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The Upper Pliocene Avifauna of Ahl al Oughlam, Morocco. Systematics and Biogeography

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ABSTRACT. The locality of Ahl al Oughlam, situated at the southeastern limit of the city of Casablanca (Morocco) at about 34° north, is dated by the biochronology of its rich mammalian fauna to about 2.5 Ma. At the present time it is 6.5 km from the Atlantic Ocean but it was on the seashore when the fossil material was deposited. Among the seabirds are *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Pelagornis mauretanicus, Calonectris* sp. cf. *C. diomedea, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua, Alca ausonia*. Among the landbirds are *Struthio asiaticus, Geronticus olsoni* n.sp., several anseriforms, *Plioperdix africana* n.sp., several otidids, *Agapornis atlanticus* n.sp., *Tyto balearica, T. alba, Surnia robusta*, and a few Passeriformes. The Recent species of albatrosses *Phoebastria albatrus* and *P. nigripes* live in the North Pacific but were also present in the North Atlantic until the Middle Pleistocene. The marine avifauna shows many similarities with that of the Yorktown Formation, in North Carolina. Unlike the mammals, which include many genera in common with the African faunas, the landbirds have more affinities with the Palaearctic region than with the Ethiopian region. They include several extinct genera or species that have been described, or identified, in the Pliocene of the Palaearctic region. The terrestrial avifauna is very different from all those that have been described from the upper Miocene and Pliocene of Africa.

RÉSUMÉ. Le gisement d'Ahl al Oughlam, situé à la limite sud-est de la ville de Casablanca (Maroc), à environ 34 ° de latitude Nord, est daté par la biochronologie de sa riche faune de mammifères d'environ 2,5 Ma. Il est actuellement situé à 6,5 km de l'Océan Atlantique mais il était sur le rivage de l'océan au moment où les fossiles ont été déposés. Parmi les formes marines on trouve *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Pelagornis mauretanicus, Calonectris* sp. cf. *C. diomedea, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua*, et *Alca ausonia*. Parmi les formes terrestres on trouve *Struthio asiaticus, Geronticus olsoni* n.sp., plusieurs ansériformes, *Plioperdix africana* n.sp., plusieurs outardes, *Agapornis atlanticus* n.sp., *Tyto balearica, Tyto alba, Surnia robusta*, et quelques Passériformes. Les espèces actuelles d'albatros, *P. albatrus*, l'Albatros à queue courte, et *P. nigripes*, l'Albatros à pieds noirs, vivent actuellement dans le Pacifique Nord mais ont vécu aussi dans l'Atlantique Nord jusqu'au Pléistocène moyen. L'avifaune marine montre beaucoup de ressemblances avec celle de la Yorktown Formation, en Caroline du Nord. Contrairement aux mammifères, qui comportent beaucoup de genres en commun avec les faunes africaines, l'avifaune

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terrestre a plus d'affinités avec celle de la province paléarctique, qu'avec celle de la province éthiopienne. Elle comporte en particulier plusieurs genres ou espèces éteints, décrits ou identifiés dans le Pliocène de la province paléarctique. Cette avifaune terrestre est très différente de celles qui ont été décrites dans le Miocène supérieur ou le Pliocène d'Afrique.

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Introduction

The fossiliferous locality of Ahl al Oughlam [AaO] is an abandoned sandstone quarry located at the southeastern fringe of the city of Casablanca, Morocco, which will probably surround it in the near future (Fig. 1). Stratigraphically the quarry exhibits a maximum marine level which is 105 m above the present sea level, referred to as the Messaoudien in the local terminology. Above this marine level, fossils were discovered by J.-P. Raynal & J.-P. Texier in 1985 in a network of fissures and interconnected galleries within a consolidated dune (calcarenite). The locality was then excavated by Denis Geraads as part of the "Programme Casablanca" of the "Institut National des Sciences de l'Archéologie et du Patrimoine" (INSAP), under the direction of Fatima-Zohra Sbihi-Alaoui and Jean-Paul Raynal.

A survey of the vertebrate faunas was published by Geraads (2006). The mammalian fauna includes at least 55 species of both micro- and macro-mammals. The genus *Equus* is absent, implying that the site is older than about 2.3 Ma (Geraads, 2006). A new species of *Hipparion, H. pomeli*, has been described subsequently from the site (Eisenmann & Geraads, 2007). The vertebrate fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards and snakes), and a few fish. The most unexpected element of the mammalian fauna is a walrus. No living or fossil walrus was previously known in the Eastern Atlantic, south of Belgium (Geraads, 2006). The site was formed in an oceanic Eulittoral environment which explains why both marine and terrestrial forms are found among the birds. The fissure fill is not stratified and, as the populations of the various rodent species from the different interconnected fissures do not significantly differ in tooth measurements, they can be considered as instantaneous at the geological scale. Although no absolute dating was possible, the biostratigraphical study of the mammals points to an age close to 2.5 Ma (Geraads, 2006).

A first published work on avifauna, describing the Struthioniformes and the Odontopterygiformes, was presented during the 2004 Sape Meeting, at Quillan (France) (Mourer-Chauviré & Geraads, 2008). The present work gives a complete systematic study of the avifauna.

Materials and methods

The highly calcareous sediments consist of loose clays with very friable bones and teeth, and concrete-hard breccias, from which bones and teeth were extracted by acid cleaning. Most of the bones, except the more robust ones, were crushed. All the material will be deposited in the collection of INSAP, at Rabat, Morocco, but casts of the most important material will be kept in the Université Claude Bernard, Lyon 1. The anatomical terminology generally follows Baumel & Witmer (1993) and, when necessary, Ballmann (1969) and Howard (1929). The biochronological stratigraphy (MN zones) follows Mein (1990). The comparative material comes from the collections of the National Museum of Natural History, Washington, D.C. (USNM); the Laboratoire d'Anatomie Comparée and the Institut de Paléontologie Humaine of the Muséum national d'Histoire naturelle, Paris (MNHN); the Paleontological Institute of the Russian Academy of Sciences, Moscow; and the Université Claude Bernard, Lyon 1 (UCB).

Figure 1. Map of the Casablanca urbanized area (in gray) with the location of the Ahl al Oughlam quarry (33°34'11"N 07°30'44"W).

Systematic Paleontology

Order Struthioniformes

Family Struthionidae

Genus *Struthio* Linnaeus, 1758

Struthio asiaticus Milne-Edwards, 1871

Mourer-Chauviré & Geraads (2008) described material belonging to this species. *Struthio asiaticus* is an ostrich characterized by its massive proportions, in particular the proportions of phalanx 1 of posterior digit III. This phalanx is more massive than that of the Recent species *S. camelus*. At Ahl al Oughlam the bones are associated with fragments of eggshells of struthioid type. The thickness of these eggshell fragments varies from 2.3 to 2.7 mm, with an average value of 2.54 mm and they are thicker than in

the Recent *S. camelus* (eggshell thickness 1.6 to 2.1 mm). The pore openings are grouped together in shallow pits, the diameters of which vary from 0.5 to 1 mm, and their density varies from 10 to 20 per cm^2. Each pit contains about 50 pore openings. *Struthio asiaticus* was widespread during the Pliocene in Europe and Asia (Mourer-Chauviré & Geraads, 2008).

Order Procellariiformes

Family Diomedeidae

Genus *Phoebastria* Reichenbach, 1852

Although albatrosses are no longer present in the North Atlantic, they were numerous during the Pliocene whith five species known from the marine deposits of the Yorktown Formation in North Carolina, USA (Olson & Rasmussen, 2001). In the Palaearctic region, an extinct species was described from England, *Phoebastria anglica* (Lydekker, 1891). It was previously known by a tarsometatarsus and pedal phalanx from the Red Crag, Foxhall, Suffolk, and by an ulna from the Coralline Crag, Orford, Suffolk (C. Harrison & Walker, 1978). To those remains have been added a complete ulna and a partial humerus from the Nordwich Crag, Suffolk (Dyke *et al*., 2007). These localities are dated to the upper Pliocene and are therefore contemporaneous with Ahl al Oughlam.

All of the fossil albatrosses found at Ahl al Oughlam belong to the genus *Phoebastria*, most of whose species live in the Pacific Ocean, generally North of the tropic of Cancer. The exception is *P. irrorata*, the Waved Albatross, or Galapagos Albatross, which lives in the intertropical zone of the East Pacific (del Hoyo *et al*., 1992). It is possible that, before the closure of the Panamanian Isthmus, there were circular oceanic currents around the earth that made it easier for organisms to be dispersed between the North Pacific and the North Atlantic. We know that species of the genus *Phoebastria* survived for at least 2 Ma in the North Atlantic after the closure of the Panamanian Isthmus because Olson & Hearty (2003) showed that a breeding colony of *P. albatrus* was present on Bermuda and was probably extirpated by the sea-level rise of the Marine Isotope Stage 11 interglacial, dated at about 400,000 years ago.

With the exception of a New Zealand population of *D. epomophora*, all the Recent albatrosses breed on islands, due to avoidance of mammalian predators. The Ahl al Oughlam albatrosses could have bred in the Canary, Salvage, Madeira, or Azores archipelagoes.

Phoebastria anglica (Lydekker, 1891)

Fig. 2A

Material. Right humerus, shaft and slightly incomplete distal part, AaO-3467; left humeri, fragment of proximal part, AaO-2691, shaft, AaO-2690, distal part, AaO-714, fragment of distal part, AaO-2621; left carpometacarpi, proximal part, AaO-2622, distal part, AaO-822; right carpometacarpus, distal part, AaO-2623; right femora, proximal part with pelagornithid vertebrae, AaO-713, proximal part, AaO-2625.

This species is also known from the Bone Valley Formation, Florida, and the San Diego Formation, California, and very numerous remains have been found in the Yorktown Formation, North Carolina (Olson & Rasmussen, 2001). Among the five albatross species identified from this locality, *P. anglica* is the largest. Unfortunately the authors above do not give measurements of elements comparable to those found at Ahl al Oughlam. Published measurements of *P. anglica* are slightly smaller than those of *Diomedea exulans*, the Wandering Albatross, and very close to those of *D. amsterdamensis*, the Amsterdam Albatross. We measured five specimens of Recent *D. exulans* and a set of subfossil postcranial bones of *D. amsterdamensis* from at least two different individuals, in the USNM collection. The elements found at Ahl al Oughlam are also characterized by dimensions smaller than those of *D. exulans* and close to those of *D. amsterdamensis* (Table 1). We consider therefore it is possible to assign them to *P. anglica*.

Phoebastria sp. cf. *P. albatrus* (Pallas, 1769)

Fig. 2B–H

Material. Posterior part of cranium, AaO-2626; right quadrates, AaO-2627, 2628; right coracoid, almost complete, and right scapula, proximal part, AaO-892; right humeri, proximal part and shaft, AaO-2624, fragment of proximal part, AaO-717, and shaft possibly from the same bone, AaO-704, distal part, AaO-716, fragment of distal part, AaO-2633; left humeri, fragment of proximal part, AaO-720, distal parts, AaO-843, 4297; articulated bones including right humerus, distal part, right ulna, proximal part and shaft, right radius, proximal part and shaft, and two sesamoids, AaO-820; right radius, proximal part, AaO-418; right carpometacarpi, proximal part, juv., AaO-4796, distal parts and shaft, AaO-2629, 2630; left carpometacarpi, almost complete, AaO-4800, proximal part, AaO-845, distal part, AaO-824; phalanx 1 of right major digit of wing, AaO-2631; phalanx 1 of left major digit of wing, proximal part, AaO-823; phalanx 2 of left major digit of wing, AaO-2632; right femora, AaO-715, distal part, AaO-847; left femora, AaO-722, proximal part, AaO-846; left tibiotarsus, distal part, AaO-2634.

The Recent North Pacific albatrosses, which belong to the genus *Phoebastria* (Nunn *et al*., 1996), have some morphological characteristics that differ from those of the genera *Diomedea, Phoebetria* and *Thalassarche*, in particular in the shape of the tarsometatarsus and in its relative length compared to the ulna (Olson & Rasmussen, 2001; Dyke *et al*., 2007). Unfortunately the tarsometatarsi are absent from the Ahl al Oughlam material. The elements listed above have been designated as *P*. sp. cf. *P. albatrus* because they are more similar, morphologically and morphometrically to this species than to any other described taxa. Some of their dimensions, however, are slightly smaller than those of a population including recent forms and subfossil forms from middens (Table 2 and Fig. 3).

Measurements of the posterior part of cranium (AaO-2626) in mm: Greatest width of the posterior part at level of zygomatic processes: 55.6; width of the calvarium at level of temporal fossae: 44.9; least width of the frontal at level of indentation between the lacrimals and the postorbital processes: 17.5.

Measurements of the coracoid and scapula (AaO-892) in mm: (on the coracoid the ventralmost tip of the acrocoracoid

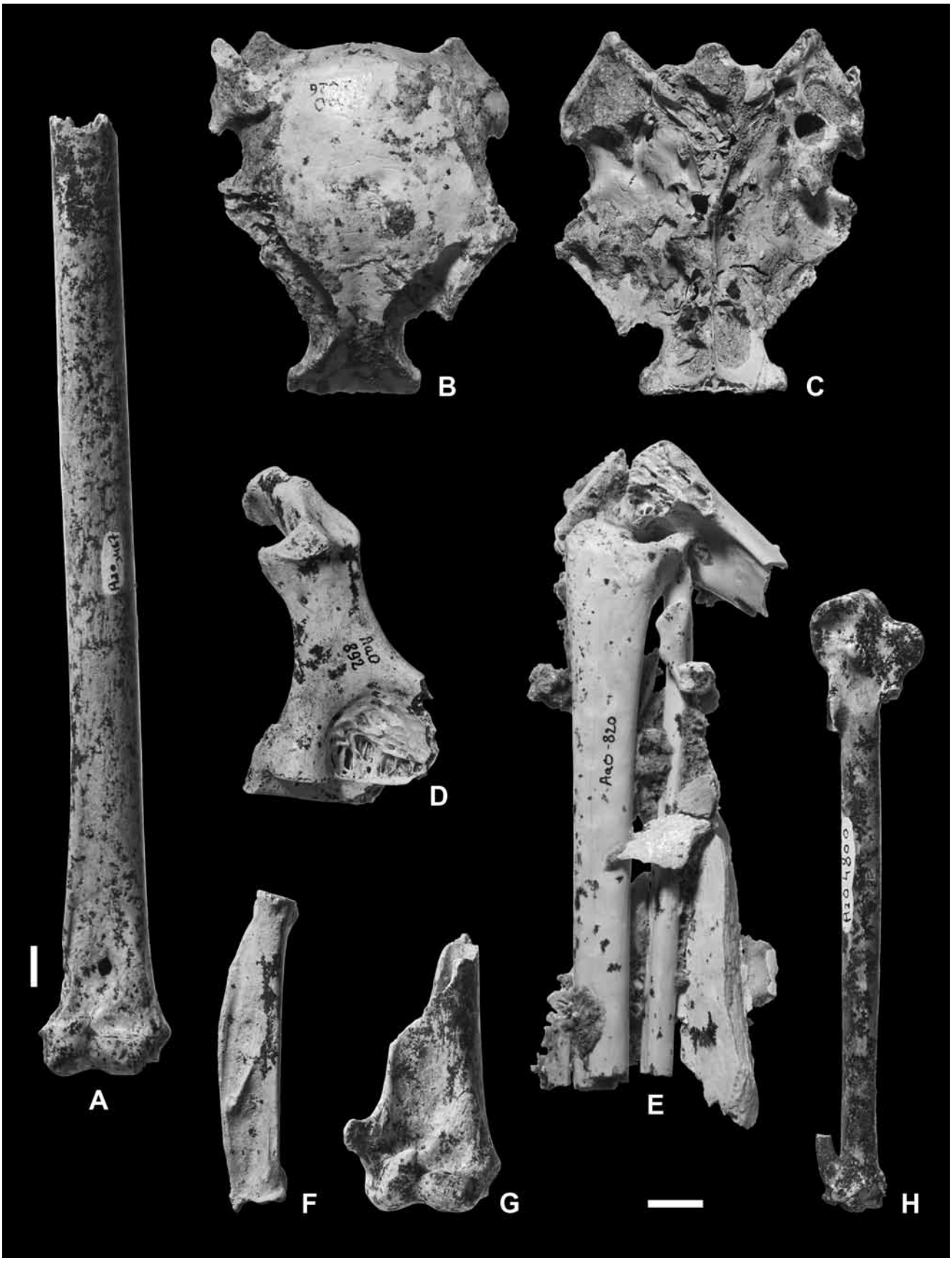

Figure 2. (*A*) *Phoebastria anglica*, right humerus, shaft and distal part, AaO-3467, cranial view. *Phoebastria* sp. cf. *P. albatrus, B–H*: (*B*) posterior part of cranium, AaO-2626, dorsal view; (*C*) idem, ventral view; (*D*) right coracoid, AaO-892, dorsal view; (*E*) right humerus, distal part, right radius and right ulna, proximal parts, articulated, and two sesamoids, AaO-820, caudal view; (*F*) phalanx 1 of right major digit of wing, AaO-2631, dorsal view; (*G*) right humerus, distal part, AaO-716, cranial view; (*H*) left carpometacarpus, AaO-4800, ventral view. The scale bars represent 1 cm. Same scale bar for *B–H*.

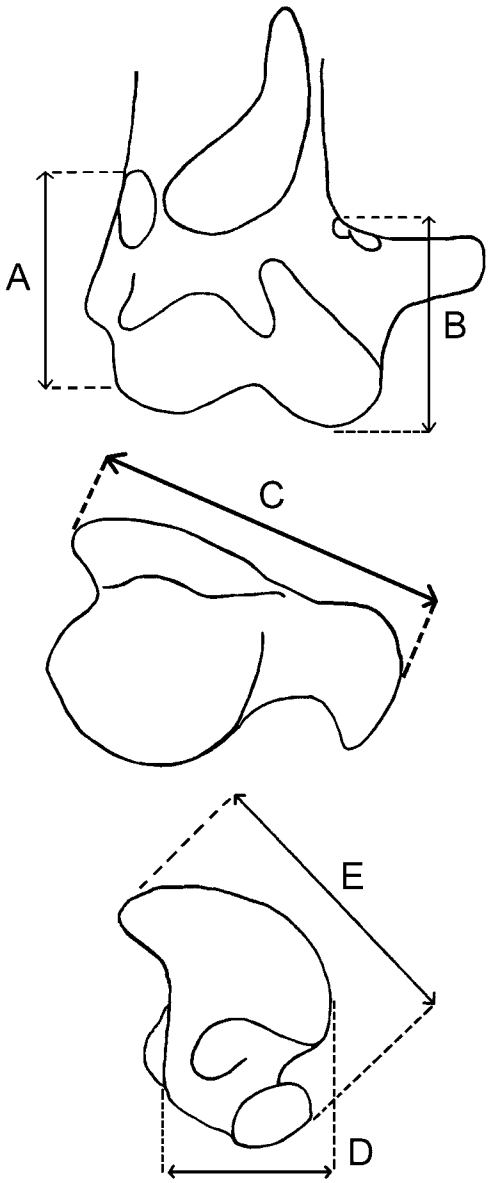

Figure 3. Diagram showing the measurements on the distal part of the humerus (*A, B*), the proximal part of the ulna (*C*), and the distal part of the carpometacarpus (*D, E*) in the genera *Phoebastria* and *Diomedea* (Tables 1 and 2).

and the tip of the procoracoid are not preserved).

Coracoid: Total length measured on the medial side, 60.2; width from the medial side of Facies scapularis to the lateral side of Facies articularis humeralis, 19.0; depth from the dorsal side of Facies scapularis to the ventral end of the acrocoracoid, ca. 30.1; width of shaft in the middle, 14.6; depth of shaft at the same level, 10.2; greatest depth of sternal facet on the medial side, 14.7.

Scapula: Proximal width from acromion to Facies articularis humeralis, 18.0.

The specimen no. AaO-820, which includes a distal humerus, a proximal ulna, and a proximal radius, all articulated, shows two sesamoids that are situated just distally compared to the place where the head of the radius comes to rest against the dorsal cotyla of the ulna. Examination of Recent skeletons of *P. albatrus* and *P. nigripes* from the USNM collection shows the occurrence, on some skeletons, of two osseous nodules, one rounded and one elongate, bound together by a supple tendon which is inserted on the dorsal side of the Processus supracondylaris dorsalis of the humerus. When the wing is flexed these two sesamoids position themselves in the space between the radius and the ulna, as in the fossil. It is possible to see these sesamoids when the skeletons still have some ligaments.

Greatest length of the elongate sesamoid on AaO-820: 17.5 mm; on a Recent *P. albatrus* (USNM 576025): 18.3 mm.

Phoebastria sp. cf. *P. nigripes* (Audubon, 1849)

Fig. 4A

Material. Left quadrate, AaO-2635; right humerus, fragment of proximal part, AaO-721; left humeri, distal parts, AaO-718, 2636; right carpometacarpus, distal part and shaft, AaO-2637; left carpometacarpus, proximal part, AaO-2692; right femur, almost complete, subadult, AaO-2638; left femur, proximal part, AaO-719.

This is the smallest of the three species of albatrosses found at Ahl al Oughlam. Its measurements correspond closely to those of the Recent *P. nigripes* (Table 2), and are larger than those of *Phoebastria* aff. *P. immutabilis*, and those of the extinct *P. rexsularum*, from the Yorktown Formation (Olson & Rasmussen, 2001).

Family Procellariidae

Genus *Calonectris* Mathews & Iredale, 1915

Calonectris sp. cf. *C. diomedea* (Scopoli, 1769)

Material. Right humerus, slightly incomplete proximal part, from a subadult individual, AaO-723; right femur, proximal part, AaO-2697.

This humerus differs from the similar-sized species of procellariid (genera *Puffinus, Pterodroma, Bulweria*) by its morphological characteristics and it is in perfect agreement with the genus *Calonectris*. In *Puffinus* the Caput humeri is more developed both in proximo-distal and craniocaudal directions and is more projecting over the Fossa tricipitalis (*sensu* Ballmann, 1969) than in *Calonectris*. The Tuberculum dorsale is proximo-distally elongate in caudal view, and is projecting proximad, whereas in *Calonectris* it is more rounded and less projecting. The Tuberculum ventrale is proportionally more developed and more caudally projecting in *Puffinus* than in *Calonectris*. In *Calonectris*, as well as in *Puffinus*, there is a small protuberance, distally directed, on the Crus dorsale of the Fossa pneumoanconaea (*sensu* Ballmann, 1969), but this protuberance is more developed in *Calonectris*. On the caudal surface, the Margo caudalis goes vertically in proximal direction, then describes a curve which joins the humeral head in *Calonectris* whereas in *Puffinus* it does not make a curve and joins the distal border of the dorsal tubercle.

The shaft of the humerus is almost circular in *Calonectris* whereas it is flattened in *Puffinus*, but unfortunately this is not visible on the fossil the shaft of which is not preserved.

In the subgenus *Thyellodroma* (species *Puffinus (Thyellodroma) pacificus*) the morphological characteristics of the proximal part of the humerus are slightly different from

Table 1. Measurements (mm) of fossil *Phoebastria anglica*, from Ahl al Oughlam, and Recent *Diomedea amsterdamensis* and *D. exulans*. Measurement A: from the proximal end of the attachment of anterior articular ligament (Howard, 1929) to a small groove situated between the processus flexorius and the condylus ventralis, on the ventral side of the distal extremity (Fig. 3). For *Diomedea exulans* the following specimens have been measured: USNM 18554, 321465, 321749, 488376, 559552. Data presented as: mean [observed range].

	Diomedea amsterdamensis Recent (n = 2)	***Diomedea exulans*** Recent (n = 5)	***Phoebastria anglica*** Ahl al Oughlam
Humerus			
depth of caput humeri	13.15 [12.1–14.2]	14.98 [14.0–16.0]	ca. 12.0
distal width	30.50 [29.0–32.0]	34.04 [33.3–34.7]	[30.5–32.0]
distal depth	18.80 [18.3–19.3]	21.96 [21.0–23.0]	[19.6–20.3]
measurement A	23.90 [22.8–25.0]	26.56 [25.8–27.0]	[25.5–25.5]
Carpometacarpus			
proximal width	10.40 [10.4–10.4]	11.66 [11.1–12.9]	10.40
proximal depth	24.35 [24.3–24.4]	26.26 [25.9–26.6]	ca. 23.0
width of metacarp. maj. at midpoint	8.00 [8.0–8.0]	7.76 [7.2–8.2]	7.50
depth of metacarp. maj. at midpoint	8.30 [8.0–8.6]	8.56 [8.3–9.0]	8.60
distal width	11.05 [10.7–11.4]	12.52 [12.0–13.1]	[10.2–10.2]
distal depth	16.60 [16.2–17.0]	17.64 [16.8–18.4]	[ca. 16–16.3]
Femur			
proximal width	21.20 [20.8–21.6]	22.72 [22.1–23.4]	[ca. 21.6–22.9]
proximal depth	13.40 [13.2–13.6]	15.74 [15.6–15.9]	[14.5–14.7]

those of the subgenus *Puffinus* (species *Puffinus (Puffinus) griseus*) but they are more similar to the subgenus *Puffinus* than to the genus *Calonectris*.

In the genera *Pterodroma* and *Bulweria* the ventral tubercle is more projecting ventrally and the Crista delto-pectoralis is more projecting dorsally than in the genus *Calonectris*. In *Pterodroma* the humeral head forms a well defined ledge, with a rounded lobe, above Fossa tricipitalis, and the dorsal tubercle is in the continuation of the humeral head, i.e. there is no space between the humeral head and the dorsal tubercle. Still in *Pterodroma* the Fossa pneumoanconaea has a lozengic shape, obliquely elongate both in proximodistal and dorsoventral directions, whereas in *Calonectris* this fossa is more rounded. Finally in *Pterodroma* there is no protuberance directed distally on the Crus dorsale fossa.

In the Recent species *Calonectris diomedea* there are great differences in size between the two subspecies. The largest one is *C. diomedea borealis*, which breeds on the Azores, the Canaries, the Berlengas, and Madeira (Jouanin & Mougin, 1979), and the smallest one is *C. diomedea diomedea*, which breeds on the Mediterranean islands. *Calonectris edwardsii*, which breeds on the Cape Verde islands, is now considered as a distinct species (Olson, 2008) and it is smaller than the two subspecies of *Calonectris diomedea*. By its dimensions (prox. width of humerus, from tip of tuberculum ventrale to tuberculum dorsale 17.2 mm; depth of caput humeri, 4.7 mm; proximal width of the femur, 8.6 mm; proximal depth, 4.7 mm) the Ahl al Oughlam form is closer to *C. d. diomedea*. Its dimensions also correspond to those of *C. leucomelas*, which breeds on the offshore islands of the West Pacific. It is smaller than the extinct species *Calonectris krantzi* from the Pliocene of the Yorktown Formation, North Carolina (Olson & Rasmussen, 2001).

An extinct species, *Calonectris wingatei*, has recently been described from the Middle Pleistocene of Bermuda (Olson, 2008). In this species the total length of most of the bones is similar to that of *C. diomedea diomedea*, but the femur is longer and all the long bones are more robust. In the Ahl al Oughlam material the femur is similar in size to *C. d. diomedea* and it is smaller than the femur of *C. wingatei*.

The genus *Calonectris* has been reported from the lower Pliocene of Duinefontein (age 5 Ma), in South Africa (Olson, 1985a), where it is represented by a carpometacarpus slightly larger and morphologically different from that of *Calonectris diomedea*, and *Calonectris* aff. *diomedea* is present in the deposits of Lee Creek Mine, North Carolina, probably from the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001).

Order Odontopterygiformes

Family Pelagornithidae

Genus *Pelagornis* Lartet, 1857

Pelagornis mauretanicus Mourer-Chauviré & Geraads, 2008

The Odontopterygiformes, or pseudodontorns, were giant marine birds which presented bony tooth-shaped excrescences on the jaws. These pseudoteeth are unique among birds. They had a very large wingspan, up to 5.5 to 6 m, and their skeleton was highly modified. *Pelagornis mauretanicus* was approximately the same size as *P. miocaenus*, the type species of the genus, but differed morphologically. The material from Ahl al Oughlam allowed the description of several elements of the post-cranial skeleton. The pseudodontorns were distributed on the oceans all over the world from the Late Paleocene onwards. During the Pliocene, they were still present in North America, New Zealand, Japan, and Peru. The Ahl al Oughlam form, dated from 2.5 Ma, is the most recent, accurately dated form known to date (Mourer-Chauviré & Geraads, 2008).

Table 2. Measurements (mm) of fossil *Phoebastria* sp. cf. *P. nigripes* and *P.* sp. cf. *P. albatrus*, from Ahl al Oughlam, and Recent *Phoebastria nigripes* and *P. albatrus*. Measurement A: as for Table 1. Measurement B: from the proximal part of the insertion of the processus supracondylaris dorsalis on the shaft, to the distal part of the condylus dorsalis. For the ulna, the proximal diagonal (C) is measured on the caudal face, from the ventral side of the olecranon, to the dorsal side of the cotyla dorsalis. On the carpometacarpus there is a small tubercle situated proximally to the distal articular surface, on the ventral side of the shaft. The distal width (D) is measured directly on the distal articular surface, without this tubercle (Fig. 3). Data presented as: mean (n) [observed range].

	Phoebastria nigripes **Recent**	***Phoebastria* sp. cf. *P. nigripes*** **Ahl al Oughlam**	***Phoebastria albatrus*** **Recent + middens**	***Phoebastria* sp. cf. *P. albatrus*** **Ahl al Oughlam**
Quadrate				
maximal height	22.68 (20) [21.4–ca. 24.5]	23.5	25.29 (8) [ca. 24–26.1]	[25.0–25.4]
Humerus				
depth of caput humeri	9.06 (18) [8.2–9.6]	9.3	11.02 (18) [10.2–11.9]	[10.3–10.6–10.7]
distal width	23.18 (18) [21.2–24.2]	[21.7–23.8]	26.59 (18) [25.6–27.8]	[25.3–25.8]
distal depth	15.17 (18) [14.0–15.7]	[15.2–15.5]	17.22 (18) [16.6–18.0]	[16.1–16.6]
measurement A	19.21 (18) [17.6–21.0]	19.6	22.22 (18) [21.3–23.2]	21.1
measurement B	17.61 (18) [16.1–19.4]	[17.2–18.2]	20.47 (18) [19.0–22.2]	[19.5–20.0–ca. 22]
Ulna				
proximal diagonal (C)	19.86 (17) [18.6–20.7]	—	22.70 (2) [22.4–23.0]	21.3
Radius				
greatest diam. of shaft at midpoint	4.78 (17) [4.4–5.3]	—	5.88 (4) [5.6–6.3]	[6.1–6.5]
depth measured perpendicularly	3.65 (17) [3.2–4.0]	—	4.55 (4) [4.4–4.7]	[4.5–4.6]
Carpometacarpus				
total length	108.63 (16) [101.5–113.7]	—	113.87 (13) [107.2–120.8]	115.7
proximal width	8.03 (16) [7.7–8.4]	7.9	9.14 (13) [8.6–9.5]	[8.7(subadult)–9.0]
proximal depth	19.88 (16) [19.0–20.7]	19.6	21.68 (13) [20.2–23.1]	[21.1(subadult)–21.4]
width metacarp. maj. at midpoint	5.30 (16) [4.9–5.6]	5.8	6.74 (13) [6.2–7.4]	[6.4–6.7–6.7]
depth metacarp. maj. at midpoint	6.38 (16) [5.8–6.9]	6.1	7.10 (13) [6.2–8.0]	[6.7–7.0–7.6]
distal width (D)	8.79 (16) [7.6–9.4]	ca. 8	10.25 (12) [9.8–10.7]	[9.2–9.2–10.2]
distal depth (E)	13.04 (16) [12.2–14.1]	—	14.47 (12) [13.7–15.3]	[13.2–13.6]
Phalanx I major wing digit				
length	53.77 (16) [50.1–57.8]	—	58.2 (1)	59.2
Femur				
total length	78.25 (18) [74.1–82.3]	ca. 79 (subadult)	89.79 (15) [86.6–94.7]	[81.7–87.0]
proximal width	15.76 (18) [15.0–17.2]	[15.5(subadult)–16.4]	18.68 (13) [17.5–19.3]	[17.6–18.3–ca. 19]
proximal depth	10.61 (18) [9.9–11.4]	[9.8–10.2 (subadult)]	12.61 (14) [12.0–13.4]	[10.4–ca. 10.5–12.3]
maximal width of shaft at midpoint	7.50 (18) [7.0–7.9]	7.7 (subadult)	8.73 (15) [8.1–9.5]	[8.2–8.7]
depth of shaft at midpoint	6.66 (18) [6.1–7.1]	7.4 (subadult)	7.73 (15) [7.3–8.5]	[8.0–8.0]
distal width	16.71 (18) [15.8–17.9]	ca. 17 (subadult)	19.60 (14) [18.7–21.3]	[17.8–19.8]
distal depth	13.17 (18) [11.8–14.0]	—	14.51 (14) [13.8–15.4]	[14.3–ca. 15]

Order Pelecaniformes

Family Sulidae

Genus *Morus* Vieillot, 1816

Morus peninsularis Brodkorb, 1955

Fig. 4B–D

Material. Right quadrates, AaO-727, 827; left quadrate, AaO-728; vertebrae, AaO-819, 828, 829, 830, 831, 832, 833, 834, 871; right coracoid, sternal part and shaft, AaO-725; left coracoid, almost complete, AaO-2108; right humerus, fragment of distal parts, AaO-730, 2639; left humerus, distal part, AaO-726; right ulna, distal part, AaO-2642; left ulna, proximal part, AaO-2641; right carpometacarpi, AaO-2643, 2644; alar phalanges, AaO-2645, 2646, 2647; left femora, AaO-724, proximal part, AaO-2648; right tibiotarsus, distal part, AaO-729; right tarsometatarsus, distal part, AaO-731, trochlea of digit IV, AaO-732.

The species *Morus peninsularis* was described by Brodkorb (1955) from the Upper Bone Valley locality, in Florida, which is dated to the lower Pliocene, age about 5 to 4.5 Ma (Becker, 1987a,b). This species is very abundant in the Pliocene Yorktown Formation, North Carolina (Olson & Rasmussen, 2001). The holotype of the species is an almost complete coracoid. Compared to the holotype, the Ahl al Oughlam coracoid AaO-2108 is of similar length but slightly more robust. The length of the dorsal and ventral sternal facets is longer, the acrocoracoid bulges a little more, and the pneumatic foramina are slightly more developed. In *Morus bassanus* the scapular facet is strongly projecting dorsally, but it is less projecting in *M. peninsularis*. Also in *M. bassanus* the clavicular facet is medioventrally oriented while in *M. peninsularis* it is more ventrally oriented. By these two characteristics the coracoid AaO-2108 is more similar to *M. peninsularis*.

The dimensions of the specimens referred to *Morus peninsularis* are similar to the dimensions of those from the Yorktown Formation preserved in the USNM collection and illustrated by Olson & Rasmussen (2001, pl. 12 and 13), except for the distal part of tibiotarsus AaO-729, which is slightly smaller (Table 3). The carpometacarpus AaO-2643 has a large pneumatic foramen on the ventral face, in the Fossa infratrochlearis, but this is not visible on the specimen AaO-2644 which is incompletely preserved. Both carpometacarpi have another, small, foramen, going right through the Processus alularis, at the level of the junction

Table 3. Measurements (mm) of fossil *Morus peninsularis* and *Morus* sp. cf. *M. bassanus*, from Ahl al Oughlam.

	Morus peninsularis			*Morus* **sp. cf.** *M. bassanus*		
Quadrate	AaO-727	AaO-728	AaO-827			
total length	19.3	19.8	20.8			
width at the top of proc. oticus	10.2	9.8	9.9			
max. width of proc. mandibularis	14.8	15.7	16.8			
Coracoid	AaO-2108	AaO-725				
internal length	55.3	—				
width of ventral sternal facet	17.3	—				
width of dorsal sternal facet	13.5	13.5				
length from head to procoracoid	24.7	—				
depth of head	13.6	—				
depth at level of scapular facet	19.3	—				
least depth of shaft	7.4	7.2				
Humerus	AaO-726	AaO-730		AaO-733	AaO-734	AaO-4801
depth of head	—	—		9.8	—	—
length of deltoid crest [a]	—	—		49.0	—	—
width of shaft at midpoint	—	—		10.3	—	—
depth of shaft at midpoint	—	—		9.5	—	—
distal width	20.5	—		—	ca. 23.5	23.3
distal depth	—	14.0		—	—	14.6
Ulna	AaO-2641	AaO-2642		AaO-2640		
proximal width	15.2	—		16.3		
proximal depth	—	—		16.0		
width of shaft at midpoint	—	—		9.0		
depth of shaft at midpoint	—	—		9.1		
depth of internal condyle	—	11.6				
Carpometacarpus	AaO-2643	AaO-2644		AaO-747		
total length	81.2	ca. 85		—		
proximal width	9.0	—		—		
proximal depth	17.6	—		—		
width of maj. metacarp. at midpoint	5.1	6.0		—		
depth of maj. metacarp. at midpoint	6.7	6.8		—		
distal width	ca. 8	8.0		7.9		
distal depth	11.7	12.2		12.7		
Phalanx 1 major wing digit	AaO-2645	AaO-2646	AaO-2647			
total length [b]	41.5	44.6	39.3			
Femur	AaO-724	AaO-2648		AaO-826		
total length	71.5	—		—		
proximal width	14.2	—		—		
proximal depth	11.6	10.4		—		
depth of head	7.2	—		—		
width of shaft at midpoint	ca. 7.0	6.4		7.0		
depth of shaft at midpoint	7.9	7.4		7.4		
distal width	14.8	—		16.5		
distal depth	12.8	—		12.8		
Tibiotarsus	AaO-729					
distal width	12.5					
distal depth	12.1					
Tarsometatarsus	AaO-731					
distal width	14.7					
distal depth	8.3					

[a] From the dorsal tubercle to its attachment to the shaft.
[b] Without the internal index process.

between the alular and the major metacarpals. The femora also have a pneumatic foramen on the cranial face, distal to the Crista trochanteris. These pneumatic foramina are less developed in Recent species of the genus *Morus*.

Morus sp. cf. *M. bassanus* (Linnaeus, 1758)

Fig. 4E–F

Material. Right humerus, proximal and distal parts, probably from the same bone, AaO-733, 734; right humerus, distal part, AaO-4801; left ulna, proximal part and shaft, AaO-2640; left carpometacarpus, distal part, AaO-747; right femur, distal part, AaO-826.

The dimensions of the remains referred to *Morus* sp. cf. *M. bassanus* are included in the variation range of a series of 14 Recent individuals from the USNM collection (Table 3). There is not much difference in the femur dimensions between *Morus peninsularis* and *M.* sp. cf. *M. bassanus* from Ahl al Oughlam. The main difference is in the distal width which is slightly larger in the Moroccan form. This is related to the fact that the medial condyle is more medially projecting in *Morus bassanus* than in *Morus peninsularis*.

The large forms, larger than *Morus bassanus* (*Morus*, undescribed species 1 and 2), that were present in the Yorktown Formation (Olson & Rasmussen, 2001) are not represented at Ahl al Oughlam.

Order Ciconiiformes

Family Threskiornithidae

Genus *Geronticus* Wagler, 1832

Geronticus olsoni n.sp.

Fig. 4G–K

Holotype. Left coracoid, AaO-741.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Left coracoid, slightly incomplete, AaO-837.

Referred material. Right humeri, distal part and shaft, AaO-838, distal parts, AaO-736, 746; left humeri, proximal part, juv., AaO-4804, distal part, AaO-739; right ulna, shaft, AaO-2649; left ulna, proximal part, AaO-4802; right radius, distal part, AaO-2650; left radii, proximal part, AaO-3099, distal part, AaO-4798; right carpometacarpi, distal parts, juv., AaO-742, 848, 2651; left carpometacarpi, distal part, AaO-737, 745, 2662, distal part, juv., AaO-738; phalanges 1 of major digit of wing, AaO-740, 743, 744; right femur, incomplete, AaO-2652; left tibiotarsi, proximal parts, AaO-825, 2653, distal part, AaO-2654; right tarsometatarsus, two trochleae, AaO-752; left tarsometatarsus, almost complete, AaO-2655.

Diagnosis. Species belonging to the genus *Geronticus* and differing from the two Recent species, *G. eremita*, the Northern Bald Ibis, and *Geronticus calvus*, the Southern Bald Ibis, and from the extinct species *G. apelex*, by its larger size.

Measurements. See Table 4.

Etymology. To Storrs L. Olson, Senior Scientist at the Smithsonian Institution in recognition of his help during the time Cécile Mourer-Chauviré spent at the USNM, in Washington, and in recognition of Helen James' and Storrs' hospitality in their home, during the same period.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. Detailed osteological comparisons with the genera of Threskiornithidae present in the collections of USNM, UCBL, and Institut de Paléontologie Humaine, MNHN Paris, make it possible to refer this material to the genus *Geronticus*. Generally, in the genus *Geronticus*, the medial part of the sternal facet of the coracoid forms a projecting point, and the medial side of the shaft is concave. However this feature may be subject to a certain amount of variation as in the two skeletons of *G. eremita* from UCBL, one has a much more projecting point than the other one. The same variation can be observed in Olson's paper on Pliocene ibises of South Africa (Olson, 1985b). The coracoid of *G. apelex* has a point that projects only slightly (Olson 1985b, fig. 5 A) while that of *G. calvus* has a slightly more projecting point (Olson 1985b, fig. 5B). On the two coracoids from Ahl al Oughlam the point is not very projecting and the medial side of the shaft is straighter. However despite this one difference the coracoids of Ahl al Oughlam are similar in all other characteristics to those of Recent members of the genus *Geronticus*. The procoracoid is well developed medially and extends farther mediad than the acrocoracoid; the Foramen nervi supracoracoidei is situated at a similarly great distance in the sternal direction from the scapular facet; the sternal facet is oblique compared to the longitudinal axis of the bone and the Processus lateralis extends very far in the lateral direction; on the dorsal face, on the medial side, just proximally to the sternal facet, there is a small elongate and flattened surface, along the medial border. This surface is also present in the Recent specimens of *G. eremita*.

The distal humeri also share the characteristics of the genus *Geronticus*. They are not very elongated ventrad. The ectepicondylar prominence forms a elongated proximad and projecting dorsad ridge. The attachment of the anterior articular ligament is not very raised compared to the cranial face. The impression of M. brachialis is shallow. There are no particular morphological characteristics on the ulna. A few Papillae remigales caudales are visible.

The distal part of the tibiotarsus is similar to *Geronticus* due to its strong elongation mediad, the medial condyle is much narrower than the lateral condyle and the Incisura intercondylaris is wide. The tubercle that is found on the lateral side of the distal opening of the Canalis extensorius is not strongly developed in the genus *Geronticus*, while it is much more developed in the genus *Threskiornis*. Both Tuberositates retinaculi extensoris are not strongly projecting in the genus *Geronticus*, while they are more developed in the closely related and potentially confusing genus *Pseudibis*.

The tarsometatarsus is short and robust as in the genus *Geronticus*. The Sulcus extensorius is deep proximally, and edged by two ridges. The hypotarsus presents two main ridges. The Crista medialis hypotarsi is incompletely preserved but the Crista lateralis is preserved and has a flattened plantar surface. The two ridges are separated by an open groove. The hypotarsus does not project far plantarly. It is separated from the Cotylae lateralis and medialis by a flattened Sulcus ligamentosus. The Cotyla lateralis has a rounded outline. On the plantar face, the Fossa parahypotarsalis medialis is deep. The lateral face of the shaft is much thicker than the medial face. The Fossa metatarsi I is situated entirely on the plantar face. The opening of the Foramen vasculare distale, on the plantar side, is situated just proximally to the Incisura intertrochlearis lateralis. In all these characteristics the Ahl al Oughlam tarsometatarsus fits the genus *Geronticus*. It differs from members of the genus *Pseudibis* which have a Cotyla lateralis with a proximally projecting tubercle in the latero-plantar corner, giving a subquadrangular shape, where the canal which separates the two hypotarsal ridges is roofed, and where the plantar opening of the Foramen vasculare distale is situated further proximally compared to the Incisura intertrochlearis lateralis.

Geronticus olsoni is, on average, 13% larger than the mean of two specimens of Recent *G. eremita*. According to the measurements given by Olson (1985b) for the main long bones of the two Recent species of bald ibises, the coracoid has the same size, but the wing bones (humerus, ulna, carpometacarpus) are distinctly shorter, the tarsometatarsus is slightly shorter, and the femur is slightly longer in *G. calvu*s than in *G. eremita*. Using the measurements given by Olson (1985b) the main long bones of *G. olsoni* are, on average, 12% larger than those of Recent *G. eremita* (n = 4) and 16% larger than those of *G. calvus* (n = 3). The only extinct species described so far in the genus *Geronticus* is *G. apelex* from the lower Pliocene of Langebaanweg, in South Africa (Olson, 1985b). On average *G. olsoni* is 28% larger

Table 4. Measurements (mm) of fossil *Geronticus olsoni* n.sp., from Ahl al Oughlam, fossil *Geronticus apelex*, from Langebaanweg, and Recent *Geronticus eremita*.

	Geronticus olsoni n.sp. Ahl al Oughlam		*Geronticus eremita*	*Geronticus apelex*
Coracoid	Holotype AaO-741	Paratype AaO-837	Recent mean (n = 2)	(Olson, 1985b)
internal length	53.0	52.4	46.55	40.4
width pars omalis [a]	14.8	—	14.10	—
depth pars omalis	13.0	12.7	12.00	—
length sternal part [b]	29.2	—	26.85	—
length sternal facet	24.7	ca. 21.3	22.55	—
depth sternal facet	6.6	6.0	4.35	—
width of shaft at midpoint	10.9	9.6	9.10	—
depth of shaft at midpoint	7.4	7.6	6.55	—
Humerus	mean (n)			
total length	est. 145 (1)		127.20	111.4
distal width	24.05 (4)		21.10	ca. 18.5
distal depth	13.07 (3)		11.30	—
width of shaft at midpoint	10.7 (1)		9.10	—
depth of shaft at midpoint	8.9 (1)		7.75	—
Ulna				
total length	est. 160 (1)		138.25	122.5
proximal width	ca. 14.5 (1)		13.60	13.3
width of shaft at midpoint	7.2 (1)		6.55	5.5
depth of shaft at midpoint	7.4 (1)		7.00	6.1
Radius				
greatest prox. diameter	8. 1 (1)		7.70	6.7
distal width	10.45 (2)		9.60	8.9
greatest diameter of shaft at midpoint	5.1 (1)		4.55	4.6
least diameter of shaft at midpoint	4.2 (1)		3.30	3.2
Carpometacarpus				
total length	est. 87 (1)		70.65	60.8
distal width	7.35 (4)		7.20	—
distal depth	11.65 (4)		10.70	9.2
width metacarp. maj. at midpoint	6.08 (6)		5.40	5.0
depth metacarp. maj. at midpoint	4.68 (6)		4.35	3.9
Phalanx 1 major wing digit				
length [c]	32.8 (3)		31.35	—
Femur				
total length	ca. 68 (1)		65.15	57.4
width of shaft at midpoint	6.9 (1)		6.35	5.5
depth of shaft at midpoint	7.0 (1)		5.90	4.9
Tibiotarsus				
total length [d]	129.0 (1)		113.80	—
proximal width	14.3 (2)		12.40	10.1
proximal depth	ca. 18.4 (1)		15.85	—
distal width	13.7 (1)		10.85	—
distal depth	14.0 (1)		11.45	—
width of shaft at midpoint	7.4 (1)		6.00	5.2
depth of shaft at midpoint	6.0 (1)		5.50	4.3
Tarsometatarsus				
total length	80.5 (1)		71.80	64.6
proximal width	15.2 (1)		13.20	11.6
proximal depth	ca. 14.0 (1)		12.00	10.9
width trochlea III	5.4 (1)		5.10	4.5
depth trochlea III	8.1 (1)		6.55	5.9
width of shaft at midpoint	7.0 (1)		5.30	4.9
medial depth of shaft at midpoint	4.4 (1)		3.70	—
lateral depth of shaft at midpoint	5.1 (1)		4.75	3.8

[a] From the glenoid facet to the procoracoid.
[b] From the angulus medialis to the processus lateralis.
[c] Without the internal index process.
[d] Without the cnemial crests.

than *G. apelex*.

The area of Casablanca where Ahl al Oughlam is situated is close to the region where *Geronticus eremita*, an endangered species (del Hoyo *et al*., 1992), is still breeding. At the present time the Northern Bald Ibis nests on cliff ledges and among boulders on steep slopes, by the sea or inland (Cramp & Simmons, 1977). Although there are no immature elements, it is likely that *G. olsoni* also nested in the Ahl al Oughlam area.

Order Anseriformes

Family Anatidae

Subfamily Anserinae

Anserini indeterminate

Material. Left carpometacarpus, proximal part, AaO-2663; left phalanx 1 of major digit of wing, AaO-735 (it is not possible to know whether they come from the same individual).

The carpometacarpus shows the morphological characteristics of the Anserini (Woolfenden, 1961) and its size corresponds to the Recent species *Branta canadensis*, the Canada Goose. Its measurements are (in mm): proximal width, 9.1; proximal depth, 20.8. It is larger than the extinct species *Branta woolfendeni*, from the upper Miocene or lower Pliocene of Big Sandy Fm. (Bickart, 1990).

On the phalanx the distal portion of the Pila cranialis phalangis is incomplete, mainly on the ventral side. This phalanx differs from that of the Anatinae by its much deeper Fossa ventralis. This Fossa ventralis is more developed in the proximal part of the phalanx. The measurements are (in mm): length (without the distal point), 32.4; proximal width (dorsoventrally), 8.0; proximal depth (craniocaudally), 7.3; maximum depth (craniocaudally) 10.4. As for the carpometacarpus, this phalanx is similar to that of the genus *Branta* but it is larger than the Recent *Branta bernicla*. Anserini (genus and species indeterminate) are present in the Pliocene of the Yorktown Formation. They are also comparable in size to *Branta canadensis* (Olson & Rasmussen, 2001).

Subfamily Anatinae

Genus *Alopochen* Stejneger, 1885

Alopochen sp. cf. *A. aegyptiacus* (Linnaeus, 1766)

Material. Right femur, proximal part, AaO-2660.

The proximal part of the Crista trochanteris is broken. This femur is similar to the genus *Alopochen* because the proximal part is mediolaterally compressed. The head is very globular and clearly raised compared to the proximal articular surface, but not very medially projecting. The neck is not very marked. There is a Linea intermuscularis cranialis that runs along the medial border of the proximal cranial surface.

The measurements are (in mm): proximal width (including head), 17.1; proximal depth, 12.4. They are included in the variation range of 10 Recent specimens of *A. aegyptiacus* from the USNM collection, the measurements of which are: proximal width, 14.9–20.6 (mean 17.31); proximal depth, 11.0–13.7 (mean 12.01).

This femur shows a deposit of medullary bone, which indicates that it belonged to a female and that this female died during the breeding season (Rick, 1975). At the present time, the Egyptian Goose is only found in Sub-Saharan Africa and in the central part of the Nile valley but formerly it was also present throughout the Nile valley, the Middle East and Southern Europe (Brown *et al*., 1982; del Hoyo *et al*., 1992). According to Cramp & Simmons (1977) it used to breed in Algeria and Tunisia.

Genus *Tadorna* Oken, 1817

Tadorna tadorna (Linnaeus, 1758)

Material. Right humeri, shaft and distal part, AaO-748, distal part, AaO-751; left carpometacarpus, almost complete, AaO-2658 (the alular metacarpal is missing).

Measurements. See Table 5.

The measurements of the distal humeri have been compared with those of the other species of the genus *Tadorna* from the USNM collection. They are smaller than those of *T. ferruginea, T. variegata, T. tadornoides, T. cana*, and larger than those of *T. radjah*. They are included in the variation range of the Recent *T. tadorna*, the Common Shelduck.

At the present time, the Common Shelduck breeds in Central Asia and on the European coasts, and winters in Southern China, Pakistan, India, Iran, Afghanistan, on the European Atlantic and Mediterranean coasts, and in North Africa. It still winters in Morocco (del Hoyo *et al*., 1992).

The Common Shelduck has been recorded from the Early Pleistocene, at Ubeidiya', in Israel (1.4 Ma), and Betfia, in Romania (1 Ma) (Tyrberg, 1998).

Tadorna sp.

Material. Right humerus, distal part, AaO-2656; left ulna, shaft and distal part, AaO-2657; right radii, proximal part, AaO-749, distal part, AaO-750.

Measurements. See Table 5.

The humerus no. AaO-2656 is larger than those referred to *T. tadorna*. It was compared with *Alopochen*, but *Alopochen* differs in the following characteristics: the distal part of the humerus is more elongated ventrad, the impression of M. brachialis is situated farther from the attachment of the anterior articular ligament, the ventral epicondyle is more projecting both caudally and distally. It was also compared with *Sarkidiornis melanotos*. In *Sarkidiornis*, as in *Alopochen*, the distal part of the humerus is more elongated ventrad than in the Ahl al Oughlam specimen. In *Sarkidiornis*, the impression of M. brachialis is small and situated more proximally. In particular, it is situated far from the attachment of the anterior articular ligament, whereas in AaO-2656 humerus it is just proximal to the attachment. In *Sarkidiornis*, the attachment of the anterior articular ligament is tilted and projecting cranially, while in the Ahl al Oughlam fossil it is less projecting and less tilted. The morphological characteristics of the fossil correspond to the genus *Tadorna*. By its dimensions, it is situated at the upper limit of the Recent *T. tadorna* and in the variation range of the Recent *T. ferruginea*, the Ruddy Shelduck. The measurements of

Table 5. Measurements (mm) of fossil *Tadorna tadorna* and *Tadorna* sp. from Ahl al Oughlam, and Recent *T. tadorna* and *T. ferruginea*. The measurements with an asterisk are taken from Woelfle (1967). The others were taken on specimens from the USNM collection.

	Tadorna tadorna Ahl al Oughlam		***Tadorna tadorna*** Recent	
			observed range	mean (n)
Humerus	AaO-748	AaO-751		
distal width	15.5	15.6	13.6–17.5	15.93 (9)
distal depth	9.4	9.3	9.1–10.7	9.97 (9)
width of shaft at midpoint	8.0	—	—	—
depth of shaft at midpoint	6.7	—	—	—
Carpometacarpus	AaO-2658			
total length	60.8		52.7–67.0*	61.40 (16)*
proximal width	6.5		—	—
width of metacarp. maj. at midpoint	5.5		—	—
depth of metacarp. maj. at midpoint	4.6		—	—
distal width	5.4		—	—
distal diagonal	8.3		7.3–9.2*	7.97 (16)*
	***Tadorna* sp.**			
Ulna	AaO-2657			
distal diagonal	11.6		10.5–12.8*	11.47 (20)*
depth of condylus dorsalis	10.0		—	—
with of shaft at midpoint	5.7		—	—
depth of shaft at midpoint	5.7		—	—
	***Tadorna* sp.**			
Radius	AaO-749	AaO-750		
greatest proximal diameter	6.2	—	5.5–7.0*	6.26 (21)*
greatest diameter of shaft at midpoint	3.7	—	—	—
least diameter of shaft at midpoint	3.2	—	—	—
distal width	—	7.6	5.7–7.7*	7.14 (21)*
distal depth	—	4.1	—	—
	***Tadorna* sp. Ahl al Oughlam**		***Tadorna ferruginea*** Recent	
Humerus	AaO-2656		observed range	mean (n)
distal width	17.2		16.7–18.2	17.58 (5)
distal depth	10.7		10.1–11.1	10.56 (5)

the other fragments of ulna and radius are included in the variation range of both *T. tadorna* and *T. ferruginea*.

At the present time the Ruddy Shelduck is a breeding resident and non-breeding Palaearctic migrant to North Africa and Western Sahara. It was formerly common and widespread, but it is now extinct as a breeding species in many regions (Brown *et al*., 1982).

The Ruddy Shelduck has been recorded as fossil in the lower Pleistocene of Dursunlu, in Turkey, in a layer dating from 0.9 to 1 Ma (Louchart *et al*., 1998), and an indetermined Tadornini has been reported in the site of Gomboré II, at Melka Kunturé, Ethiopia, dated at about 0.8 Ma (Pichon, 1979).

Genus *Mergus* Linnaeus, 1758

Mergus sp.

Material. Right carpometacarpus, proximal part, AaO-2659.

This carpometacarpus has been compared with the following genera of Oxyurinae (Worthy & Lee, 2008) (*Biziura, Heteronetta, Thalassornis, Stictonetta, Malacorhynchus*) and Anatinae (*Alopochen, Tadorna, Plectropterus, Cairina, Sarkidiornis, Nettapus, Aix, Chenonetta, Amazonetta, Merganetta, Anas, Marmaronetta, Netta, Aythya, Somateria, Polysticta, Histrionicus, Clangula, Melanitta, Bucephala, Mergus*) present in the USNM collection, and it is most similar to the genus *Mergus*. The alular metacarpal is not very projecting, both cranially and proximally. The dorsal face of this alular metacarpal has a depression that is more marked in the genus *Mergus* than in the other members of Anatinae. Its proximal craniocaudal depth, 10.9 mm, is included in the variation range of the Recent species *Mergus serrator*, the Red-breasted Merganser (Woelfle, 1967).

At the present time the Red-breasted Merganser does not winter on the Atlantic coasts of Morocco, but it is present, at the same latitude, on the Atlantic coasts of North America (del Hoyo *et al*., 1992). *Mergus* aff. *M. serrator* is also present in the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001).

Order Galliformes

Family Phasianidae

Genus *Plioperdix* Kretzoi, 1955

Plioperdix africana n.sp.

Fig. 4M–U

Holotype. Complete right humerus AaO-755.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Right humeri, almost complete, AaO-753, shaft, AaO-2687, distal parts, AaO-761, 769, 857; left humeri, distal parts, AaO-760, 762, 763, 4809.

Referred material. Left coracoids, almost complete,

Table 6. Measurements (mm) of *Plioperdix africana* n.sp. from Ahl al Oughlam, and *Plioperdix ponticus* from Ukraine, Moldova, and Central Asia (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin, 2009).

	***Plioperdix africana* n.sp.** Ahl al Oughlam		***Plioperdix ponticus***	
Coracoid	AaO-754	AaO-2688	observed range	mean (n)
internal length	est. 31	—	—	—
width of facies artic. humer.	3.4	3.4	—	—
greatest width at midpoint	3.3	3.3	—	—
depth at midpoint	2.2	2.2	—	—
width of sternal facet	9.1	—	6.1–6.1	6.10 (2)
length of sternal facet	7.0	—	—	—
depth of sternal part	2.9	—	—	—
Humerus	observed range	mean (n)		
total length	43.7–44.2	43.95 (2)	—	—
proximal width	11.0–11.6	11.30 (2)	—	—
depth of head	4.8–5.0	4.90 (2)	—	—
with of shaft at midpoint	3.7–4.0	3.90 (4)	—	—
depth of shaft at midpoint	2.8–3.2	3.05 (4)	—	—
distal width	7.5–8.1	7.89 (8)	6.9–7.1	6.95 (4)
distal depth	4.3–4.8	4.63 (6)	3.8–4.2	3.92 (5)
Ulna	AaO-4810			
proximal width	5.0			
Radius	AaO-2689			
total length	36.2		—	—
greatest diam. of shaft at midpoint	1.7		—	—
least diam. of shaft at midpoint	1.5		—	—
Carpometacarpus	observed range	mean (n)		
total length	22.5–23.8	23.23 (3)	20.9–21.5	21.2 (2)
proximal width	2.8–3.1	2.97 (6)	2.3–2.6	2.48 (5)
proximal depth	5.7–6.2	5.97 (3)	5.6–5.7	5.65 (2)
length of distal symphysis	3.8–4.1	3.95 (2)	—	—
width of metacarp. maj. at midpoint	2.2–2.3	2.28 (4)	—	2.1 (1)
depth of metacarp. maj. at midpoint	1.9–2.1	2.05 (4)	—	—
Tibiotarsus	AaO-764			
distal width	5.7		4.4–5.0	4.65 (6)
distal depth	5.6		—	5.0 (1)
Tarsometatarsus	AaO-856			
total length	34.9		—	28.4 (1)
proximal width	7.2		—	5.2 (1)
proximal depth	7.0		—	—
depth of medial cotyla	4.3		—	2.5 (1)
depth of lateral cotyla	3.4		2.4–2.4	2.40 (2)
distal width	6.5		5.2–5.5	5.33 (3)
width trochlea met. III	2.8		2.0–2.3	2.12 (6)
depth trochlea met. III	3.9		2.4–2.7	ca. 2.53 (6)
distance foramen to distal end [a]	6.0		3.3–5.1	4.17 (6)
smallest width of shaft	3.2		2.3–2.3	2.30 (4)
least depth of shaft	2.1		1.4–1.6	1.48 (5)

[a] Distance from the distal vascular foramen to the distal end of trochlea metatarsi III.

AaO-754, omal part, AaO-2688, shaft, subadult, AaO-757; left ulna, proximal part, AaO-4810; radius, almost complete, AaO-2689; right carpometacarpi, almost complete, AaO-756, 758, 858; left carpometacarpi, proximal part, AaO-759, proximal part and shaft, AaO-4811; right tibiotarsus, distal part, AaO-764; right tarsometatarsus, AaO-856.

Diagnosis. Species showing the morphological characteristics of the genus *Plioperdix* but larger than the only species known so far, *Plioperdix ponticus* (Tugarinov, 1940), from the Pliocene of Europe and Central Asia.

Measurements. See Table 6.

Etymology. *africana*, for Africa, because the only other species of this genus, *Plioperdix ponticus*, was described from Eastern Europe and Asia.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. This small galliform from Ahl al Oughlam has been compared with all the Recent African genera present in the USNM collection but it cannot be referred to any of them

The humeri have a double pneumotricipital fossa. The Fossa pneumoanconaea is widely open and penetrates up to the proximal end of the bone, under the humeral head. The Fossa tricipitalis penetrates only 1 to 2 mm under the humeral head. The tricipital fossa is continued on the caudal face of the shaft by a shallow groove, that goes distally and obliquely onto the ventral border of the shaft. This groove is very elongated distally. It is bordered on the dorsal side by a ridge, the Margo caudalis, which keeps to the Eminentia musculi latissimi dorsi posterioris (Ballmann, 1969). On the cranial side, the Sulcus transversus is very shallow and indistinctly outlined proximally.

In their description of the material referred to the genus *Plioperdix* Bocheński and Kurochkin (1987) gave three morphological characteristics for the humerus. One was this groove. Another was that the distal part of the Crista

Figure 4. (*A*) *Phoebastria* sp. cf. *P. nigripes*, left humerus, distal part, AaO-718, cranial view. *Morus peninsularis*, *B–D*: (*B*) left coracoid, AaO-2108, ventral view; (*C*) right carpometacarpus, AaO-2643, ventral view; (*D*) left femur, AaO-724, caudal view. *Morus* sp. cf. *M. bassanus*, *E–F*: (*E*) right humerus, distal part, AaO-4801, cranial view; (*F*) left ulna, proximal part and shaft, AaO-2640, craniodorsal view. *Geronticus olsoni* n.sp., *G–K*: (*G*) right humerus, distal part and shaft, AaO-838, cranial view; (*H*) left coracoid, AaO-741, holotype, dorsal view; (*I*) idem, ventral view; (*J*) left tibiotarsus, distal part, AaO-2654, cranial view; … [caption continued on facing page]

pectoralis humeri ends with a sharp step. This is not very visible on the Ahl al Oughlam humeri but it is similar to what can be seen on the cranial face of the humerus of *P. ponticus* illustrated by them (Bocheński & Kurochkin, 1987, pl. XVIII, fig. 11–12). The third feature was that the Epicondylus ventralis is sharpened distally, which is also the case on the Ahl al Oughlam humeri.

The Ahl al Oughlam humeri have been compared with the humeri of the genus *Palaeortyx*. This genus is known in many European localities, from the beginning of the Late Oligocene and generally to the Middle Miocene (Göhlich & Mourer-Chauviré, 2005), but also in the Late Miocene of Hungary (Janossy, 1976), Spain (Villalta, 1963; Cheneval & Adrover, 1993), and is present until the Early Pliocene in Gargano, in Southern Italy (Ballmann, 1973, 1976; Göhlich & Pavia, 2008). A form referred to the genus *Palaeortyx* is also present in southwestern Africa, in the lower Miocene of Elisabethfeld and in the middle Miocene of Arrisdrift, both in Namibia (Mourer-Chauviré, 2003; 2008). *Palaeortyx* differs from the Ahl al Oughlam form in that the Fossa tricipitalis penetrates very deeply under the humeral head, to the end of the bone, and consequently the Fossa pneumoanconaea penetrates less deeply than the tricipital fossa. In addition the tricipital fossa continues in the disto-ventral direction as a groove which is more oblique and shorter than in the genus *Plioperdix*.

Two other genera of small galliforms, *Palaeocryptonyx* and *Chauvireria*, are present in the European Pliocene. The Ahl al Oughlam humeri have been compared with those of the type-species of *Palaeocryptonyx, P. donnezani*, from the lower Pliocene of Perpignan (MN 15) (Depéret, 1892, 1897). On the humerus of *P. donnezani*, the tricipital fossa penetrates under the humeral head, but not deeply, and is not continued as a groove crossing the shaft obliquely, in the disto-ventral direction. The humerus of *P. donnezani* is smaller than that of *P. africana*, but its deltopectoral crest is proportionally longer. The pneumatic foramen situated in the Fossa pneumoanconaea is smaller in *P. donnezani*. In *P. africana*, the distal part of the humerus is more elongate ventrad and the ventral epicondyle projects more ventrad than in *P. donnezani*.

In *Chauvireria balcanica* Boev, 1997, from the upper Pliocene of Varshets (MN 17), Bulgaria, the humerus is straighter, whereas in *P. africana* both proximal and distal parts are ventrally incurved. In *Chauvireria*, the tricipital fossa penetrates deeply under the humeral head, but it is not prolonged as a groove. The humeral head is more swollen in the proximo-distal direction than in the genera *Plioperdix* and *Palaeocryptonyx*, and the distal part is relatively narrower than in the other two genera.

The genus *Plioperdix*, with the species *P. ponticus* (Tugarinov, 1940), has been reported in the Early Pliocene of Ukraine and Moldova, and in the Late Pliocene of Transbaikalia and northern Mongolia (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin 2009). A phasianid similar to *Plioperdix ponticus* has also been reported in the Late Miocene of Southern European Russia (Titov *et al*., 2006). Mlíkovský (1995) placed *Francolinus minor* Janossy, 1974, in synonymy with *Plioperdix ponticus* (Tugarinov, 1940), and reported this species in the locality of Stránská Skála, Musil's Talus Cone, in the Czech Republic, dated from the Early Middle Pleistocene (Tyrberg, 1998). But subsequently Mlíkovský (2002) placed the genus *Plioperdix* in synonymy with the Recent genus *Alectoris*, and the species *Plioperdix ponticus* in synonymy with *Alectoris donnezani* (Depéret, 1892). The species *donnezani* is the type-species of the genus *Palaeocryptonyx* and we have shown above that the genus *Plioperdix* differs from the genus *Palaeocryptonyx*. Therefore the occurrence of the species *Plioperdix ponticus* in the Early Middle Pleistocene relies on the correction refused of *F. minor* Janossy, 1974 to *Plioperdix* and so cannot be confirmed.

The carpometacarpi of *P. ponticus* are characterized by a Processus intermetacarpalis weakly developed, and a minor metacarpal narrow, not projecting caudally as angle, and not extending distally beyond level of Facies articularis digitalis major. Distinct fossae are located at base and in distal part of the minor metacarpal, one fossa on each side (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin, 2009). In *P. africana* the carpometacarpus is relatively shorter than in *P. ponticus*. The Processus intermetacarpalis is small and is situated very close to the proximal symphysis of the major and minor metacarpals, but it is relatively more developed than in *P. ponticus*. The minor metacarpal is only preserved on one specimen and it is very thin. The fossa which is situated on the ventral side of the distal symphysis of *P. ponticus* (Zelenkov & Kurochkin, 2009, pl. 9, figs 7b and 10b) is absent in *P. africana*.

In *P. africana*, the carpometacarpus differs from that of *Palaeortyx* because the Processus pisiformis is globular and does not extend cranially, and the Depressio muscularis interna (*sensu* Ballmann, 1969) is shallow, unlike that in the genus *Palaeortyx* (see Mourer-Chauviré *et al*., 2004, pl. 1, fig. 5). It differs from the genus *Palaeocryptonyx* as in this genus the Processus intermetacarpalis is situated farther from the proximal synostosis of the two metacarpals. *Chauvireria* is distinguished from *P. africana* by a very robust major metacarpal, and its minor metacarpal is more robust and more distant from the major metacarpal. In *Chauvireria* the Processus intermetacarpalis is well developed, the minor metacarpal protrudes very slightly distally beyond the level of the facies articularis digitalis major, and there is a fossa on the ventral side of the distal symphysis.

Bocheński & Kurochkin (1987) then Zelenkov & Kurochkin (2009) give the morphological characteristics of the coracoid of *Plioperdix*. In *P. africana* the Pars omalis of the coracoids is incomplete but the coracoid AaO-754 agrees with *P. ponticus* in having a sternal facet very short and very curved and it lacks a pneumatic foramen in the Impressio m. sternocoracoidei. Coracoids of *Palaeocryptonyx* have a longer and less curved sternal facet and the Angulus medialis projects less mediad. AaO-754 differs also from the genus

Figure 4 [caption continued from facing page]... (*K*) left tarsometatarsus, AaO-2655, cranial view. (*L*) Rallinae, right humerus, distal part, AaO-765, cranial view. *Plioperdix africana* n.sp., *M–U*: (*M*) right humerus, AaO-755, holotype, caudal view; (*N*) idem, cranial view; (*O*) right humerus, AaO-753, paratype, caudal view; (*P*) left coracoid, AaO-754, dorsal view; (*Q*) idem, ventral view; (*R*) right carpometacarpus, AaO-756, ventral view; (*S*) right tarsometatarsus, AaO-856, plantar view; (*T*) idem, dorsal view; (*U*) idem, proximal view. The scale bars represent 1 cm. Same scale bar for *A–K* and *M–T*.

Table 7. Measurements (mm) of fossil *Otis* sp., size *Otis tarda*, from Ahl al Oughlam and Recent *Otis tarda*.

Ulna		***Otis* sp.** **Ahl al Oughlam**	***Otis tarda*** **Recent**	
			males	females
		AaO-766		
proximal width	observed range	24.1	23.2–25.9	17.2–18.6
	mean (n)		24.47 (3)	18.00 (4)
proximal depth	observed range	22.0	21.8–24.4	17.0–18.0
	mean (n)		23.33 (3)	17.38 (4)
		AaO-767		
depth of condylus dorsalis	observed range	17.4	18.3–19.6	14.0–14.4
	mean (n)		18.77 (3)	14.20 (2)
distal depth [a]	observed range	ca. 16.5	17.6–20.8	14.2–15.7
	mean (n)		19.10 (3)	14.95 (2)

[a] From the tuberculum carpale to the dorsal side of the condylus dorsalis.

Chauvireria, the sternal facet of which is also longer and less curved, but the Angulus medialis more projecting. In these two genera, there is no pneumatic foramen in the Impressio m. sternocoracoidei. On the ventral face, the Ahl al Oughlam coracoid shows a strong longitudinal ridge which causes a bulge of the sternal facet, while in *Palaeocryptonyx* and *Chauvireria* the sternal part is flatter.

The tarsometatarsus AaO-856 shows the principal characteristic of the genus *Plioperdix*: the trochleae are constricted rather than splayed, causing a relatively narrow distal end. Trochlea met. II is strongly pushed back plantarly and both Trochleae met. II and IV do not project significantly on the medial and lateral sides. This tarsometatarsus is subadult. The Sulcus extensorius is very deep at its proximal part. The two proximal vascular foramina are situated at the bottom of a fossa. The medial border of the Cotyla medialis projects significantly proximad as can be seen also in *Plioperdix ponticus* (see Bocheński & Kurochkin, 1987, pl. XVIII, fig. 3–4). In the two specimens of *P. ponticus* the hypotarsus is not completely preserved. There are two ridges, a medial one, and a lateral one, separated by a canal. On the Ahl al Oughlam specimen there is a roofed canal, situated approximately in the sagittal plane, and another roofed canal, narrower, situated plantarly compared to the first one. Both canals open distally by a single orifice, situated on the medial side of the hypotarsus. On the plantar face of the hypotarsus there are two smooth ridges, separated by a shallow groove. The hypotarsus is prolonged, along the plantar face, by a short median ridge. On each side of the hypotarsus there are the Fossae parahypotarsales medialis and lateralis. The Fossa parahypotarsalis lateralis is bordered by a ridge on its lateral side. The Fossa met. I is hardly visible. As Bocheński & Kurochkin (1987) have indicated, the tarsometatarsus of *Plioperdix* is very different from that of *Ammoperdix*. The most striking characteristic of the *P. africana* tarsometatarsus is that its distal width is less than its proximal width.

The measurements of *P. africana* are given in Table 6. On average, the dimensions of *P. africana* are 30% larger than those of *P. ponticus*.

Order Gruiformes

Family Rallidae

Rallinae size *Porzana pusilla* (Pallas, 1776)

Fig. 4L

Material. Right humerus, distal part, AaO-765.

Among all the Recent genera with which it was compared, it looks most similar to the genus *Porzana*. It differs from *Porzana*, however, by the strong deepening of its Fossa m. brachialis. Its distal width is 3.7 mm. In one Recent *Porzana pusilla* the distal width is also 3.7 mm.

Family Otididae

Genus *Otis* Linnaeus, 1758

Otis sp., size *Otis tarda* Linnaeus, 1758

Fig. 5A–B

Material. Right ulna, proximal part, AaO-766, and distal part, AaO-767.

Measurements. See Table 7.

Comparison with Recent forms. This fossil was compared with the genera having species of large size today in today Africa: *Ardeotis, Neotis, Lissotis, Afrotis*, and *Otis*. The proximal part of the ulna differs from those of *Ardeotis* because, in that genus, there is almost no separation between the dorsal and ventral cotylae, whereas in the Ahl al Oughlam fossil, as in *Otis*, there is a Crista intercotylaris. On the ventral side, the Impressio brachialis is very deep and forms a fossa which is ventrally bordered by a projecting ridge. In *Ardeotis*, the Impressio brachialis is very wide and extends to the median axis of the bone. In the Ahl al Oughlam fossil, as in *Otis*, the Impressio brachialis is narrower, shallower, not bordered by a ridge, and does not extend to the middle of the cranial face of the shaft.

In the genera *Neotis* and *Lissotis*, the shaft becomes much narrower distally compared to the proximal part, the Impressio brachialis also forms a fossa bordered by a projecting ridge, as in *Ardeotis*. The shaft becomes wider

again at the distal part, and the tuberculum carpale strongly projects craniad. In the Ahl al Oughlam fossil, as in the genus *Otis*, the shaft does not become much narrower distally compared to the proximal part.

In the genus *Afrotis*, the shapes of the cotylae are different. The dorsal cotyla is almost as wide as the ventral cotyla and has the shape of a parallelogram, whereas in the Ahl al Oughlam fossil, as in *Otis*, the dorsal cotyla is much narrower than the ventral cotyla.

Compared to a Recent *Otis tarda*, in the fossil the olecranon is less proximally projecting and narrower at its base, and the dorsal cotyla is prolonged distally on the cranial face by a shorter lip. At the distal part, the shape of the articular surface is craniocaudally narrower, and both dorsal and ventral condyles are more distally projecting than in the Recent form. The same characteristic has been described for an *Otis* sp. from the upper Pliocene of Saint-Vallier, the age of which is similar (Mourer-Chauviré, 2004, fig. 4). Finally, the Tuberculum carpale is situated further in the proximal direction and is dorsoventrally narrower than in the Recent form. The Papillae remigales, or quill knobs, are often very projecting in the Otididae. On the caudal face of the proximal part one can see three papillae, the first one slightly flattened, the other ones circular and very projecting.

Comparison with fossil forms. *Otis lambrechti* Kretzoi, 1941, a species comparable in size to *Otis tarda*, has been reported in several southern European localities (Hungary, Romania, Austria) dated from MN 18 to MNQ 22 (Mourer-Chauviré, 2004), but no ulna was found in any of these localities. A larger form, *Iorotis gabunii* Burchak-Abramovich & Vekua, 1981, has been described from the Pliocene (MN 16) of oriental Georgia, but it is larger than the Recent males of *O. tarda*. The other extinct species of the genus *Otis* are smaller than *Otis tarda*.

Genus *Chlamydotis* Lesson, 1839

Chlamydotis sp. cf. *C. mesetaria* Sánchez-Marco, 1990

Fig. 5C–E

Material. Right tarsometatarsus, proximal part and shaft, AaO-2664.

Measurements. See Table 8.

This tarsometatarsus shows the morphological characteristics of the genus *Chlamydotis* as follows. There is a strong difference in level between the lateral and the medial cotylae. The lateral cotyla is offset clearly lower in the distal direction than the medial cotyla. The lateral cotyla has an almost octogonal shape. It has two articular facets on its lateral side, a cranial one and a plantar one. There is a small groove on the cranial side of the medial cotyla, on the medial side of the Eminentia intercotylaris. In the hypotarsus there is a large roofed groove. The Crista medialis hypotarsi does not project plantarly as far as in the genus *Otis*, but it is extended by a straight ridge on the medioplantar side.

At the present time, the genus *Chlamydotis* only includes one species, *Chlamydotis undulata*, the Houbara bustard, but an extinct species, *C. mesetaria*, has been described from the locality of Layna, Spain (Sánchez-Marco, 1990), dated to be from the end of the mammal reference-level MN 15, or about 3.5 Ma (Daams *et al*., 1999). This species is only known by a tibiotarsus. It is characterized by a slightly larger size than in the Recent species *C. undulata*, and the width of the shaft in the middle, as well as just proximally to the condyles, shows that it was a proportionally more robust form. In the Ahl al Oughlam form, the measurements are very slightly larger than in the Recent species, but the shaft is clearly stronger. For that reason we designate it as *Chlamydotis* sp. cf. *C. mesetaria*, the age of which is also comparable.

Table 8. Measurements (mm) of fossil *Chlamydotis* sp. cf. *C. mesetaria* from Ahl al Oughlam and Recent *Chlamydotis undulata*.

Tarsometatarsus	***Chlamydotis* cf. *mesetaria*** Ahl al Oughlam	***Chlamydotis undulata*** Recent	
		males	females
	AaO-2664	(n=2)	(n=2)
proximal width	15.5	15.8–16.6	13.3–15.3
proximal depth	13.3	13.2–13.2	11.4–12.8
width of shaft at midpoint	ca. 6.3	5.3–5.4	4.8–5.4

A bustard, designated as cf. *Chlamydotis undulata* has been reported from the Middle Miocene of Maboko Island, in Kenya (C. Harrison, 1980).

Genus *Lophotis* Reichenbach, 1839

cf. *Lophotis* sp.

Fig. 5F–G

Material. Almost complete right coracoid, AaO-768.

Measurements (in mm): internal length, 41.4; length from the top of acrocoracoid to the sternal part of the scapular facet, 14.0; proximal width from the medial side of the scapular facet to the lateral side of the glenoid facet, 7.7; least width of shaft, 4.4; depth of shaft at the same level, 3.9; depth of the sternal facet, 4.4.

On this coracoid, the ventral-most tip of the acrocoracoid, the Angulus medialis, and the lateral side of the sternal part are missing. This coracoid has been compared with those of the genera *Tetrax, Eupodotis, Afrotis, Lissotis*, and *Lophotis*, and it is most similar to the genus *Lophotis*. Its morphological chracteristics are as follows: its shape is elongate and more slender than in the other genera; the impression of the M. sternocoracoidei is not strongly indicated; the procoracoid protrudes from the shaft very close to the scapular facet, it is narrow at its base, whereas it is wider in the other genera. In the genus *Lissotis*, the shaft strongly widens in the sternal direction below the scapular facet, whereas this is not the case in the Ahl al Oughlam fossil. Among bustards there is a difference in the shape of the acrocoracoid: in the genera *Tetrax* and *Lissotis* it forms a very long point directed medially and ventrally, whilst in *Afrotis* and *Lophotis* it is shorter, unfortunately it is not possible to see this characteristic on the fossil. This coracoid cannot belong to the same species as the tarsometatarsus referred to *Chlamydotis* sp. cf. *C. mesetaria*: it corresponds

to a smaller form. Its dimensions are slightly larger than those of three comparative specimens of *Lophotis ruficrista gindiana* from the USNM.

Order Charadriiformes

Family Charadriidae

Genus *Pluvialis* Brisson, 1760

cf. *Pluvialis* sp.

Material. Left humerus, proximal part, AaO-770.

This humerus resembles *Pluvialis apricaria* and *P. squatarola*. It differs from them because the ledge of the humeral head which overhangs the tricipital fossa is less developed than in these two Recent species. *Pluvialis* aff. *squatarola* has been reported in the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001). At the present time both species occur on the Atlantic coasts of Morocco.

Genus *Charadrius* Linnaeus, 1758

cf. *Charadrius* sp.

Material. Left humerus, almost complete, AaO-773.

At the present time several species of the genus *Charadrius* occur on the Atlantic coasts of Morocco. According to the estimated length of the humerus (ca. 32 mm) the plover present at Ahl al Oughlam was slightly larger than the Recent species *Charadrius dubius* and *C. alexandrinus* and was closer to the Recent species *Charadrius hiaticula*.

Family Stercorariidae

Genus *Catharacta* Brünnich, 1764

Catharacta sp. cf. *C. skua* Brünnich, 1764

Fig. 5I

Material. Right humerus, distal part and shaft, AaO-4793.

Measurements (in mm): distal width, 18.7; distal depth, 11.5; width of shaft in the middle, 8.5; depth of shaft in the middle, 7.5.

This humerus is morphologically similar to that of the Recent species *Catharacta skua*, and its dimensions agree with that of a Recent specimen from the Paris MNHN as well as with those given by Olson & Rasmussen (2001) for the Recent forms. A *Catharacta* sp., the size of *Catharacta skua* or *C. maccormicki*, has been reported from the Lee Creek Mine, coming probably from the Yorktown Formation (Olson & Rasmussen, 2001). In Florida, the locality of Richardson Road Shell Mine, dating to 2.4–2.0 Ma, has yielded a coracoid of a *Stercorarius* sp., intermediate in size between the Recent species of the genus *Catharacta* and the Recent species of the genus *Stercorarius* (Emslie, 1995). At the present time the Great Skua breeds mainly on islands in the North Atlantic and winters on the continental shelf, on both sides of the Atlantic Ocean and in Western Mediterranean, young individuals reaching Cape Verde Islands and Brazil (del Hoyo *et al*., 1996).

Family Alcidae

Genus *Alca* Linnaeus, 1758

Alca ausonia (Portis, 1889)

Fig. 5J–M

Material. Right humerus, proximal part, AaO-781; left humerus, shaft and distal part, AaO-2666; left scapula, cranial part, AaO-2665; left ulna, distal part, AaO-2667; left radius, shaft and distal part, AaO-841; left carpometacarpus, distal part, AaO-2668; right femur, distal part, AaO-2661; left tibiotarsus, proximal part and shaft, AaO-2693.

This material shows the morphological characteristics of the genus *Alca* and differs from the other members of Alcidae. Alcids are very numerous in the Pliocene of the Yorktown Formation and include, from the smaller to the larger, *Alca* aff. *torda, A. ausonia, Alca grandis* and *Alca stewarti* (Olson, 2007; Wijnker & Olson, 2009). There are no detailed measurements, but it is possible to see that the distal width of the humerus is comprised between ca. 11.8 and 12.8 mm for *Alca ausonia*, and between ca. 13.5 and 14.5 mm for *A. grandis* (Olson & Rasmussen, 2001, fig. 9). In the Ahl al Oughlam specimen the distal part of humerus is incomplete, but it is possible to estimate the distal width (from the cranial face of the Condylus dorsalis to the caudal face of the Epicondylus ventralis) at ca. 11.9 mm. On a cast of the holotype of *Alca ausonia* (IGF 14875), this distal width is 12.3 mm. The Ahl al Oughlam Alcidae is therefore attributed to the extinct species *Alca ausonia*. The measurements are given in Table 9. Compared to a Recent specimen of *Alca torda islandica*, the dimensions of the specimens referred to *Alca ausonia* here from Ahl al Oughlam are on average 24% larger.

In addition to the fossil forms from the Yorktown Formation, alcids belonging to the genus *Alca* have also been reported on the coasts of the Old World. *Alca ausonia* has been described from the Middle Pliocene of Orciano Pisano, in Tuscany, close to the Mediterranean (Delle Cave, 1996). *Alca* sp. has been reported from the Pliocene of El Alamillo, southeast Spain, in marine deposits (Sánchez-Marco, 2003). This form is slightly larger than *Alca torda* and could belong to *Alca ausonia. Alca ausonia* has been reported in the lower Pliocene of the Kattendijk Sands Formation at Kallo, Belgium (Dyke & Walker, 2005). However the total length given for a complete ulna (55 mm) seems too small for this

Table 9. Measurements (mm) of fossil *Alca ausonia* from Ahl al Oughlam.

	Alca ausonia Ahl al Oughlam
Humerus	AaO-781
proximal. width	20.0
depth of humeral head	8.1
Humerus	AaO-2666
maximal distal width	ca. 11.9
max. width of shaft [a]	8.2
max. depth at the same level	4.8
Scapula	AaO-2665
maximal width of omal part	12.7
Ulna	AaO-2667
distal diagonal	ca. 10.5
width of shaft at midpoint	4.4
depth of shaft at midpoint	7.2
Radius	AaO-841
width of shaft at midpoint	4.4
depth of shaft at midpoint	3.0
distal width	6.4
distal depth	4.1
Carpometacarpus	AaO-2668
width major metacarp. at midpoint	3.1
depth major metacarp. at midpoint	4.3
Femur	AaO-2661
width of shaft at midpoint	4.7
depth of shaft at midpoint	4.7
distal width	ca. 9.0
distal depth	ca. 8.6
Tibiotarsus	AaO-2693
proximal width	8.0
proximal depth with crista cnemialis cranialis [b]	12.6
height of crista cnemialis cranialis [c]	8.0
width of shaft at midpoint	4.8
depth of shaft at midpoint	4.0

[a] At 40 mm from the distal end, in proximal direction.
[b] From the facies articularis medialis to the cranialmost part of the crista cnemialis cranialis.
[c] From the articular plane to the tip of the cristal cnemialis cranialis.

species. Four different species of *Alca* (including probably *A. ausonia*) are present in the Early Pliocene (age 3.5 Ma) of the Netherlands (E. Wijnker, pers. comm.).

At the present time alcids still occur on the Moroccan coasts (Urban *et al*., 1986).

Order Columbiformes

Family Columbidae

Genus *Columba* Linnaeus, 1758

Columba sp. cf. *C. pisana* (Portis, 1889)

Fig. 5H

Material. Right humerus, distal part and shaft, AaO-2672.

Measurements (in mm): distal width, 10.6; distal depth, 7.3; width of shaft in the middle, 5.2.

Given the current environment of Ahl al Oughlam the presence of members of Pteroclidae could be expected, but the humerus AaO-2672 agrees well with the columbids and differs from the pteroclids because in the pteroclids the entepicondyle projects caudad much more than in the columbids, and it is clearly distinct from the ventral condyle.

The species described by Portis (1889) from Orciano Pisano, in Tuscany, as *Falco pisanus*, actually corresponds to a columbid (Mourer-Chauviré, in Olson, 1985c). Mlíkovský (2002) placed this species in the genus *Columba* and he placed it in synonymy with *Columba omnisanctorum* described by Ballmann (1976) from the Gargano. These two species are almost contemporaneous, early Pliocene (MN 14–15) for the Gargano, middle Pliocene (MN 15–16) for Orciano Pisano (Delle Cave 1996). It is not possible to compare these two species directly because they are not represented by the same elements, but they are compatible in size. The ulna of *Columba pisana* is slightly larger than that of Recent *Columba livia* and *Columba oenas*, and the different elements of *Columba omnisanctorum* are included in the range of variation of the Recent *C. oenas* (see measurements in Fick, 1974). *Columba palumbus* is bigger than both species (Fick, 1974). In the Ahl al Oughlam humerus the distal width is 10.6 mm whereas in *C. omnisanctorum* the distal width is 11 mm (Ballmann, 1976).

Columba sp. size *C. palumbus* Linnaeus, 1758

Material. Left carpometacarpus, proximal part, AaO-782.

Measurements (in mm): proximal width, 5.8; proximal depth, 11.2.

The dimensions of this carpometacarpus are larger than those of the Recent *C. livia* and *C. oenas*, and they fall within the range of variation of the Recent *C. palumbus* (see measurements in Fick, 1974).

Order Psittaciformes

Family Psittacidae

Genus *Agapornis* Selby, 1836

Agapornis atlanticus n.sp.

Fig. 5N–Q

Holotype. Almost complete right humerus AaO-786.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Incomplete right humeri, AaO-788, 789, 791, 2670; right humeri, proximal part, AaO-784, 790, 793, 800; right humeri, distal part, AaO-794, 2700, 2701, 2702, 4812; left humeri, AaO-785, 2671; left humeri, almost complete, AaO-783, 787, 853, 854; left humeri, distal part, AaO-2703, 2704, 2705, 2706. The humeri AaO-790, 794, 2700, and 4812 show a deposit of medullary bone.

Referred material. Right ulnae, proximal part and shaft, AaO-797, proximal part, AaO-4814; right ulnae, distal part, AaO-799, 4816; left ulna, almost complete, AaO-792; left ulnae, proximal part, AaO-795, 796, 4815; left ulna, distal part, AaO-4817; right carpometacarpi, almost complete, AaO-775, 776, 778; right carpometacarpus, proximal part, AaO-798; left carpometacarpi, proximal part, AaO-779, 4813.

Diagnosis. Species larger than the Recent or fossil species of the genus *Agapornis*. The humeral head shows a distal extension on the caudal face. On the dorsal side of

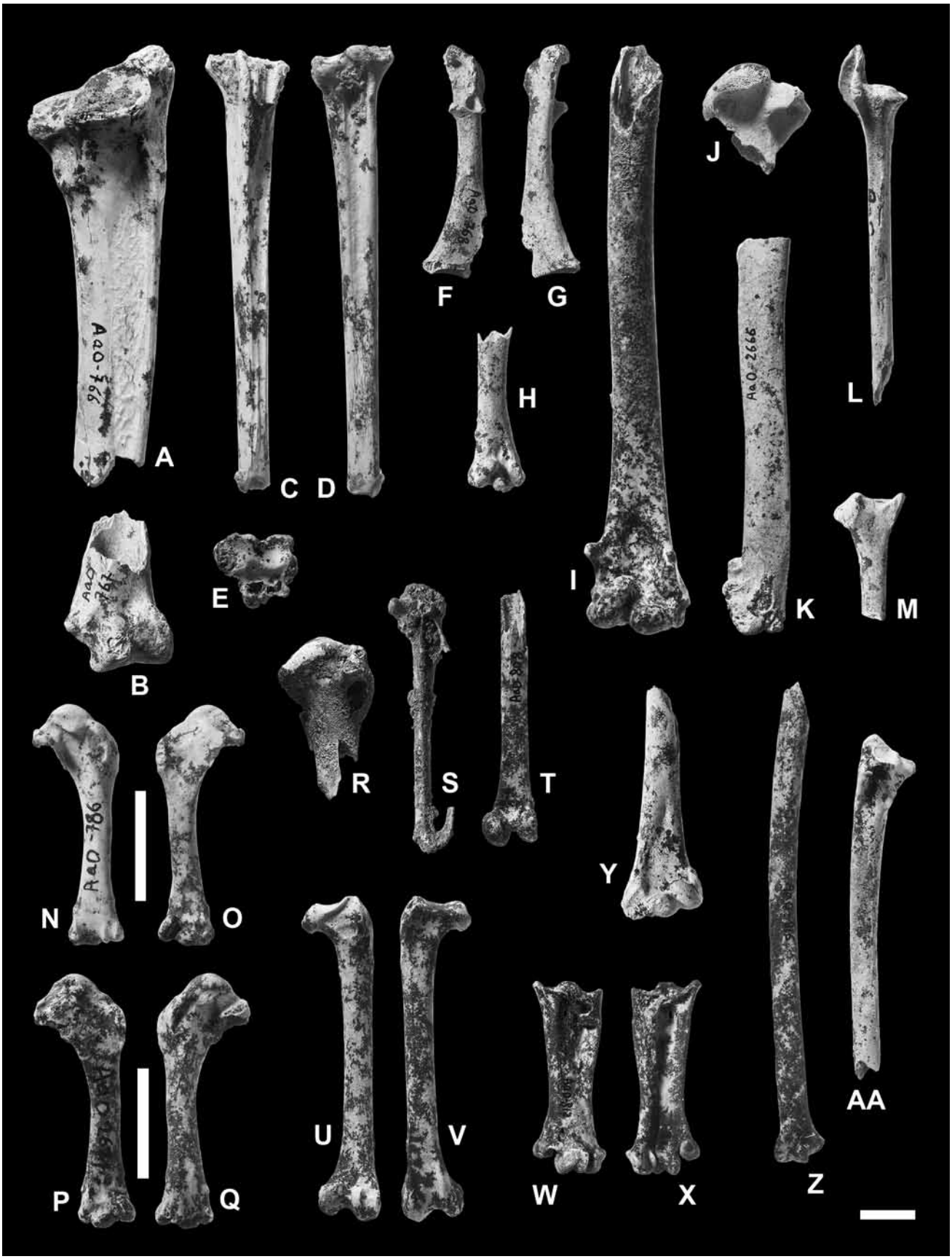

Figure 5. *Otis* sp. size *Otis tarda*, *A–B*: (*A*) right ulna, proximal part, AaO-766, cranial view: (*B*) right ulna, distal part, AaO-767, ventral view. *Chlamydotis* sp. cf. *C. mesetaria, C–E*: (*C*) right tarsometatarsus, proximal part and shaft, AaO-2644, caudal view; (*D*) idem, cranial view; (*E*) idem, proximal view. cf. *Lophotis* sp., *F–G*: (*F*) right coracoid, almost complete, AaO-768, dorsal view; (*G*) idem, ventral view. (*H*) *Columba* sp. cf. *C. pisana*, right humerus, distal part and shaft, AaO-2672, cranial view. (*I*) *Catharacta* sp. cf. *C. skua*, right humerus, distal part and shaft, AaO-4793, cranial view. … [caption continued on facing page]

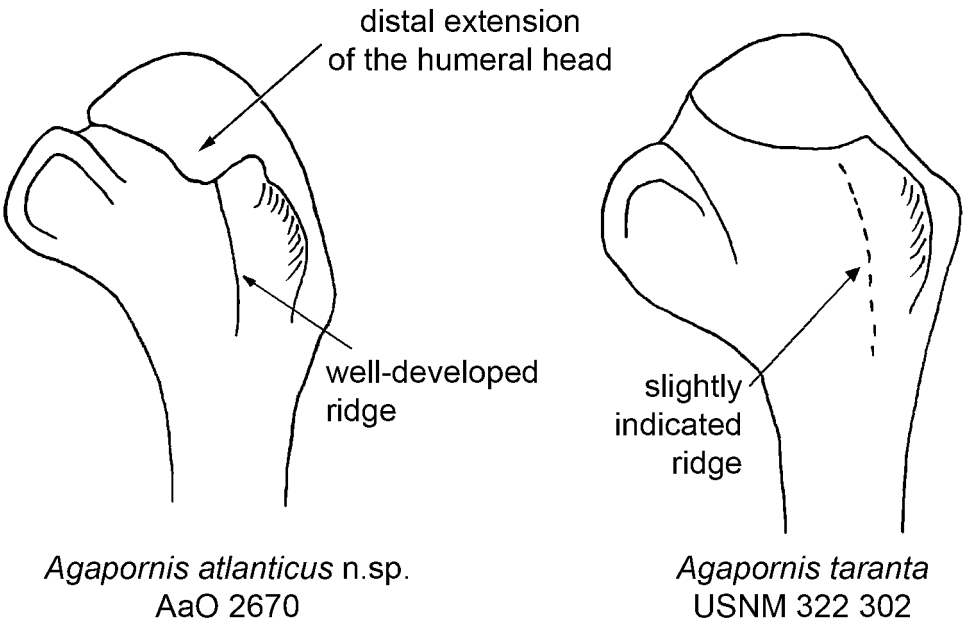

Figure 6. Diagram showing the differences between the proximal humerus of *Agapornis atlanticus* n.sp., from Ahl al Oughlam, and that of a Recent specimen of *Agapornis taranta*, USNM 322302.

the humeral head there is a longitudinal ridge which is more developed than in the Recent species.

Measurements. See Table 10.

Etymology. *atlanticus*, from the Atlantic Ocean, because the locality of Ahl al Oughlam was on the Atlantic shore at the time of the deposit.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. These parrot specimens have been compared with all of the genera that occur in Africa at the present time and which are present in the USNM collection. The fossils can be attributed to the genus *Agapornis*. Among the Recent species of this genus there is a size variation, the smallest one being *A. lilianae*, then by increasing size *A. pullarius, A. personatus, A. fischeri, A. roseicollis*, and *A. taranta*. There was no comparative skeleton of *A. nigrigenis* but this species is similar in size to *A. lilianae*. The Ahl al Oughlam *Agapornis* remains are large and, by their dimensions, they are closer to the Recent species *A. taranta*. Compared to a sample of six individuals of *A. taranta*, the total length of the humerus is similar, but the distal width is smaller and the width of the shaft in the middle is larger in the Moroccan form. In the ulna the mean values of the proximal width and width of shaft in the middle are larger, and for the carpometacarpus the total length and the proximal depth are also larger in the Ahl al Oughlam species.

Morphologically the humerus of *Agapornis atlanticus* differs from the Recent species by the presence of a distal extension of the humeral head on the caudal face. This extension does not exist in the Recent *Agapornis*. There is also a longitudinal ridge that begins on the dorsal side of the humeral head and extends distad. It delimits an elongate fossa, situated between this ridge and the crista m. supracoracoidei. This ridge is very faintly visible in the Recent *Agapornis* (Fig. 6). At the distal end, the attachment of the anterior articular ligament is strongly projecting. Proximal to this attachment, the impression of M. brachialis is situated entirely on the ventral half of the bone. There is a tubercle proximal to the dorsal condyle but it is very slightly indicated and it is visible only on one half of the humeri. This characteristic is different from that described by Stidham for the Recent and fossil *Agapornis* from South Africa, where "the humeri exhibit the character of having a tubercle proximal to the space in between the dorsal and the ventral condyles" (Stidham, 2006, p. 199). In the Ahl al Oughlam parrots the dorsal condyle measures about 2.5 mm proximo-distally and the tubercle is situated about 1 mm proximally to the condyle. This position is different from what we have observed in the genus *Poicephalus* where a tubercle is present and situated proximally to the dorsal condyle, but on the

Figure 5 [caption continued from facing page]… *Alca ausonia, J–M*: (*J*) right humerus, proximal part, AaO-781, caudal view; (*K*) left humerus, distal part and shaft, AaO-2666, cranial view; (*L*) left tibiotarsus, proximal part and shaft, AaO-2693, lateral view; (*M*) left scapula, cranial part, AaO-2665, lateral view. *Agapornis atlanticus* n.sp., *N–Q*: (*N*) right humerus, almost complete, AaO-786, holotype, caudal view; (*O*) idem, cranial view; (*P*) left humerus, almost complete, AaO-2671, paratype, cranial view; (*Q*) idem, caudal view. *Tyto balearica, R–S*: (*R*) left humerus, proximal part, AaO-4805, caudal view; (*S*) right carpometacarpus, AaO-2684, ventral view. (*T*) *Tyto alba*, left tibiotarsus, distal part, AaO-808, cranial view. *Surnia robusta, U–AA*: (*U*) left femur, AaO-814, caudal view; (*V*) idem, cranial view; (*W*) right tarsometatarsus, almost complete, AaO-817, cranial view; (*X*) idem, caudal view; (*Y*) left humerus, distal part, AaO-839, cranial view; (*Z*) left ulna, distal part and shaft, AaO-816, ventral view; (*AA*) left ulna, proximal part and shaft, AaO-815, ventral view. The scale bars represent 1 cm. Same scale bar for *A–M* and *R–AA*.

Table 10. Measurements (mm) of fossil *Agapornis atlanticus* n.sp. from Ahl al Oughlam and Recent *Agapornis taranta* (s = standard deviation).

	***Agapornis atlanticus* n.sp.** Ahl al Oughlam				***Agapornis taranta*** Recent			
	mean	observed range	n	s	mean	observed range	n	s
Humerus								
total length	22.50	22.0–23.4	8	0.53	22.78	21.7–23.8	6	0.78
prox. width [a]	7.37	7.1–7.6	7	0.20	—	—	—	—
distal width	4.83	4.7–5.0	11	0.12	5.08	4.8–5.4	6	0.26
width of shaft at midpoint	2.68	2.4–2.9	13	0.16	2.05	1.9–2.3	6	0.14
Ulna								
total length	ca. 27.0	—	1	—	27.67	26.5–28.7	6	0.84
prox. width	4.00	3.9–4.1	4	0.08	3.78	3.5–4.0	6	0.19
width of shaft at midpoint	2.00	1.9–2.1	4	0.12	1.93	1.9–2.1	6	0.08
Carpometacarpus								
total length	21.20	21.0–21.4	2	0.28	17.48	16.6–18.7	6	0.78
prox. depth	5.58	5.5–5.7	4	0.10	4.70	4.4–4.9	3	0.26

[a] From the ventral side of the crista bicipitalis to the dorsal side of the crista m. supracoracoidei.

median side of this condyle and closer to it.

Extinct psittacids exist in the Neogene of the Palaearctic region, such as *Archaeopsittacus verreauxi*, from the early Miocene of Saint-Gérand-le-Puy (MN 2a) (Milne-Edwards, 1867–1871), *Xenopsitta fejfari* from the early Miocene of Merkur (MN 3) (Mlíkovský, 1998a), and *Pararallus dispar* (syn. *Psittacus lartetianus*) from the middle Miocene of Sansan (MN 6) (Cheneval, 2000). Indeterminate psittacids have also been reported in the middle Miocene of the Nördlinger Ries (MN 6) and of Steinheim (MN 7) (Heizmann & Hesse, 1995). In Africa, psittacids were present in the late Miocene and the early Pliocene of Langebaanweg (Rich, 1980; Stidham, 2006), and *Agapornis* sp. is reported from two localities of Olduvai, Bed I, lower Pleistocene (Brodkorb, 1985), and from the Pleistocene of Kromdraai B (Stidham, 2006).

The presence of an *Agapornis* species in Morocco is surprising because all of the Recent species of this genus live South of the Sahara, and most of them have a very limited distribution area in the southern part of the African continent. These different species live in variable environments, moist savannah, lowland primary and secondary forests, montane forests, wooded steppe (Fry *et al*., 1988), but one species, *A. roseicollis*, lives close to the western coast of Southern Africa (Angola, Namibia, South Africa) in dry wooded and subdesert steppe. This species may sometimes nest in rock crevices. The presence of medullary bone (Rick, 1975) inside the medullary cavity of several humeri indicates that *Agapornis atlanticus* was nesting in the vicinity of the fossiliferous site. It it possible that this species nested in the blocks of consolidated sands in which the fossils were deposited, while the other species of this genus nest in termitaria or in trees (Fry *et al*., 1988).

Order Strigiformes

Family Tytonidae

Genus *Tyto* Billberg, 1828

Tyto balearica Mourer-Chauviré, Alcover, Moya & Pons, 1980

Fig. 5R–S

Material. Left humerus, proximal part, AaO-4805; left ulnae, proximal parts, AaO-4794, 4806; left radii, distal parts, AaO-852, 2686; right carpometacarpus, almost complete, AaO-2684; left carpometacarpus, distal part, AaO-2685; right tibiotarsus, distal part, AaO-2698; left tibiotarsi, distal parts, AaO-4807, 4808.

Measurements (in mm): humerus, proximal width, ca. 17.0; proximal depth, 9.8. Ulnae, proximal width, 9.9 and 10.1. Radii, least width of shaft, 2.8 and ca. 2.9. Carpometacarpus, total length, est. 48.5. Tibiotarsi, distal width, 10.7 and 11.2.

The dimensions of these elements are clearly larger than those of the Recent *Tyto alba* and they are either included in the size-variation of the extinct species *T. balearica*, or are close to them (Mourer-Chauviré & Sánchez-Marco, 1988; Louchart, 2002). *Tyto balearica* was described from three insular localities of the Balearics (Mourer-Chauviré *et al*., 1980), then was found again in several continental localities of Spain and the south of France, where it is present until the Plio-Pleistocene boundary (summary statement in Sánchez-Marco, 2001). It has also been found in the Middle Pleistocene of Corsica and Sardinia where it is represented by a particular subspecies, *T. balearica cyrneichnusae* (summary statement in Louchart, 2002). On the other hand,

the remains from the upper Miocene of Aljezar B (MN 12) (Cheneval & Adrover, 1993), of Valdecebro (MN 12) (Sánchez-Marco, 2001), and some remains from the Mio-Pliocene of Gargano referred by Mlíkovský (1998b) to *T. balearica*, do not belong to this species (Louchart, 2002).

Tyto balearica is thus known during a time span extending from the Early Pliocene (MN 15) to the Middle Pleistocene. In all these localities it does not coexist with *Tyto alba*. The only locality where *T. balearica* is found together with another species of the genus *Tyto* is the Middle Pleistocene locality of Castiglione 3 CG, in Corsica, where an indeterminate species of *Tyto* is represented by a pedal phalange (Louchart, 2002).

Tyto alba (Scopoli, 1769)

Fig. 5T

Material. Left ulna, distal part and shaft, AaO-801; distal part, AaO-850; right radii, distal parts, AaO-802, 803; right carpometacarpus, distal part, AaO-805; left carpometacarpi, proximal part, AaO-806, distal part, AaO-4797; right femora, shaft, AaO-804, distal part, AaO-807; right tibiotarsi, distal part and shaft, AaO-4799; left tibiotarsi, distal parts, AaO-808, 809, 810; right tarsometatarsi, proximal part, AaO-813, distal parts, AaO-849 (juvenile), 4803; left tarsometatarsi, proximal part, AaO-2699, distal part, AaO-812, shaft AaO-811.

The dimensions of the Ahl al Oughlam Barn Owl are slightly larger than the maximal values for a population of Recent *Tyto alba alba* and *T. alba guttata* (Louchart, 2002) but there are a large number of subspecies with strong size variation. The Recent species *Tyto alba* has been reported in the Middle Miocene (MN 7, Mein 1990) of Beni Mellal in Morocco (Brunet, 1971) but it is only represented by an alar phalange (Brunet, 1961). It cannot be excluded that this phalange could have belonged to an earlier species of the genus *Tyto*, as for example *Tyto sanctialbani*, the dimensions of which are similar to those of the Recent *Tyto alba* (Lydekker, 1893). Apart from this reference, the oldest mention of the presence of *Tyto alba* is from the locality of Olduvai, Bed I, dating between 1.85 and 1.70 Ma (Brodkorb & Mourer-Chauviré, 1984a).

Family Strigidae

Genus *Surnia* Duméril, 1806

Surnia robusta Janossy, 1977

Fig. 5U–AA

Material. Rostrum maxillare, AaO-818; left humerus, distal part, AaO-839; left ulnae, proximal part and shaft, AaO-815, distal part and shaft, AaO-816; left femur, AaO-814; right tarsometatarsus, almost complete, AaO-817 (only the Crista medialis hypotarsi is missing).

Measurements. See Table 11.

This species was described by D. Janossy from material from four Plio-Pleistocene localities of Hungary (Janossy, 1977; 1983), and it has not been reported from any other locality. It is characterized by its size which is much larger than in the Recent and fossil forms of the species *Surnia ulula*, the Hawk Owl, the only present-day species of the genus *Surnia*.

This material shows the morphological characteristics of the genus *Surnia*, with its particularly short and robust tarsometatarsi. On the rostrum maxillare the ventral face of the os premaxillare is flattened. In the Recent *Surnia ulula* this surface is variable, it is flattened in half of the individuals, and grooved in the other half. The distal humerus shows the same characteristics as are found in the genus *Surnia*. It is strongly ventrally elongated. The impression of M. brachialis is very long and extends very far proximad along the shaft. The ectepicondylar prominence is broken on the fossil, but it is possible to see that it was situated just proximally to the dorsal condyle. In the genus *Surnia*, it is small, but clearly projecting and its top forms a right angle. On the proximal ulna, on the cranial side, distally to the cotylae,

Table 11. Measurements (mm) of *Surnia robusta* from Ahl al Oughlam and the Carpathian Basin (Janossy, 1977) and Recent *Surnia ulula*.

	Surnia robusta Ahl al Oughlam	***Surnia robusta*** Janossy, 1977	***Surnia ulula*** Recent, mean
Rostrum maxillare			(n = 6)
length [a]	ca. 15.5	—	9.85
Humerus			(n = 7)
distal width	ca. 15.5	15.5–16.0 [f]	12.16
distal depth	7.8	—	6.10
width of shaft at midpoint [b]	6.3	6.7	4.83
depth of shaft at midpoint [b]	5.5	—	4.40
Ulna			(n = 12)
proximal width	10.2	—	8.02
proximal depth [c]	8.7	—	6.75
distal width [d]	8.6	—	6.75
depth of internal condyle	8.5	—	6.32
width of shaft at midpoint	4.9–5.0	—	3.64
depth of shaft at midpoint	5.1–5.3	—	3.70
Femur			(n = 15)
total length	59.2	—	49.17
proximal width	12.7	—	9.72
proximal depth	8.4	—	6.13
distal width	12.1	12.0	9.39
distal depth	10.1	—	7.71
width of shaft at midpoint	5.2	5.3	4.01
depth of shaft at midpoint	5.5	—	4.05
Tarsometatarsus			(n = 12)
total length	35.3	37.2	25.91
proximal width	12.7	12.6	9.68
partial proximal depth [e]	6.9	—	5.86
distal width	13.3	12.6–15.0 [g]	10.08
distal depth	9.6	—	7.23
width of shaft at midpoint	8.4	7.3	6.05
depth of shaft at midpoint	3.6	—	2.78

[a] Length of the rostrum maxillare from the tip of the rostrum to the cranial border of the nasal aperture.
[b] On the Ahl al Oughlam humerus, the width and depth of shaft are not measured at midpoint, but just distal to the break.
[c] From the cranial border of the ventral cotyla to the top of the olecranon.
[d] From the dorsal border of the dorsal condyle to the top of the tuberculum carpale.
[e] On the Ahl al Oughlam tarsometatarsus the crista medialis hypotarsi is broken. The proximal depth is measured from the dorsal side of the cotylae to the top of the crista lateralis hypotarsi.
[f] n = 3
[g] n = 4

the bicipital attachment forms a proximodistally elongated and sharply defined ridge. In the Recent *Surnia ulula*, this ridge projects less and has a variable shape, but it is rather dorsoventrally oriented. The distal ulna does not differ from the Recent *S. ulula* except by its size. The femur also shows the morphological characteristics of the genus *Surnia*. On the femoral head the Fovea lig. capitis is very deep. On the caudal face the lateral condyle extends proximally by a ridge. This ridge closes the Fossa poplitea on its medial side and delimits laterally a deep fossa that is situated proximally compared to the lateral and fibular condyles. On the tarsometatarsus, the Crista medialis hypotarsi is missing. This tarsometatarsus shows the same proportions as in the Recent species, *S. ulula*, but it is larger. Its dimensions are very close to those of the holotype tarsometatarsus of *Surnia robusta*, from Villány 3, which is almost of the same age as Ahl al Oughlam (MN 17, ca. 2–2.5 Ma) (Tyrberg, 1998). The Ahl al Oughlam material has been compared with a sample of 6 to 15 individuals of Recent *S. ulula*, including males and females, from the collections of the MNHN (Laboratoire d'Anatomie comparée and Institut de Paléontologie humaine), in Paris, the NMNH, in Washington, the UCB, in Lyon, and the Paleontological Institute of the Russian Academy of Sciences, in Moscow. On average the postcranial elements of the Moroccan *Surnia robusta* are 31% larger than those of the Recent *Surnia ulula*.

As Janossy has pointed out, the Recent species lives in the taiga zone of Eurasia and North America, and in the mountain regions of Central Asia. "It is a question whether the Lower Pleistocene form had the same ecological significance, in view of the fact that most of the remains originate—as we have seen—from the Submediterranean region of the Villány Mountains" (Janossy, 1977, p. 14). The occurrence of this species at Ahl al Oughlam is not accidental because it is represented by at least two individuals.

Order Passeriformes

A few elements can be attributed to species of the family Alaudidae. Some other elements cannot be identified more accurately, mainly because of the lack of comparative material.

Discussion

It is difficult to compare the Ahl al Oughlam avifauna with the other avifaunas from the upper Miocene and Pliocene of Africa, because these other African faunas include a large proportion of aquatic species, non-marine but living on the shores of rivers and freshwater, saline, or alkaline lakes. In Ethiopia and Chad the late Miocene avifaunas include species belonging to the families Podicipedidae, Phalacrocoracidae, Anhingidae, Ardeidae, Ciconiidae (with large sized forms), Anatidae (with a small sized swan, *Afrocygnus chauvireae*), Gruidae and Heliornithidae (Louchart *et al*., 2005a; Louchart *et al*., 2005b; Louchart *et al*., 2008). Although the Recent African species *Leptoptilos crumeniferus* is not strictly aquatic, forms belonging to the genus *Leptoptilos* are almost always associated with these avifaunas.

The same predominance is found again in the Late Miocene avifaunas of Eastern and Northern Africa. In Kenya the avifauna of Lothagam (Harris & Leakey, 2003) is mainly composed of species of Pelecanidae, Anhingidae, Ciconiidae (*Leptoptilos* cf. *crumeniferus*), Ardeidae, Anatidae and Rallidae. In North Africa, in the Beglia Formation of Tunisia (Rich, 1972), there are species of the families Phalacrocoracidae, Anhingidae, Balaenicipitidae(*Paludiavis richae*, C. Harrison & Walker, 1982), and Ciconiidae (*Leptoptilos richae* C. Harrison, 1974, the size of *Leptoptilos crumeniferus*) (Louchart *et al*., 2005c). In the locality of Sahabi, in Libya, which is probably older than the Mio-Pliocene boundary, there are species of the families Phalacrocoracidae, Anhingidae, Ciconiidae (*Leptoptilos* sp.), and Anatidae [in particular the small swan *Afrocygnus chauvireae* (Ballmann, 1987; Louchart *et al*., 2005a)]. The only locality that has yielded a terrestrial avifauna is Lemudong'o, in Kenya, but the material is very fragmentary and has been only identified at the ordinal or familial level (Stidham, 2007).

The African Pliocene and early Pleistocene avifaunas also include a very large proportion of aquatic forms. In Chad, the avifaunas of Kossom Bougoudi (age 5 Ma) and Koro Toro (age 3–3.5 Ma) only include aquatic forms: phalacrocoracids, anhingids, ardeids, the very large ciconiid, *Leptoptilos falconeri*, and anatids (Louchart *et al*., 2004; Louchart *et al*., 2005c). In Ethiopia, the Pliocene localities of Hadar and Omo have yielded anhingids (Brodkorb & Mourer-Chauviré, 1982) and again the very large ciconiid *Leptoptilos falconeri* (Louchart *et al*., 2005c). In Tanzania, the locality of Olduvai, Bed I, has yielded a great quantity of birds that correspond primarily to aquatic forms, or species of the following families: Podicipedidae, Anhingidae, Phalacrocoracidae, Pelecanidae, Phoenicopteridae, Ardeidae, Balaenicipitidae, Ciconiidae (including possibly *Leptoptilos falconeri*), Anatidae, Rallidae, and charadriiforms belonging to at least seven families (Jacanidae, Rostratulidae, Charadriidae, Scolopacidae, Recurvirostridae, Glareolidae, Laridae) (Brodkorb & Mourer-Chauviré, 1982; Brodkorb & Mourer-Chauviré, 1984b; Brodkorb, 1985). Again in Tanzania, the Upper Pliocene phosphorites of Minjingu have yielded phalacrocoracids (Schlüter, 1991).

In contrast to all these avifaunas with predominant aquatic forms the Pliocene locality of Laetoli, in Tanzania, has yielded bird remains and fossil eggs belonging only to terrestrial forms (Struthionidae, Accipitridae, Phasianidae, Numididae, Columbidae and Strigidae) (Watson, 1987; T. Harrison, 2005; T. Harrison & Msuya, 2005). In South Africa, in the locality of Langebaanweg, the Quartzose Sand Member, lower Pliocene, has yielded a very rich avifauna where the most abundant birds are species of Phasianidae (58% of the Minimal Number of Individuals = MNI). Among the aquatic forms, procellariiforms and charadriiforms are relatively numerous (8% of the MNI), but other families were represented by only 1% (Phalacrocoracidae) or less than 1% (Spheniscidae, Podicipedidae, Sulidae, Ciconiidae, Rallidae) of the MNI (Rich 1980), and the ardeids, phoenicopterids and balaenicipitids are not represented (Olson, 1985b). Another difference is the presence of a large, extinct, stork, *Ciconia kahli* (Haarhoff, 1988), whereas in the other upper Miocene and Pliocene localities of Africa, the ciconiids are represented by very large forms of Leptoptilini (genera *Leptoptilos* and *Ephippiorhynchus*) (Louchart *et al*., 2005c; Louchart *et al*., 2008).

The Ahl al Oughlam avifauna is made up partly of marine forms and partly of terrestrial forms. The marine forms

are: *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Calonectris* sp. cf. *C. diomedea, Pelagornis mauretanicus, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua*, and *Alca ausonia*. Among the terrestrial forms, it is possible to distinguish forms whose recent or past distribution can be both Eurasiatic and African, or Palaearctic, or only African. The Eurasiatic and African forms are: *Struthio asiaticus, Geronticus olsoni* n.sp., *Alopochen* sp. cf. *A. aegyptiacus, Tadorna tadorna, Otis* sp. size *O. tarda, Chlamydotis* sp. cf. *C. mesetaria, Columba* sp. size *C. palumbus, Tyto alba*. The Palaearctic forms are: *Mergus* sp., the genus *Plioperdix, Columba* sp. cf. *C. pisana, Tyto balearica*, and *Surnia robusta*. The uniquely African forms are: cf. *Lophotis* sp. and *Agapornis atlanticus* n.sp.

The marine avifauna of Ahl al Oughlam is very similar to the slightly older avifauna of the Yorktown Formation, North Carolina, and it is very different from the Early Pliocene avifaunas of South Africa (Langebaanweg, Olson, 1985d, and Duinefontein, Olson 1985a). A very rich marine avifauna from the Early Pliocene of Netherlands (about 3.5 Ma) is currently under study by Erik Wijnker. It also presents great affinities with the Yorktown Formation avifauna (E. Wijnker, pers. comm.). The marine avifauna of Ahl al Oughlam, with its three species of albatrosses, one extinct, and the other two closely related to Recent forms of the North Pacific, and the most recent member of Pelagornithidae known so far, is very different from the present day avifauna and shows that there has been a considerable modification in the Atlantic avifauna since the end of the Pliocene. However, this modification occurred progressively because albatross colonies were still present in the North Atlantic until the Middle Pleistocene (Olson & Hearty, 2003).

Among the mammals, most of the genera identified at Ahl al Oughlam are also known in Eastern or Southern Africa (Geraads, 2006). Unlike the mammals, the terrestrial bird fauna does not look like the other terrestrial avifaunas from the Pliocene of Africa, with the exception of the ostriches, which are present in almost all the localities. In particular, galliforms are represented at Ahl al Oughlam by the Eurasiatic genus, *Plioperdix*, whereas the African Pliocene avifaunas generally include species of the genus *Francolinus*, and sometimes *Coturnix* (Brodkorb, 1985), or *Pavo* (Louchart, 2003; Pickford *et al*., 2004). This shows that, as far as the birds are concerned, Morocco already belonged to the palaearctic zoogeographical region in the late Pliocene. The only really African elements are a bustard, referred to the genus *Lophotis*, and the small *Agapornis* parrot. The avifauna does not include any oriental component.

Paleoecological significance

The pollen record of the ODP site 658, situated at 21°N, makes it possible to follow the evolution of the vegetation over a long period, from 3.7 Ma to 1.7 Ma (Leroy & Dupont, 1994). According to these authors (1994, p. 309) "The oxygen isotope record of ODP Site 658 shows high glacial values for stages 104 (2.60 Ma), 100 (2.53 Ma) and 98 (2.49 Ma) resembling the strong fluctuations of the Quaternary. These stages are expressed in the pollen spectra by high percentages of dry elements, such as Amaranthaceae-Chenopodiaceae, Caryophyllaceae, *Artemisia* and *Ephedra*. During this period, probably desert vegetation developed in Northwestern Africa, as a response to severe aridification in combination with increased trade winds". The ODP site 658 is situated too far away from the Casablanca region to give information about the vegetation of this region, but nevertheless it indicates a growing aridification of northwestern Africa during this period. This is confirmed also by what is known in the Mediterranean area where a first steppe appears at about 2.5 Ma, indicating a cooler and more arid climate.

As already mentioned the marine avifauna of Ahl al Oughlam is very similar to the slightly older avifauna of the Yorktown Formation, which is situated almost at the same latitude (35°23'22"N, Olson & Rasmussen, 2001), and it does not indicate anything concerning the temperature. The mammals, by the absence of tree-dwelling monkeys, the virtual absence of forest or even woodland antelopes, and the abundance of gerbillids, point to an open landscape (Geraads, 2006). Most of the landbirds, with the presence of ostriches, ibises, bustards, small partridges, larks, also correspond to an open environment. The abundance of the small parrot, *Agapornis atlanticus* n.sp., is surprising, but in the genus *Agapornis* one species, *A. roseicollis*, lives in dry wooded and subdesert steppes (Fry *et al*., 1988). The oddest element is the presence of the genus *Surnia*, the only Recent species of which, *Surnia ulula*, lives in the forest tundra and boreal taiga of the North of the Holarctic region and the mountains of Central Asia, but avoids the dense coniferous forests (del Hoyo *et al*., 1999). At the present time forests of cork-oaks and holm oaks are present in the El Katouat massif, to the South East of Casablanca, which reaches its highest point at 1058 m, but this massif is situated at about 60 km from the site. It seems therefore probable that the ecological requirements of the extinct species *Surnia robusta* were different from those of the Recent species *Surnia ulula*.

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