The Struthionidae and Pelagornithidae (Aves: Struthioniformes, Odontopterygiformes) from the late Pliocene of Ahl Al Oughlam, Morocco

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ABSTRACT - The Pliocene locality of Ahl al Oughlam is situated at the southeastern limit of the city of Casablanca, in Morocco, on an ancient seashore of the Atlantic Ocean. It has yielded a very rich vertebrate fauna (macro- and micromammals, birds, reptiles, amphibians and fishes) including both terrestrial and marine forms. On the basis of biostratigraphy, the fauna has been dated at about 2.5 Ma, which corresponds to the latest Pliocene. The avifauna is very diverse and includes birds belonging to twelve different orders. In this paper we describe only the Struthionidae and the Pelagornithidae. Ostriches are represented by a large-sized form, referred to the extinct species *Struthio asiaticus* Milne-Edwards, and its eggshells, of struthioid type, are comparable to those of the recent species *Struthio camelus*, but thicker. The Pelagornithidae, giant marine birds with bony pseudoteeth, are represented by an extinct species of the genus *Pelagornis*. As far as we know, this species was probably the latest representative of the order Odontopterygiformes.

Keywords - Aves, Ostriches, Pseudodontorns, Pelargornis mauretanicus n. sp., Pliocene, Morocco

Les Struthionidae et les Pelagornithidae (Aves, Struthioniformes et Odontopterygiformes) du Pliocène final d'Ahl al Oughlam, Maroc – Le gisement pliocène d'Ahl al Oughlam est situé à la limite sud-est de la ville de Casablanca, au Maroc, sur un ancien rivage de l'Océan Atlantique. Il a livré une très riche faune de Vertébrés (macro- et micromammifères, oiseaux, reptiles, amphibiens et poissons), appartenant surtout à des formes terrestres, mais comportant aussi des formes marines. Des arguments biostratigraphiques ont permis de dater cette faune de 2,5 Ma, ce qui correspond au Pliocène final. L'avifaune est très diversifiée et comporte des oiseaux appartenant à douze ordres différents. Dans cette étude nous décrivons seulement les Struthionidae et les Pelagornithidae. Les autruches sont représentées par une forme de grande taille, attribuée à l'espèce éteinte *Struthio asiaticus* Milne-Edwards, et leurs coquilles d'œufs, de type struthioïde, sont comparables à celles de l'espèce actuelle *Struthio camelus*, mais sont plus épaisses. Les Pelagornithidae, oiseaux marins géants à pseudodents, sont représentés par une espèce éteinte du genre *Pelagornis*. Les restes trouvés à Ahl al Oughlam correspondent probablement aux derniers réprésentants connus de l'ordre des Odontopterygiformes.

Mots Clés - Oiseaux, Autruches, Oiseaux à pseudodents, Pelagornis mauretanicus n. sp., Pliocène, Maroc

INTRODUCTION

The fossiliferous locality of Ahl al Oughlam was discovered in 1985 by J.-P. Raynal and J.-P. Texier. It is situated at the southeast boundary of the city of Casablanca, Morocco, 6.5 km from the present-day Atlantic shore (Raynal *et al*., 1990). This locality was then excavated by Denis Geraads, within the framework 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. All the material comes from a network of fissures and interconnected galleries, in a jumble of calcarenites blocks, at the foot of what was once a cliff on the shore. The fact that this site was formed along the oceanic seashore explains that both marine and terrestrial forms were found among the birds. The mammals include mainly terrestrial forms but the remains of a walrus and of two small cetaceans were also found.

The biostratigraphical study of the mammals made it possible to date this locality to the Late Pliocene and to attribute to it an age of about 2.5 Ma (Geraads, 1997). The mammals are very numerous and include more that 55 species. The list of the identified taxa is given by Geraads, 1993, 1995, 1996, 1997, 2004, 2006; Geraads *et al.,* 1998; Geraads & Amani 1998; Alemseged & Geraads, 1998; Geraads & Metz-Muller, 1999; and Eisenmann & Geraads, 2007.
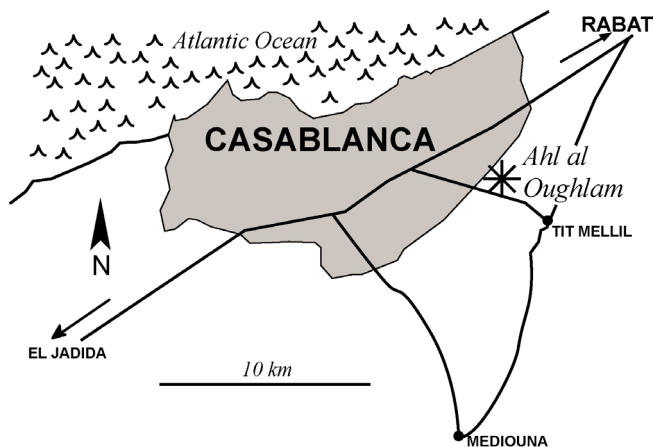
Figure 1 - Location map of the Ahl al Oughlam locality.

In addition to mammals and birds, fishes, amphibians, and reptiles have also been found. The amphibians and the reptiles other than chelonians have been studied by S. Bailon (2000). The material belongs to the collection of IN-SAP, at Rabat.

Birds are very diverse and include Struthioniformes, Procellariiformes, Odontopterygiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Galliformes, Gruiformes, Charadriiformes, Columbiformes, Psittaciformes, Strigiformes, and Passeriformes. The present study concerns only the Struthionidae and Pelagornithidae. The anatomical terminology generally follows Baumel & Witmer (1993), and Howard (1929) when necessary. The following museum acronyms are used: BMNH, The Natural History Museum, London (formerly, British Museum (Natural History)); MNHN, Muséum National d'Histoire Naturelle, Paris; UCB, Université Claude Bernard, Lyon; USNM, collections of the former United States National Museum, now in the National Museum of Natural History, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Order STRUTHIONIFORMES (Latham, 1790)
Family STRUTHIONIDAE Vigors, 1825
Genus *STRUTHIO* Linnaeus, 1758

Struthio asiaticus Milne-Edwards, 1871
fig. 2-3

Material
Dorsal vertebra and fragment of dorsal vertebra, AaO 835, 1444; 3 fragments of pelvis, AaO 703, 874, 875; fragment of rib, AaO 876; several pieces of a left femur, AaO 873; left femur, distal part, AaO 700; shaft of left femur, juv., AaO 3468; right femur, distal part, AaO 701; fragment of right femur, distal part, AaO 702; left tibiotarsus, distal part, AaO 1443; left tibiotarsus, distal part, juv., AaO 2214; right tarsometatarsus, distal part, and left tarsometatarsus, distal part, from the same individual, trochleae not preserved, AaO 2860, 2218; left tarsometatarsus, proximal part, incomplete,

AaO 2928; shaft of left tarsometatarsus, AaO 2216; shaft of right tarsometatarsus, juv., AaO 2217; left tarsometatarsus, distal part, juv., AaO 2215; phalanx 1, AaO 836, and 2, AaO 2219, of right posterior digit III; phalange 3 of posterior digit III, AaO 2973; phalanx 4 of posterior digit III, incomplete, AaO 877; 20 fragments of eggshells.

Dimensions
The material is very fragmentary and it is not always possible to take the standard measurements such as width and depth of the proximal and distal parts, but when taking partial measurements and comparing them with the same measurements taken on recent *Struthio camelus*, it is found that they are on average 20 % larger than on a large male individual (fig. 2).
The measurements which could be taken are as follows (in mm):
Proximal femur (AaO 873): maximum proximal width: 134; minimum depth of collum femoris: 51 ; depth of caput femoris: 57.5.
Proximal tarsometatarsus (AaO 2928): proximal width: estimate superior to 92; width of the shaft at the level of the distal end of the tuberosities for M. tibialis cranialis: ca. 47; depth of the shaft at the same level: ca. 51.
Distal tarsometatarsi AaO 2218 and AaO 2860: width of the shaft 10 cm proximad to the distal foramen 39.2; depth of the shaft at the same level: 27.8; AaO 2218: distal width at the level of the distal foramen: 64.0.
The measurements of the phalanges are given in table 1.

Description
Very numerous fossil forms of ostriches have been described from the Late Miocene, the Pliocene, and the Pleistocene of Eurasia, both on osteological and eggshell remains. According to Kurochkin & Lungu (1970), and Mikhailov (1992), all the European and Asiatic Pliocene forms, described from osteological remains, are very similar and have been synonymized with the species *Struthio asiaticus* Milne-Edwards, described from the Pliocene of the
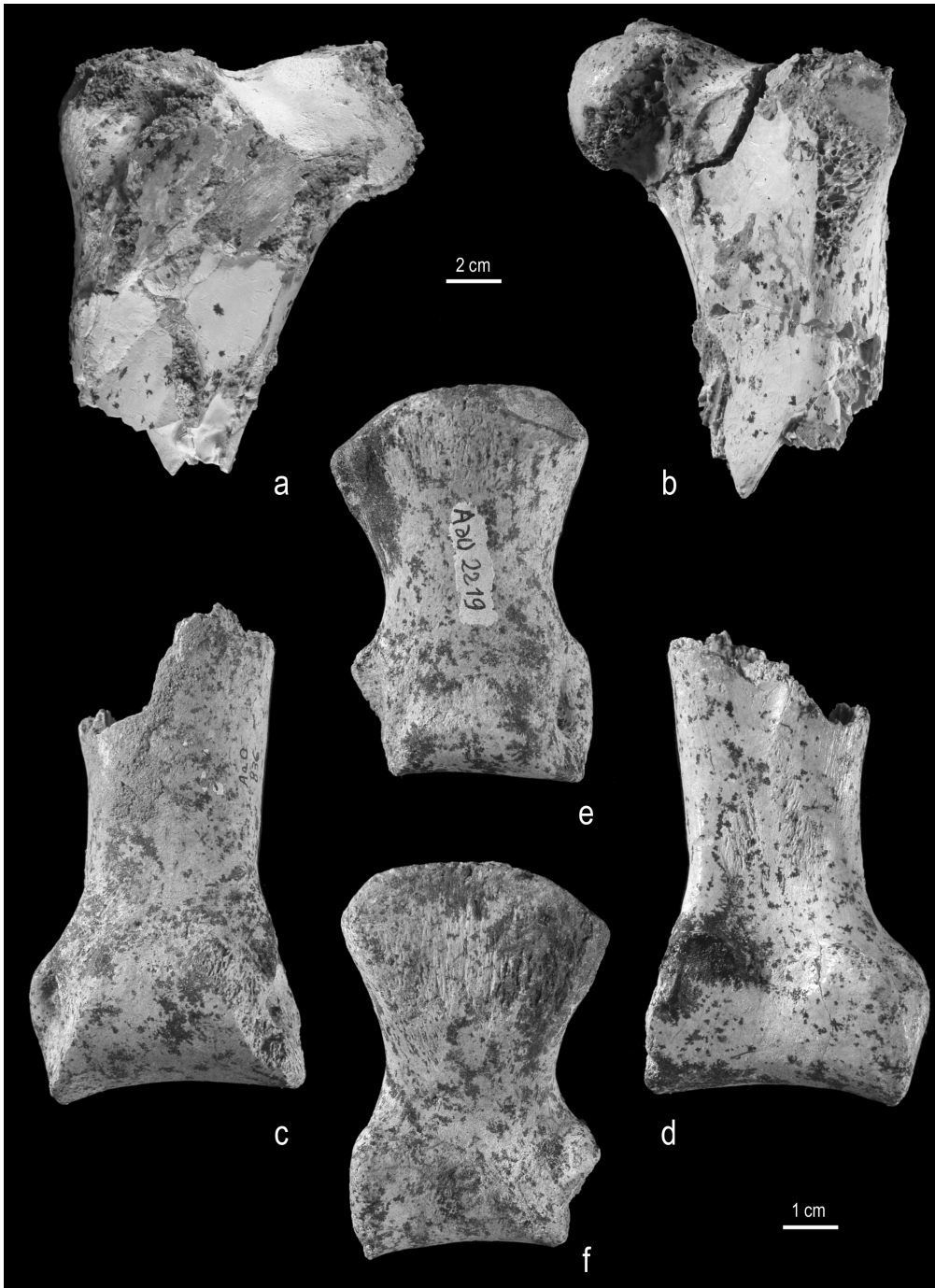
Figure 2 - *Struthio asiaticus*, Ahl al Oughlam.
a-b: left femur, proximal part, AaO 873; a) caudal view, b) cranial view. Same scale for a and b.
c-d: phalanx 1 of right posterior digit III, distal part, AaO 836; c) dorsal view, b) plantar view.
e-f: phalanx 2 of right posterior digit III, AaO 2219; e) dorsal view, f) plantar view. Same scale for c, d, e, and f.

Siwaliks (Milne-Edwards, 1867-71). However, according to Mikhailov (1992: p. 370) "the eggshell remains… are distinct and the features of each "eggshell morphotype species" evolved independently from the Miocene to the Pleistocene". The "eggshell species" need to have their own names, at least parataxonomic ones. For that reason the eggshells are referred to three different species: *S. asiaticus*, which has struthioid type eggshells, *S. chersonensis*, which has mixed aepyornithoid-struthioid type eggshells, and *S. transcaucasicus*, which has aepyornithoid type eggshells (Mikhailov, 1988, 1992).

All the species described from osteological remains from the Late Miocene, the Pliocene, and the Early Pleistocene of Europe and Asia, with the exception of *S. orlovi*, from the Late Miocene of Moldavia (Kurochkin & Lungu, 1970), are massive, heavy ostriches, characterized by dimensions and robustness larger than those of the recent ostrich, *S. camelus*. This also applies to the ostriches which have been described after the publication of Kurochkin and Lungu's (1970) work, for example *S. dmanisensis*, from the Early Pleistocene of Georgia (Burchak-Abramovich & Vekua, 1990). Although *S. asiaticus* is not taller than the recent os-
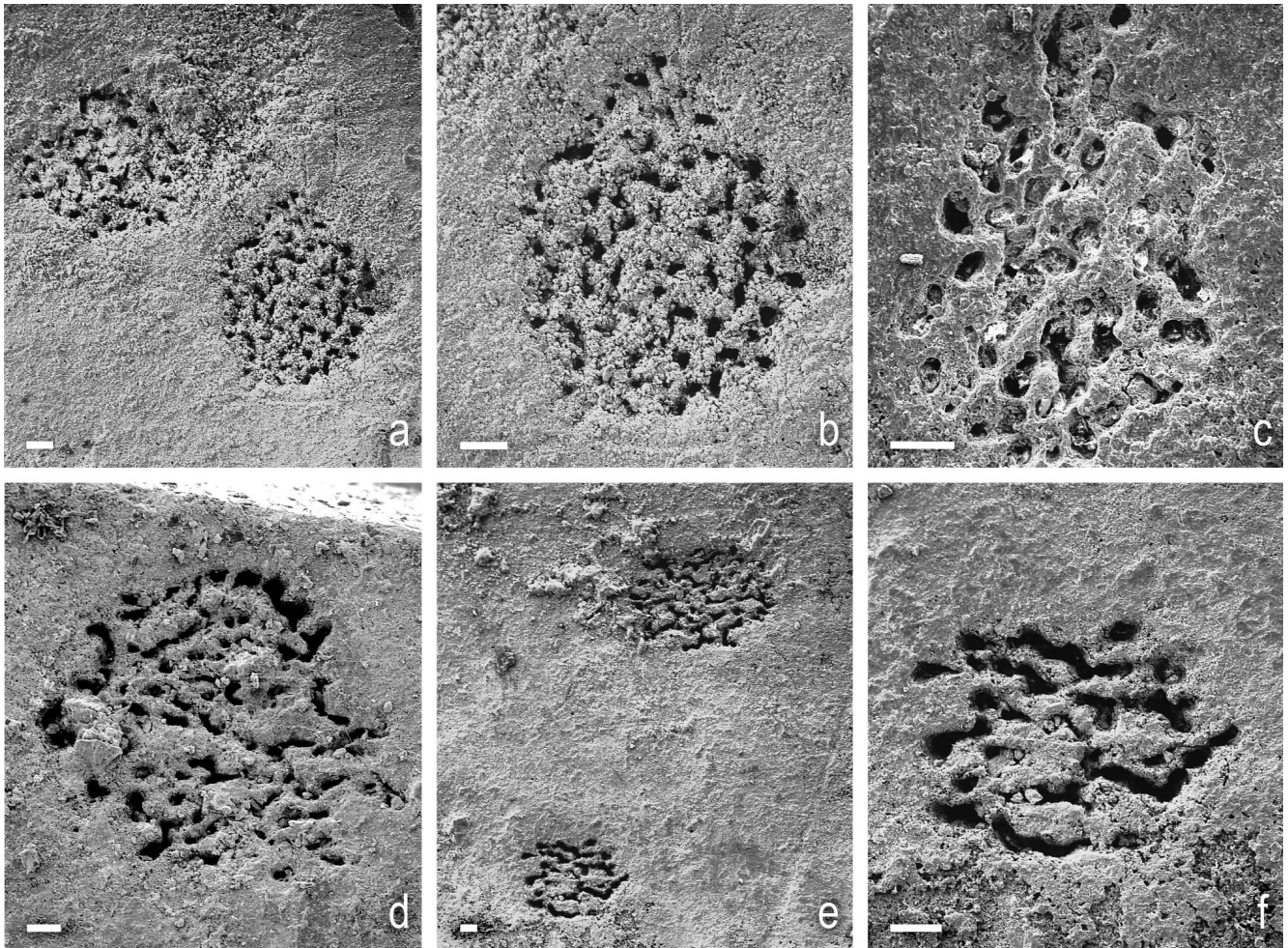
Figure 3 - *Struthio asiaticus*, Ahl al Oughlam. Scanning electron microscope pictures of eggshell fragments showing the complexes of pore openings: a-b: eggshell n° 7; c: eggshell n° 8; d-f: eggshell n° 20. For the eggshell fragment n° 20, the pore openings are particularly visible because of deposits of Mn salts inside them. (Scale bars = 0.1 mm)

trich, it is also a massive form, as shown by the proportions of the phalanx 1 of posterior digit III (table 2).

It is not always possible to compare all these forms with each other since they have been described on the basis of different elements, but for a certain number of species, the dimensions of phalanx 1 of posterior digit III are known (Sauer, 1979). For *S. asiaticus*, the dimensions of the proximal part of this phalanx are known (Davies, 1880; Lydekker, 1884-1886) and for the Ahl al Oughlam ostrich the dimensions of the distal part are known. For all these fossil ostriches, the ratio between proximal width and minimum width of shaft is comprised between 1.57 and 1.68, whereas in the recent *S. camelus* it varies from 1.68 to 1.92. Likewise the ratio distal width/minimum width of the shaft is comprised between ca 1.37 and 1.58 in the fossil ostriches, while it varies from 1.54 to 1.86 in the recent ones (table 2). For *S. asiaticus*, as well as for the Ahl al Oughlam ostrich, the measurements of this phalanx indicate that they were massive ostriches.

Comparisons with the African forms

In Africa *Struthio oldawayi* was described by Lowe (1933) from fragments of pelvis coming from Olduvai, Bed I, Tanzania, dated from 2 - 2.1 to 1.7 Ma (Leakey, 1967; Hay 1976). Lowe indicates that the fossil form only differs from the recent subspecies of *S. camelus* by its larger size but does not give its dimensions. Leakey (1967: pl. 96 and 97) illustrates some bones of a very large ostrich, also coming from Olduvai, Bed I. These bones are at least 33 % larger than those of a large recent male ostrich. Later on, Arambourg (1979) described the species *Struthio barbarus* from the Villafranchian locality of Aïn Boucherit, in Algeria, also characterized by its dimensions that are larger than those of the recent forms. This locality is dated from the Plio-Pleistocene boundary and thus it is slightly younger than Ahl al Oughlam (Geraads, 1993). The dimensions of *S. barbarus* are on average 20 % larger than those of a large recent male ostrich. However, among the forms which have been synonymized

with *S. asiaticus*, some are up to 50 % larger than the recent ones (Kurochkin & Lungu, 1970). According to the different types of fossil eggshells, there were different forms of ostriches in Africa during the Pliocene and the Early Pleistocene (aepyornithoid-type eggshells at least until the Mio-Pliocene, and several different struthioid-type eggshells). Due to the lack of information concerning the type of eggshells of *S. oldawayi* and *S. barbarus*, it is not possible to know if they were really different from each other.

Comparisons with fossil eggshells
Introduction

The difference between the aepyornithoid- and the struthioid-type eggshells lies in the arrangement and the surface openings of the pore canal systems. "The *Aepyornis* eggs have simply isolated canals, each of which opens to the surface in its own elongate and sometimes forked pore groove" (Sauer, 1966: p. 10). Also in the *Aepyornis* eggs, "the deeply grooved pore openings [are] oriented parallel, and interspersed with short comma and sting (or "dagger point") pores" (Sauer, 1966: p. 11). "In the [recent] Struthionidae the eggs have multi-branched pore canals with multiple openings in roundish pits" (Sauer, 1966: p. 10).

As mentioned above, the eggshells of the fossil ostriches belonging to the genus *Struthio* show pore openings which can be aepyornithoid, mixed, or struthioid. In the recent forms of *Struthio camelus* the eggshells are of struthioid type, but the different subspecies show different types of pore openings. Five types of pore openings have been defined for the five subspecies *S. c. camelus*, *S. c. spatzi*, *S. c. australis*, *S. c. massaicus* and *S. c. molybdophanes* (Schönwetter, 1927; Sauer, 1972). However Sauer (1972) indicates that the association between the subspecies and the type of pore openings is not always as constant as indicated by Schönwetter (1927).

Description of the Ahl al Oughlam eggshells (fig. 3)

On the eggshells from Ahl al Oughlam, when they have not been altered by erosion or by diagenesis, one can see multiple pore openings grouped together in shallow pits. Each pit includes about 50 openings. The diameter of the pits varies from 0.5 to 1 mm and their number varies from 10 to 20 per cm2, depending on the fragments. This structure is close to that of the recent subspecies *S. c. molybdophanes*, which lives in Somalia, in the south-east and south of Ethiopia, the south-east of Sudan, and in Kenya (Mayr & Cottrell, 1979), and differs from that of the subspecies which live in geographically closer areas, such as *S. c. camelus* (South of Sahara and Mauritania, and from Senegal to Sudan and Eritrea), or *S. c. spatzi* which used to live in the Rio de Oro region, but which is now merged with *S. c. camelus* (Brown *et al.*, 1982).

At Ahl al Oughlam the thickness of the eggshell fragments varies from 2.3 to 2.7 mm, with an average value of 2.54. These eggshells are thicker that those of *S. camelus*, which are generally from 1.6 to 2.1 mm thick, with an exception for the recently extinct subspecies *S. c. syriacus*, in which eggshell thickness was from 1.3 to 2.1 mm (Sauer, 1966).

The eggshells attributed to *Struthio asiaticus* and coming from Nullas, on the Ken river, Banda district, in India, also show the same type of pore openings as the recent subspecies *S. camelus molybdophanes*, and their thickness varies from 2.2 to 2.4 mm (Bidwell, 1910; Sauer, 1968).

Comparison with the other fossil eggshells described from Africa
1° Eggshells from the continental Mio-Pliocene of Morocco

Sauer and Sauer (1978) have described struthious eggshells found in Mio-Pliocene continental deposits of southern Morocco. These eggshells show pore openings which are aepyornithoid, struthioid, or mixed A-S. It is sometimes possible to find two different types on the same eggshell, aepyornithoid pore openings in the equatorial region, and struthioid pore openings in the polar region. There is some correlation between the thickness of the shell and the type of pore openings. The eggshells with struthioid pores are generally from 1.55 to 2 mm thick and the eggshells with aepyornithoid pores are generally from 1.95 to 2.7 mm thick, but there are many exceptions in both groups. Sauer and Sauer think that there is an evolution between the aepyornithoid-type eggshells and the struthioid-type eggshells, with all the intermediates between them. However the struthioid-type eggshells of these deposits have a type of pore openings which resembles those of the recent subspecies *S. c. camelus* and *S. c. australis*, and are therefore different from the Ahl al Oughlam eggshells.

2° Eggshells of the genus *Psammornis*

The genus *Psammornis*, based on eggshells, includes two species: *P. rothschildi*, from eggshells found in Algeria, and *P. lybicus*, from one fragment found in Lybia. In addition, some fragments found in Arabia have been referred to *Psammornis* sp. This material was revised by Sauer (1969).

These eggshells are thick and the Algerian and Arabian forms correspond to large-sized eggs. According to Sauer the original thickness of the eggshell is 4.0 mm in *P. rothschildi*, 3.1 mm in *Psammornis* sp., and 2.80 mm in *P. lybicus*. The size of the egg is estimated at about 250 x 190 mm in *P. rothschildi*, 210 x 172 mm in *Psammornis* sp., and 143 x 127 in *P. lybicus*. Their age is not accurately known but according to Sauer (1969), the size of the eggs and the thickness of the shells suggest that they are Pliocene. The arrangement of the pore openings is typically struthioid and resembles more particularly that of the subspecies *S. c. camelus*. The eggshells of the Ahl al Oughlam ostrich are distinct from the different forms of *Psammornis*; they are not so thick and the disposition of the pore openings corresponds rather to that of *S. c. molybdophanes*.

3° Eggshells from Namibia

Very numerous eggshell localities have been discovered in Namibia and have made it possible to establish a biostratigraphy based on these stratigraphically collected eggshells (Pickford *et al.*, 1995; Senut & Pickford, 1995; Senut *et al.*, 1998; Pickford & Senut, 2000; Senut 2000). Several eggshell localities have also yielded fossil mammals "which permit the ages of the strata to be determined within reasonable limits" (Senut & Pickford, 1995, p. 33). This biostratigraphy demonstrates the succession of three genera, *Namornis*, from the Middle Miocene (approx. - 16 to - 15 Ma), then *Diamantornis*, with four species from the Middle and Late Miocene (approx. - 15 to - 8 Ma), then the genus *Struthio* with three species, *S. karingarabensis*, from the Late Miocene (approx. - 8 to - 5 Ma), *S. daberasensis*, from the Pliocene (approx. - 5 to - 2 Ma), and lastly *S. camelus*, from the Early Pleistocene to the Recent (Pickford & Senut, 2000; Senut, 2000).

In the genus *Diamantornis* the pore openings are clustered in very large numbers to form megapores, circular in surface area, and funnel-shaped in section, the diameter of which varies from 2.7 to 10 mm according to the species; the shell thickness varies from 2.1 to 4.2 mm.

In the two extinct species of the genus *Struthio*, the pore openings are clustered to form pore complexes but they are distinctly smaller than in the genus *Diamantornis*. In *Struthio karingarabensis* the diameter of the pore complexes varies from 2.4 to 2.7 mm and the thickness of the shell varies from 2.95 to 3.2 mm. In *S. daberasensis* the diameter of the pore complexes varies from 0.5 to 2.2 mm and their number varies from 4 to 5 per cm2. The shell thickness is situated between 1.7 and 2.6 mm, with a mode of 2.3 mm. The Ahl al Oughlam eggshells are close to those of *S. daberasensis* by their thickness but differ from them by the generally smaller size of the pore complexes (0.5 to 1mm) and by their larger density (10 to 20 per cm2).

4° Eggshells from East Africa

Harrison & Msuya (2005) have described struthionid eggshells from the localities of Laetoli, in Tanzania, Lothagam and Kanapoi, in Kenya, the ages of which are comprised between 7.4 and ca. 2.6-2.7 Ma. They have found again the chronological succession of two species of *Diamantornis*, then *Struthio* cf. *karingarabensis*, *S. kakesiensis*, a new species, morphologically intermediate between *S. karingarabensis* and *S. daberasensis* from Namibia, then *S. camelus* which appears in East Africa at approximately 3.6 - 3.8 Ma. Aepyornithoid eggshells have also been found at Lothagam, in a layer dated from ca. 6.5 to 6.7 Ma, thus in the Late Miocene, while in Namibia aepyornithoid eggshells are only found in Early Miocene and early Middle Miocene layers (Pickford & Senut, 2000; Senut, 2000).

At last, in Malawi, struthioid eggshells referred to *S. daberasensis* have been reported in the Mid-Pliocene (ca. 3.0 - 3.5 Ma) of the Chiwondo Beds (Stidham, 2004 a).

Conclusion

It seems important to remind here that the species *Struthio coppensi*, from the Early Miocene of Namibia, which is a true didactylous ostrich, was associated with aepyornithoid eggshells (Mourer-Chauviré *et al.*, 1996). The presence of aepyornithoid eggshells does not mean that the birds which laid them were Aepyornithidae. In absence of skeletal remains it is not possible to write about an aepyornithoid eggshell : "This record confirms that elephant birds survived in mainland Africa until at least the Late Miocene" (Harrison & Msuya, 2005, p. 313).

Two different types of ratite eggshells are found simultaneously in the Neogene of Africa and Southern Eurasia:

–eggshells with relatively simple aepyornithoid, or struthioid of solitary needle-point type, or intermediate aepyornithoid-struthioid openings, such as those described by Sauer & Sauer (1978) in the Mio-Pliocene continental deposits of Morocco. In these forms, pore complexes including a large number of openings are not found. In East Africa, aepyornithoid eggshells are found until the Late Miocene, at about 6.5 to 6.7 Ma (Harrison & Msuya, 2005).

–struthious eggshells with large pore complexes grouping together a large number of openings, as described in the four species of the genus *Diamantornis*, and in the three extinct species *Struthio karingarabensis*, *S. kakesiensis*, and *S. daberasensis*. These eggshells have been first described in Namibia but they are also present in South Africa (Pickford & Senut, 2000), East Africa (Malawi, Tanzania, Kenya), and in Arabia (Harrison & Msuya, 2005; Stidham, 2004 a). These large pore complexes are still found in one of the subspecies of the recent ostrich, *S. camelus molybdophanes*.

At Ahl al Oughlam the diameter and the density of the pore complexes are similar to that of this recent subspecies, but the thickness of the shell is larger, and closer to that of the extinct species *S. daberasensis*. *S. daberasensis* is found in deposits dating from approximately 2 to 5 Ma in Namibia, and in deposits dating from ca. 3.0 to 3.5 in Malawi. The eggshells found at Ahl al Oughlam are thus consistent with the chronological position of this locality.

Struthionid skeletal remains associated with eggshells have rarely been found in the same fossiliferous locality. The case of Ahl al Oughlam is particularly interesting because it shows the association of skeletal remains of a massive ostrich, *Struthio asiaticus*, with thick eggshells, thicker than those of the recent *S. camelus*, and the pore openings of which are similar to those of the recent subspecies *S. c. molybdophanes*.

Order ODONTOPTERYGIFORMES Howard, 1957

Family PELAGORNITHIDAE Fürbringer, 1888

The Pelagornithidae are members of a group of extinct birds which can be designated as pseudodontorns.

They 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. They had a superficial similarity with the Procellariiformes but they were more closely related to the Pelecaniformes. However, recent works on the skull of very early pseudodontorns show that they form a monophyletic group and that they are not included in the Pelecaniformes (Bourdon, 2004). It is thus preferable to place them in their own order, the Odontopterygiformes Howard, 1957. A large number of forms have been described (Harrison & Walker, 1976; Olson, 1985), but, according to Olson and Rasmussen (2001: p. 259): "So far, all of the considerable material of these birds found in late Oligocene and Neogene deposits around the North Atlantic appears to be referable to a single genus - *Pelagornis* - although this includes a variety of species ".

The pseudodontorns are known since the Late Paleocene of Central Asia (Averianov *et al*., 1991) and the Early Eocene of England (Harrison & Walker, 1976) and Morocco (Gheerbrant *et al*., 2003; Bourdon, 2006). As early as this, they were probably present on all the oceans because they are also known in the Late Eocene or the Early Oligocene of Antarctica (Tonni, 1980; Tonni & Tambussi, 1985). They were widespread during the Miocene but they are more rarely reported from later deposits. During the Pliocene they are present in North America, as shown by material from the Yorktown Formation, at Lee Creek, North Carolina (Olson & Rasmussen, 2001), dated from 4.5 to 5 Ma. They have also been reported from New Zealand (Mc Kee, 1985), where new discoveries show them to be present up to layers dated from 3.6 to 3.1 Ma (Mc Kee, pers. comm.). In Japan Ono (1980) described a femur from the Upper Pliocene Dainichi Fm., Kakegawa Group of Shizuoka Pref., which was later attributed to a pseudodontorn (Matsuoka *et al*., 1998). In Peru, in the Pisco Formation, pseudodontorns are present in the locality of Sacaco, dated from about 3 Ma (Chavez & Stucchi, 2002). The Moroccan form, dated ca. 2.5 Ma, is therefore the most recent, accurately dated, form known so far.

Genus *PELAGORNIS* Lartet, 1857

This genus only includes one species, *Pelagornis miocaenus* Lartet, 1857, and this species is only known by humeri and a shaft of ulna. The holotype is an almost complete left humerus coming from the "Molasse coquillère marine de l'Armagnac", department of Gers. Its age is Middle Miocene, Serravallian (Cahuzac, pers. comm.), equivalent of the mammalian biozones MN 6-7-8, age between 16.5 and 11 Ma (BiochroM'97, 1997). It has been illustrated by Milne-Edwards (1867-71: pl. 45) and it is kept in the Paris MNHN, uncatalogued. The other elements attributed to this species come from the localities of Léognan, near Bordeaux, and Condom, in Gers. The locality of Léognan (Cestats) is Early Miocene, Burdigalian or Orleanian, MN 3 zone, age between 20 and 18 Ma (Duranthon & Cahuzac, 1997). Ac-cording to B. Cahuzac (pers. comm.) the *Pelagornis* from Condom could also come from the "Molasse coquillère marine" of the Middle Miocene, and its age would be the same as that of the holotype. This material is conserved in the Museum of Bordeaux collection and casts are kept in the collections of BMNH, London, and UCB, Lyon.

Pelagornis mauretanicus n. sp.
fig. 4-10

Holotype.
Right humerus, distal part, AaO 705 (fig. 4, a-b)

Horizon and Locality.
Late Pliocene, age about 2.5 Ma. Ahl al Oughlam, south-east boundary of the city of Casablanca, Morocco.

Paratypes.
Mandible, fragments of the right and left ramus, AaO 884; fragments of rostrum, AaO 881, 882, 896; fragments of rostrum or mandible with pseudoteeth, AaO 880, 883; isolated pseudoteeth, AaO 711; right quadrate, AaO 707; right pterygoids, AaO 708 et 878; vertebrae, AaO 879, 886, 888, 889, 890, 893, 898, 2620; fragment of sacrum, AaO 887; fragments of proximal left humerus, AaO 895, proximal right humerus, AaO 710, distal right humerus, AaO 706; right ulna, distal part, right radius, distal part, and right os carpi radiale, associated, AaO 709; left ulna, distal part, and left radius, distal part, associated, AaO 894; right radius, proximal part, AaO 885; fragment of right radius, distal part, AaO 899; right os carpi ulnare, AaO 712; fragment of left carpometacarpus, proximal part, AaO 891; fragment of wing phalanx, AaO 821; right femur, almost complete, AaO 897.

All the pseudodontorn material from Ahl al Oughlam has been referred to a single species, *P. mauretanicus*, because all these elements are compatible in size. This material consists mainly in isolated bones, and it has rarely been found several representatives of the same bone. For the distal part of the radius, however, there are three elements, the dimensions of which are similar (table 9). When it is possible to compare with other pseudodontorns, e.g. those from the Lee Creek Mine (Olson & Rasmussen, 2001), the Ahl al Oughlam form is consistently slightly larger than *Pelagornis* sp. 2, and clearly larger than *Pelagornis* sp. 1 (tables 5 and 10).

Diagnosis.
Species comparable in size to *Pelagornis miocaenus*. Processus supracondylaris dorsalis projecting both dorsally and cranially, and clearly separated by a groove from the condylus dorsalis. This processus extends in proximal direction by a wing which obliquely merges with the craniodorsal angle of the shaft. Two depressions are present in the fossa m. brachialis, one proximal to the condylus dorsalis, and the other one, deeper, proximal to the condylus ventralis. The epicondylus ventralis is strongly developed cranio-
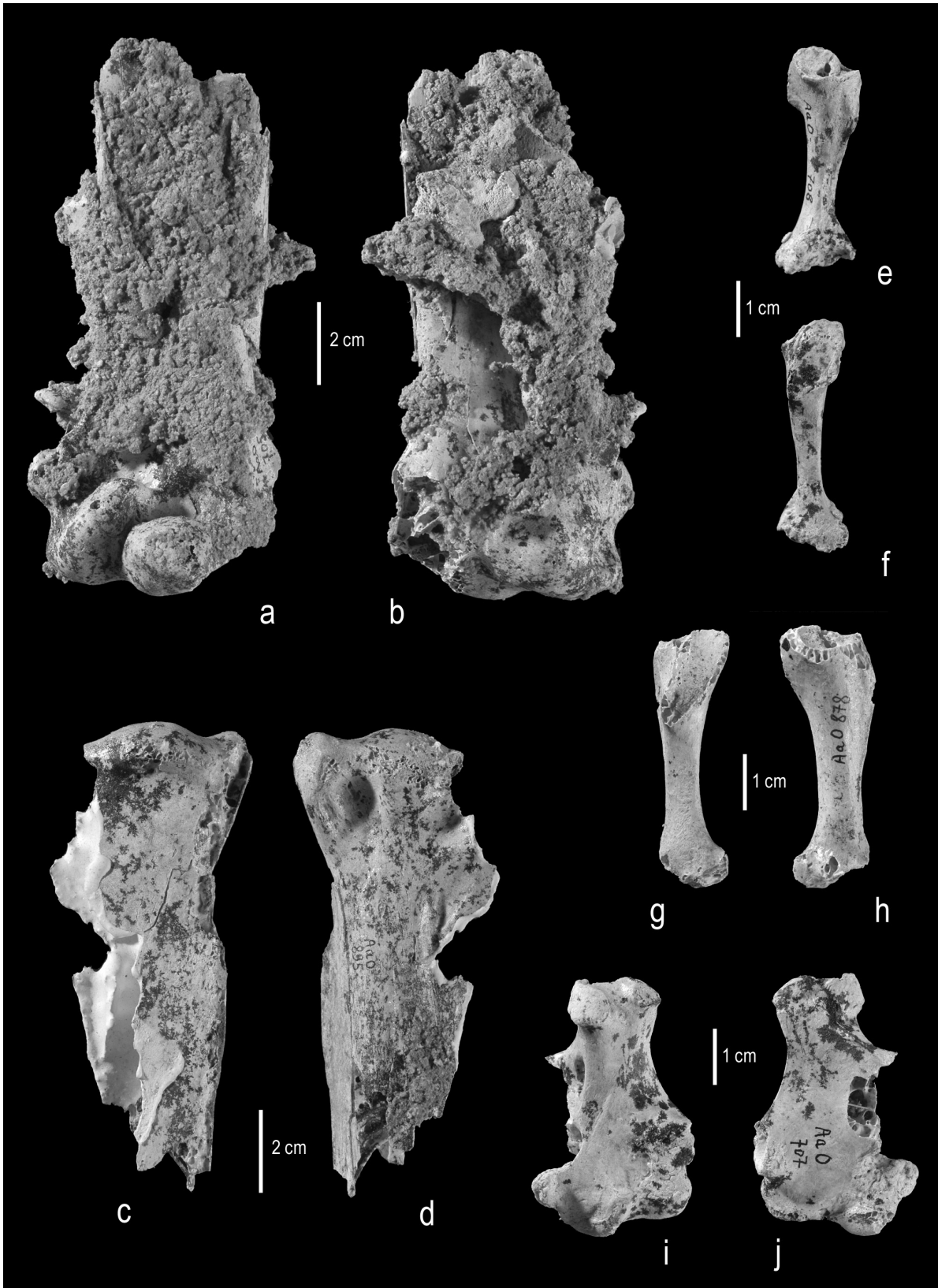
Figure 4 - *Pelagornis mauretanicus* n. sp., Ahl al Oughlam. a-b: right humerus, distal part, AaO 705, holotype; a) cranial view, b) caudal view; c-d: left humerus, proximal part, AaO 895, paratype; c) cranial view, d) caudal view; e-f: right pterygoid, AaO 708, paratype; e) dorsal view, f) lateral view; g-h: right pterygoid, AaO 878, paratype; g) dorsal view, h) lateral view; i-j: right quadrate, AaO 707, paratype; i) medial view, j) lateral view.
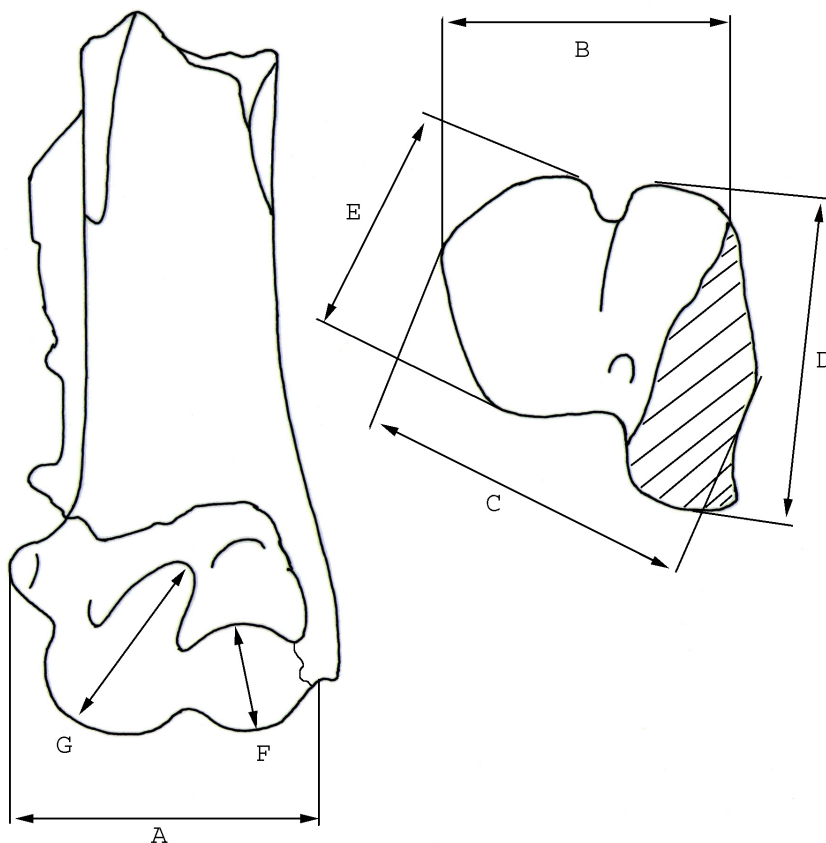
Figure 5 - Diagram showing the way of measuring the distal part of the humerus of *Pelagornis mauretanicus* n. sp. The hatched area corresponds to an incompletely preserved part.

caudally.

Dimensions: see tables 4-10.

Etymology.
From Mauretania, name of the ancient Roman province, which encompassed a part of present-day Morocco.

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

Description and comparisons

Harrison and Walker have given an emended diagnosis of the humerus of *Pelagornis*. They indicate that at the proximal part, on the caudal face: "a deep hollow extends up towards external tuberosity and another hollow undercuts the proximal head, leaving a distal ridge, with marked internal curvature, on the anconal surface" (Harrison & Walker, 1976: p. 29). This can also be expressed by saying that the caput humeri is extended distally by a ridge, recurved in ventral direction and situated between two depressions. This ridge is clearly visible on the holotype left humerus from Armagnac, illustrated by Milne-Edwards (1867-71: pl. 45) and on the right humerus from Léognan illustrated by Harrison and Walker (1976: pl. 10, fig. A et B) but it is not a

constant characteristic because it is hardly visible on another right humerus from Léognan (original in Bordeaux, cast in Lyon n° O. 758), as well as on a humerus attributed to the genus *Pelagornis* and coming from New Zealand (Scarlett, 1972; Harrison & Walker, 1976: pl. 10, fig. C). On the latter two humeri, the distal outline of the caput humeri only forms a slight expansion. This expansion is situated between two depressions, the first one corresponds to the incisura capitis, and the second one is a fossa situated distally compared to the tuberculum dorsale, but it does not form "a distal ridge with marked internal curvature". The two proximal parts of humerus of Ahl al Oughlam, although they do not present a recurved distal ridge, can nevertheless be attributed to the genus *Pelagornis*.

Comparison of the humeri with those of *Pelagornis miocaenus* (fig. 4, a-d)
The Ahl al Oughlam remains are slightly larger than the holotype of *P. miocaenus* but these differences are not significant because, as already mentioned by Milne-Edwards (1874), there are large size differences between the different humeri attributed to this species (table 3). The humerus from Condom is almost 25 % larger than the holotype humerus, or the Léognan humerus (cast n° A 167, BMNH).
The distal parts of humerus from Ahl al Oughlam differ from those of *P. miocaenus* by the following characters: in *P. miocaenus* the processus supracondylaris dorsalis

Figure 6 - Diagram of quadrates of Pelagornithidae. a-b: *Pelagornis mauretanicus* n. sp., Ahl al Oughlam, right quadrate, AaO 707; a) medial view, b) cranial view; c-d: *Pelagornis* sp. 1 or *Pelagornis* sp. 2, Yorktown Fm., Lee Creek Mine, right quadrate, USNM 446495; c) medial view, d) craniolateral view; e: indetermined Pelagornithidae, Calvert Fm., right quadrate, USNM 237189, cranial view. The hatched areas correspond to incompletely preserved parts.
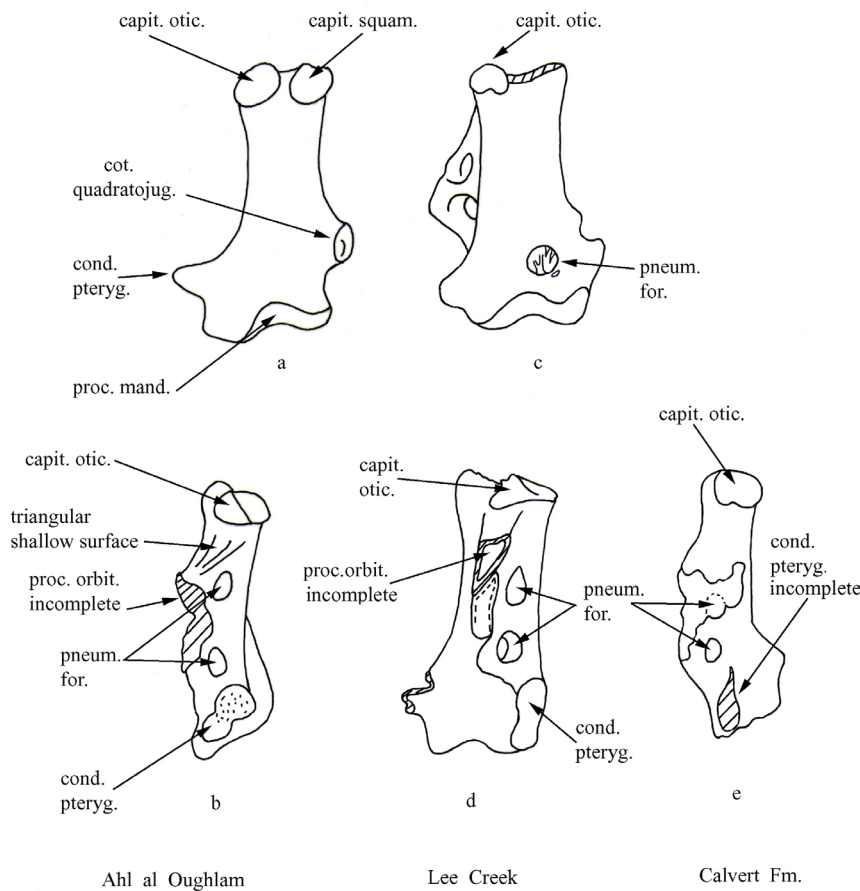
is weakly projecting, both on the dorsal and cranial faces, in the Ahl al Oughlam form it is more projecting both dorsally and cranially, and it is clearly separated from the condylus dorsalis by a groove. Proximally it is extended by a wing which obliquely merges with the craniodorsal angle of the shaft. In *P. miocaenus* the surface of the shaft situated proximally to the condyles is flattened, while in the Ahl al Oughlam form it shows two fossae, one proximal to the dorsal condyle, the other, deeper, proximal to the ventral condyle. In *P. miocaenus* the ventral condyle is slightly flattened in the proximodistal direction, while in the Ahl al Oughlam form it is more rounded. On the caudal face, the fossa olecrani is absent but the epicondylus ventralis, although incomplete in *P. miocaenus* as well as in *P. mauretanicus*, was probably more developed and caudally projecting, and was probably extending further proximally in the Ahl al Oughlam form.

In distal view, due to the great extension of the epicondylus ventralis, the Ahl al Oughlam humerus is craniocaudally larger than the *P. miocaenus* humerus (fig. 5 and table 4).

Considering these morphological differences and the great interval of time (17.5 to 8.5 Ma) which separates them, we attribute the Ahl al Oughlam form to a new species.

Description of the other elements

A. Quadrate AaO 707 (fig. 4, i-j, fig. 6 and table 5)

On this specimen the tip of the processus orbitalis is broken. The processus oticus ends in two condyles, the capitulum oticum and the capitulum squamosum, separated by a distinct incisura intercapitularis. The capitulum squamosum is rounded, the capitulum oticum is formed by two
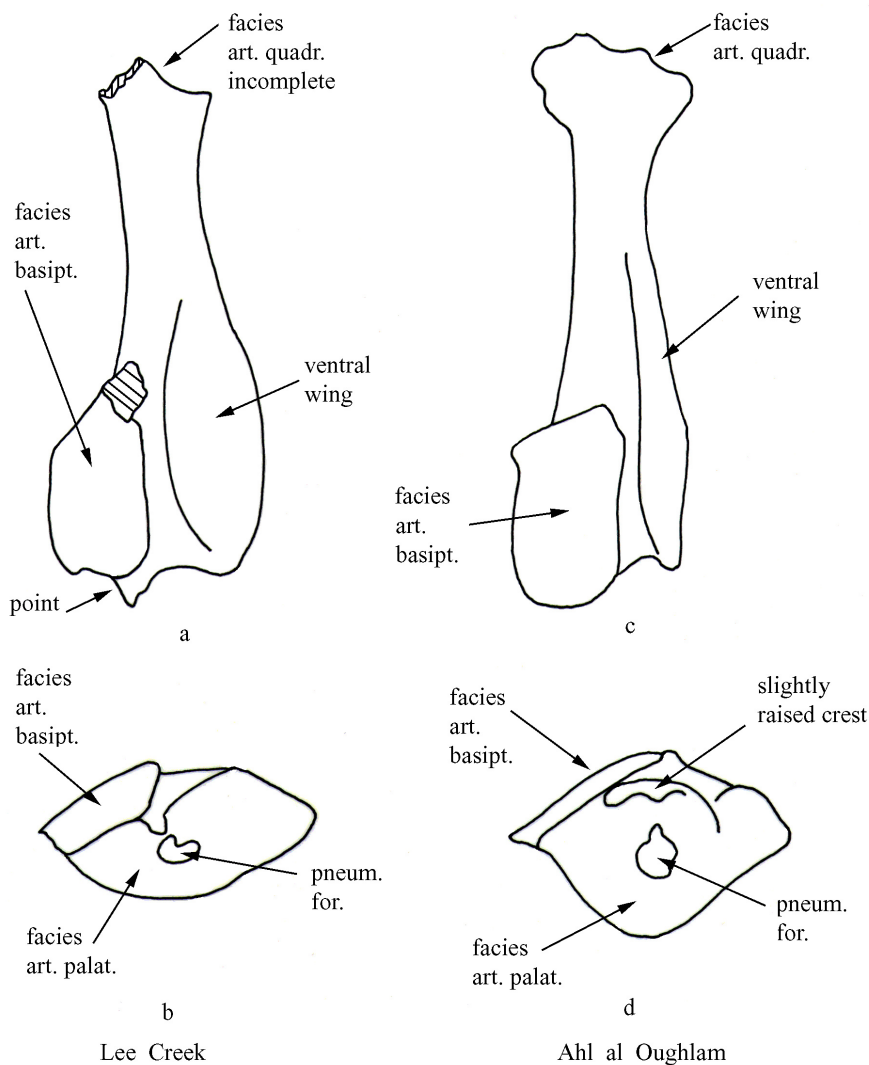
Figure 7 - Diagram of pterygoids of *Pelagornis* ssp. a-b: *Pelagornis* sp. 1 or *Pelagornis* sp. 2, Yorktown Fm., Lee Creek Mine, right pterygoid, USNM 425110; a) dorsomedial view, b) cranial view; c-d: *Pelagornis mauretanicus* n. sp., Ahl al Oughlam, right pterygoid, AaO 708; c) dorsomedial view, d) cranial view.

flat surfaces, one medially oriented and the other one cranially oriented, joined along an oblique edge. Distally to the capitulum oticum, on the cranial face, the dorsal side of the processus orbitalis forms a triangular surface, moderately deep, and bordered by two thin ridges. Distally to this triangular surface, on the medial side of the processus orbitalis, there are two large pneumatic foramina. The cotyla quadratojugalis is socket-shaped and surrounded by a thick rim. It is situated at about the distal third of the bone. The processus mandibularis is formed by two rounded protuberances, the condylus medialis and the condylus lateralis, separated by an oblique groove. The condylus pterygoideus is short and looks like a synostosed articulation.

This quadrate was compared with that of a Pelagornithidae from the Calvert Formation, dated from the Middle Miocene (USNM 237 189), the processus orbitalis of which is also broken. It differs from that from Ahl al Oughlam because the capitulum oticum is not formed of two flat sides but rounded, and because it does not show a triangular shallow surface on the proximal side of the processus orbitalis, distally to the capitulum oticum. It was also compared with the quadrate of *Pelagornis* sp., from the Early Pliocene of Lee Creek (USNM 446 495, Olson & Rasmussen, 2001: pl. 11, f), the processus orbitalis of which is not preserved. The Ahl al Oughlam quadrate is extremely similar to the latter one, which also shows a capitulum oticum formed by two flat sides. The only difference is that in medial view the Lee Creek quadrate shows a pneumatic foramen situated proximally to the articular mandibular surface, at the level of the groove which separates the condylus medialis from the condylus lateralis. At the location of this pneumatic foramen there is only a shallow depression on the Ahl al Oughlam
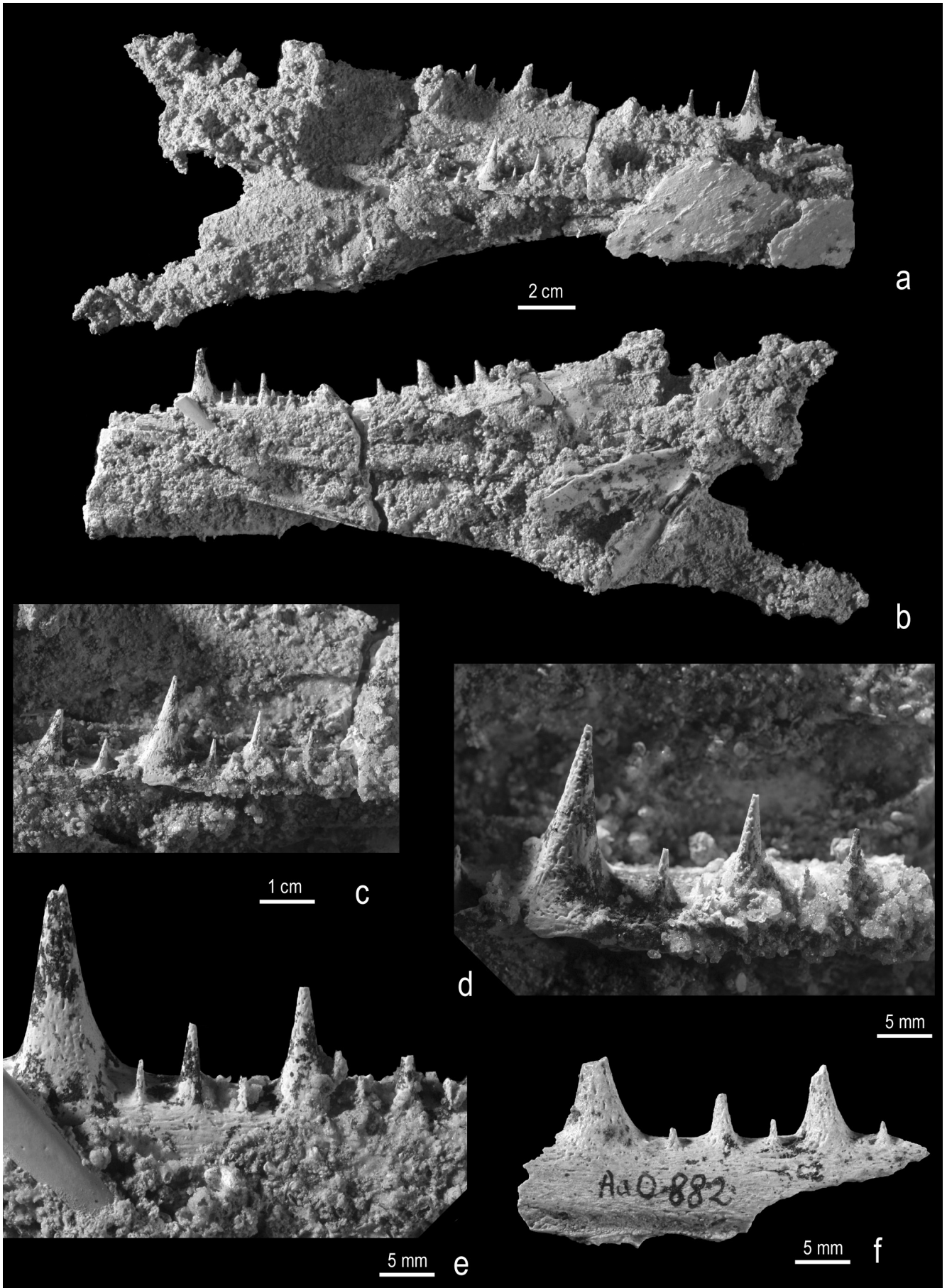
quadrate.

A pseudodontorn quadrate, designated as *Osteodontornis* sp., was described from the Middle Miocene of Japan (Ono, 1989). It also looks very similar in shape and size to that from Ahl al Oughlam but it only shows a small pneumatic foramen, on the medial face, at the level of the middle part of the processus orbitalis.

Among the recent Pelecaniformes the quadrate of *Pelagornis* looks more similar to that of Sulidae and Phaethontidae. The characteristics shared with these two families are a socket-shaped articulation for the quadrato-jugal, a processus oticus showing two distinct condyles, a pneumatic foramen situated on the medial face, dorsally compared to the condylus pterygoideus and at the same level as the ventral edge of the processus orbitalis. It differs however because in the Sulidae and Phaethontidae the quadrato-jugal socket is situated at the end of a peduncle which extends laterally and ventrally, while this is not the case in *Pelagornis*. In addition, the shape of the mandibular articulation is very different in *Pelagornis* from that of the Sulidae and Phaethontidae. The characteristics in common between *Pelagornis*, the Sulidae and the Phaethontidae are also found in the Diomedeidae and, in the shape of the mandibular articulation, the quadrate of *Pelagornis* also resembles that of *Diomedea*.

B. Pterygoids AaO 708 and 878 (fig. 4, e-h, fig. 7 and table 5)

The two pterygoids differ slightly from each other: AaO 878 is larger and the facies articularis quadratica shows a rounded cotyla and a pneumatic foramen while on AaO 708 this articular facet is a little synostosed with bony excrescences around it and does not show that pneumatic foramen. The facies articularis basipterygoidea is quadrangular in AaO 708, elongate and more elliptical in AaO 878. The ventral wing is slightly projecting in AaO 708, and more projecting in AaO 878. The facies articularis palatina shows a pneumatic foramen on both specimens, it is more circular in AaO 708 and more elongate in AaO 878.

The pterygoid AaO 878 is very similar to a pterygoid of *Pelagornis* sp. from the Pliocene of Lee Creek (USNM 425 110, Olson & Rasmussen 2001: pl. 11, d). On this specimen there is a projecting point at its cranial end, cranially to the facies articularis palatina. This point was probably present in AaO 878 but has been broken. It does not exist in AaO 708 where there is at the same place a slightly raised crest but no point.

In pseudodontorns, the pterygoid was described in *Odontopteryx toliapica*, from the Early Eocene of England (Harrison & Walker, 1976). Both pterygoids from Ahl al Oughlam, as well as the Lee Creek one, have the same general shape as that of *Odontopteryx*. In the latter, the facies articularis basipterygoidea is well developed and elongate, and there is a point cranially to the facies articularis palatina but this point is much more projecting in *Odontopteryx*.

Aslanova and Burchak-Abramovich (1999: p. 428) mention the presence of the pterygoid of *Caspiodontornis* and indicate that it strongly differs from that of *Odontopteryx* and looks more similar to that of the recent genus *Pelecanus*. However, in *Pelecanus*, the pterygoid is narrow and elongate and there is no basipterygoid facet. In addition, the shape of the facies articularis palatina is very different from that of *Pelagornis* and *Odontopteryx*, it is concave and dorsoventrally elongated. It seems therefore that the pterygoid of *Caspiodontornis* was different from that of the other pseudodontorns.

In all the recent Pelecaniformes, the perygoid has the shape of a narrow, elongate stick, triangular in section in the Pelecanidae, circular or subcircular in section in the Phaethontidae and Fregatidae, laterally flattened in section in the Phalacrocoracidae, Anhingidae and Sulidae. The pterygoid of *Odontopteryx*, and even more that of *Pelagornis*, differs from that of the recent Pelecaniformes by its short and cranially wide shape. In the recent Diomedeidae the pterygoid also has the shape of a narrow, elongate stick and the facies articularis basipterygoidea is semicircular and it is situated almost at the cranial end of the bone. By these two characteristics the pterygoid of *Pelagornis* differs from that of Diomedeidae.

C. Mandible and pseudoteeth (fig. 8-9)

The mandible AaO 884 includes the two mandibular rami resting against each other and covered by sand and concretioned sediments. It is not possible to free them because the bones are completely crushed. It is possible to see, on both rami, the position of the intraramal joint (Zusi & Warheit, 1992). A part of the posterior ramus of the right mandible is preserved over 9 cm posteriorly to the intraramal joint, and cranially to the joint the right and left intermediate rami are preserved over 18 cm, but the pseudoteeth are not preserved on the anteriormost parts. The part corresponding to the mandibular symphysis is absent. On the lateral face of the left ramus the mandibular lateral longitudinal sulcus (Harrison & Walker, 1976), or external groove (Stidham, 2004 b) is clearly visible.

The pseudoteeth are always arranged according to the same pattern. The largest ones, of order 1, are separated by about 40 mm (table 6). In the middle of this space there are smaller ones, of order 2. In the middle of the space between

Figure 8 (opposite) - *Pelagornis mauretanicus* n. sp., Ahl al Oughlam. a-e: mandible AaO 884, paratype; a) right lateral view, b) left lateral view, c) detail of the pseudoteeth of the right ramus, caudally to the break of the mandible, d) closer detail of pseudoteeth of the right ramus. From the left to the right: pt. order 1, needle not preserved, pt. order 3, needle, pt. order 2, needle, pt. order 3, needle, e) closer detail of pseudoteeth of the left ramus, cranial part. From the left to the right: pt. order 1, needle, pt. order 3, needle, pt. order 2, needle, pt. order 3, needle. f: fragment of rostrum AaO 882, paratype. From the left to the right: pt. order 1, needle, pt. order 3, needle, pt. order 2, needle.
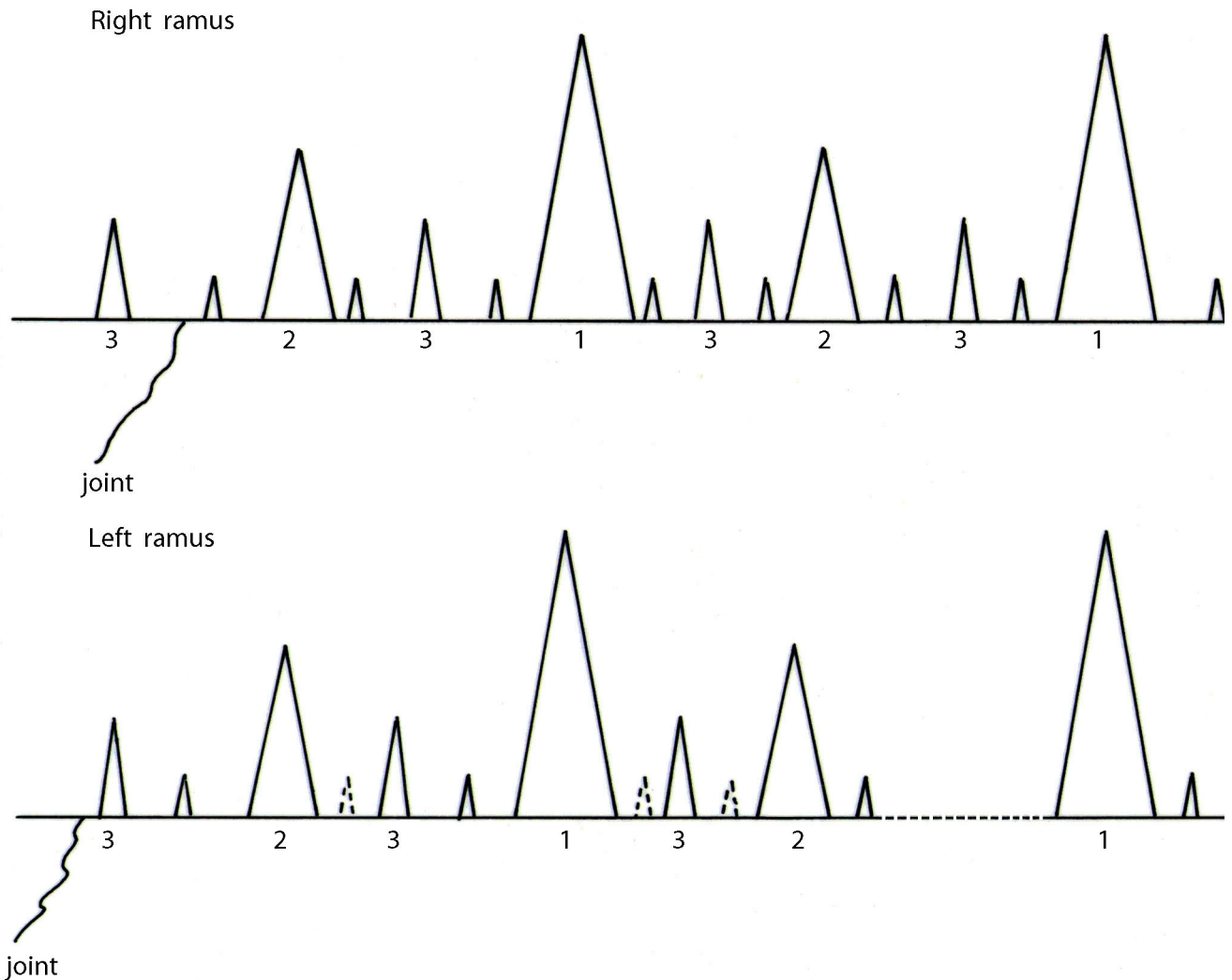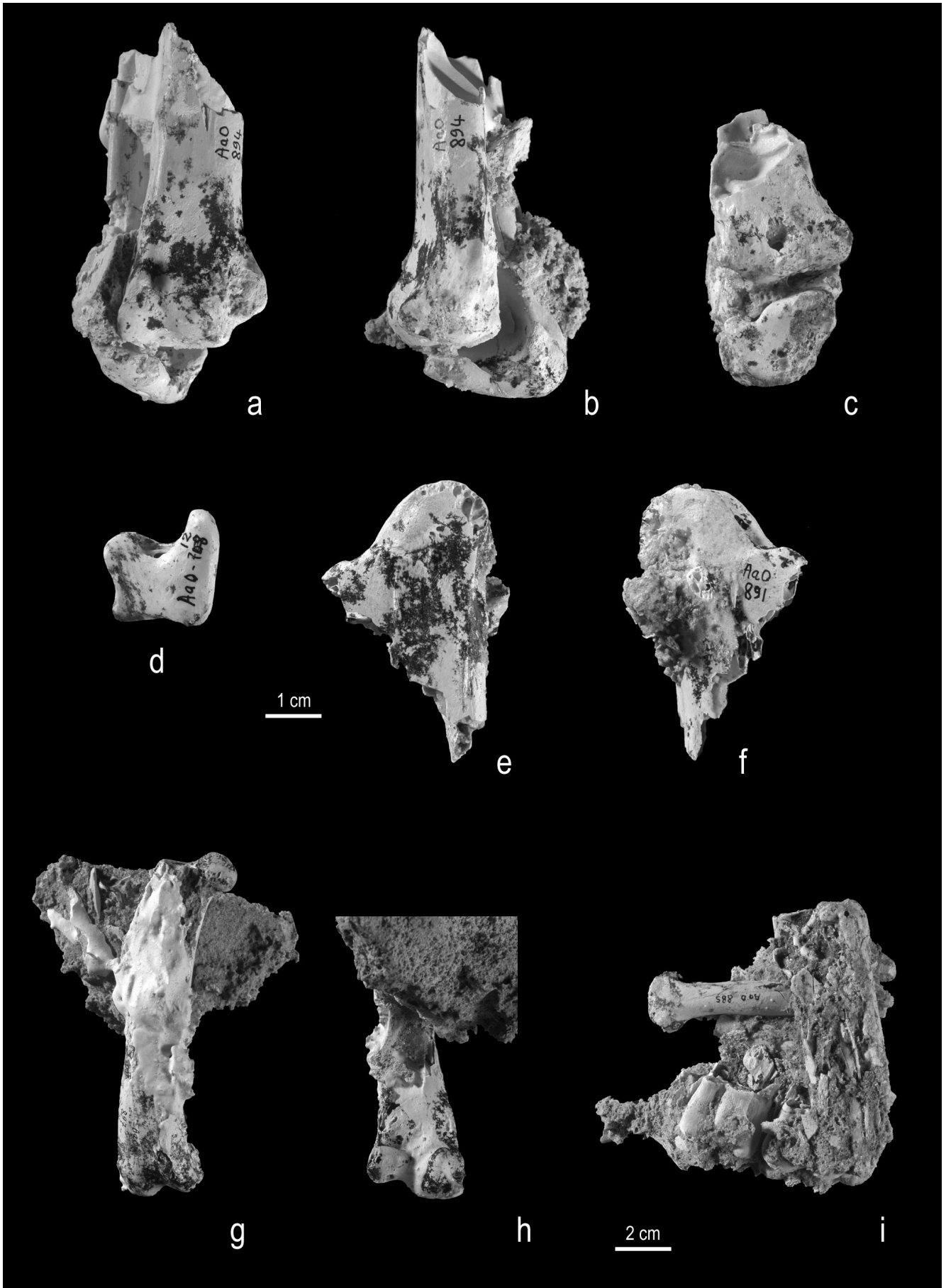
Right ramus

joint

Left ramus

joint

Figure 9 - Diagram showing the position of order 1, 2 and 3 pseudoteeth and needles, on the right and left rami of the AaO 884 mandible. The needles in dotted lines have been broken but their trace is visible on the mandible. Their is a small discrepancy, of 1 or 2 mm, between the position of the pseudoteeth on the right and left rami. This can be due to the imprecision of the measurement, or to a slight postdepositional displacement. The pseudoteeth are slightly closer together on the caudal part than on the cranial part.

Figure 10 (opposite) - *Pelagornis mauretanicus* n. sp., Ahl al Oughlam. a-b: left ulna, distal part, and left radius, distal part, AaO 894, paratype; a) ventral view, b) cranial view; c: right ulna, distal part, right radius, distal part, and right radial carpal, AaO 709, paratypes. Ulna and radius, ventral view, radial carpal, distal view; d: right ulnar carpal, AaO 712, paratype, medial view; e-f: left carpometacarpus, proximal part, AaO 891, paratype; e) dorsal view, f) cranioventral view. Same scale for a, b, c, d, e, and f. g-h: right femur, AaO 897, paratype; g) cranial view, h) caudal view of the distal part; i: jumble of bones showing a large mammal tooth and the proximal part of a left radius of *P. mauretanicus* n. sp., AaO 885, paratype, caudal view. On the left, there are a left radius and a left ulna, distal parts, crushed. Same scale for g, h, and i.

the order 1 and order 2 teeth are smaller ones, of order 3. Finally, in the middle of the space between the teeth of order 1 or 2 and the teeth of order 3 there are extremely thin pseudoteeth, which are truly needles of bone. These pseudoteeth are not always perfectly preserved, but even when they are broken it is possible to see their location on the dorsal face of the mandible. For the needles the trace is a thin line. The needles are not situated quite on the top of the mandibular

ramus, but on its lateral side. The measurements of the pseudoteeth on the mandible AaO 884 are given in table 7.

The order 1 and 2 pseudoteeth are not regularly elliptical in section. They show a ridge situated either on the laterocaudal angle, or on the mediocaudal angle. The order 3 pseudoteeth and the needles are craniocaudally flattened, their width is larger than their depth. The whole set of pseudoteeth is oriented perpendicularly compared to the longitu-

dinal axis of the mandible, and they are not inclined cranially.

The last two visible pseudoteeth, of order 3, are situated either cranially, or just caudally, to the intraramal joint. Caudally to these two last ones, there are no more traces of pseudoteeth.

The pattern of the pseudoteeth corresponds to what has been described by Harrison and Walker (1976) for the largest part of the mandible of the genus *Osteodontornis*. It differs from the pattern of a mandible illustrated by Zusi and Warheit (1992) for an indetermined Pelagornithidae (ChM PV 4768) from the Charleston Museum. However almost the same pattern can be found on a partial rostrum of Pelagornithidae (probably *Osteodontornis orri*) from the Miocene of California illustrated by Olson (1985: p. 195, fig. 9) and on a dentary of *Osteodontornis* sp. from the late Early Miocene of Japan (Matsuoka *et al.,* 1998). New material of *Osteodontornis orri* has been found in the Middle Miocene of Sharktooth Hill, in California (Stidham, 2004 b). Its age is between 15.2 and 16.0 Ma, which corresponds to the beginning of the Middle Miocene. The arrangement of the teeth on the mandible is slightly different from what can be observed on the Ahl al Oughlam mandible, but this may be due to the fact that this fragment corresponds to a more anterior part than that preserved on the Moroccan mandible.

The Ahl al Oughlam pattern is also different from that which was described for *Caspiodontornis kobystanicus*, from the Middle Oligocene of Azerbaijan (Aslanova & Burchak-Abramovich, 1999), where the succession of large, medium, and small "teeth", separated by a variable number of "toothlets", is not as regular as in the Moroccan form. In addition, in the Azerbaijan form, certain pseudoteeth of the mandible are slightly cranially inclined.

D. Fragments of rostrum (fig. 8, f)

The fragment of rostrum AaO 896 is completely crushed and it is not possible to see many details except for the edge of both tomia with incomplete pseudoteeth. On the lateral side of the left tomium one can see the rostral lateral longitudinal sulcus, or rostral groove, and on the crushed palate one can see a deep tooth pit. Fragments AaO 881 and 882 show pseudoteeth of order 1, 2, and 3, incomplete, and needles. They are considered as fragments of rostrum because they show a rostral groove which is situated at a small distance from the tomial edge. On these fragments the dimensions of the pseudoteeth are smaller than on mandible AaO 884 (table 8). These fragments perhaps correspond to a more anterior part of the jaws than the part preserved on mandible AaO 884.

E. Distal ulnae (fig. 10, a-c)

The two distal ulnae AaO 709 and AaO 894 seem to come from the same individual. The distal articular surface is rather flat while it is usually rounded in birds, both condyles, dorsalis and ventralis, are very slightly projecting on the ventral face, and the condylus dorsalis is weakly elongated

in proximal direction. These two condyles are practically indistinguishable from the surface of the shaft. On the contrary the tuberculum carpale is strongly separated from the shaft and proximodistally elongated. There is a depression on the dorsal face of the tuberculum carpale. Dimensions (mm): diagonal width from the caudalmost side of condylus dorsalis to tuberculum carpale, 24.4; depth of condylus dorsalis: 21.7.

F. Radii (fig. 10, a-b, i, and table 9)

The proximal part of the radius (AaO 885) shows an oval, dorsoventrally elongated proximal articular surface and, on each side, a strong tuberculum bicipitale radii. The distal part of the radius is ventrally incurved and forms a kind of niche in which the distal part of the ulna comes to lodge. This disposition is reminiscent of what can be observed for example in frigatebirds, but the hollow of the radius is more pronounced in *Pelagornis*. As in Fregatidae, the distal part of the radius is inflated cranially, while in other Pelecaniformes (Pelecanidae, Phaethontidae, some Phalacrocoracidae, Sulidae) the distal part of the radius is widened, like a paddle, but not ventrally incurved and cranially inflated. In the genus *Anhinga*, however, it is slightly cranially inflated, but not ventrally incurved.

G. Ulnar carpal AaO 712 (fig. 10, d)

This bone is relatively narrow and the two crura are not very divergent. The crus longum is not much longer than the crus breve and there is a large pneumatic foramen in the incisura metacarpalis. Among the recent Pelecaniformes it is most similar to the Pelecanidae, but in the latter the bone is much more pneumatized. It strongly differs from that of the Diomedeidae in which the crus longum is much longer than the crus breve. Dimensions (mm): total length or length of crus longum: 21.2; length of crus breve: 16.0; maximum width at the top of the two crura: 21.1; width at the base: 18.2.

H. Radial carpal AaO 709 (fig. 10, c)

This bone has an overall trapezoidal shape, with a flattened and almost semicircular distal surface. It is higher cranially than caudally. In its general shape it is reminiscent of the Pelecanidae, Phalacrocoracidae, Phaethontidae and Sulidae, and differs from the Fregatidae and Diomedeidae. Dimensions (in mm): maximum width of the distal articular surface: 20.8; maximum depth of the distal articular surface: 14.0; proximodistal length on the cranial side: 15.0; proximodistal length on the caudal side: 10.5.

I. Proximal carpometacarpus AaO 891 (fig. 10, e-f)

The alular metacarpal is incomplete but it is possible to see that it was situated very far distally from the proximal extremity, and that it was very slightly projecting in proximal direction. On the caudal face, distally to the trochlea carpalis, the os metacarpale minus is not separated from the os metacarpale majus, which indicates that the two met-

acarpal bones were fused proximally over a long distance. This shape is reminiscent of that in the genus *Pelecanus*, but in the latter the fovea carpalis cranialis is more developed, the median groove between the two ridges, dorsal and ventral, of the trochlea carpalis, is deeper, and these two ridges are much more projecting, while in *Pelagornis* the median groove is hardly indicated. Dimensions (mm): dorsoventral width of the trochlea carpalis at the proximal end: 17.5.

J. Femur (fig. 10, g-h, and table 10)

The femur AaO 897 was crushed in the locality, its shaft was entirely plastered and it is partly covered by concretioned sediments. It is not very different from a femur of recent *Pelecanus* but its collum femoris is not so contracted, and its trochanter femoris is not so projecting caudally, so that the proximal articular surface has a more rectangular outline.

The distal part of this femur is widened and flattened as in the recent Pelecanidae, and it is especially widened on the lateral side. On the cranial face the two condyles are very slightly projecting and the sulcus patellaris is wide and shallow. On the caudal face the Ahl al Oughlam femur differs from that of a recent *Pelecanus* because the sulcus fibularis (fibular groove of Howard, 1929) is hardly indicated and thus the lateral and fibular condyles are practically united. The part situated proximally to the condyles (fossa poplitea) seems to have been rather flat but it is partly masked by plaster.

Among the pseudodontorns the femur is known in *Palaeochenoides miocaenus* (Shufeldt, 1916; Wetmore, 1917) the age of which can be considered as Late Oligocene (Olson 1985). The Ahl al Oughlam femur differs from it because in *P. miocaenus* the condylus lateralis is very clearly separated from the condylus fibularis.

The femur of *Pelagornis mauretanicus* is very similar to that of *Pelagornis* sp., small form, from the Pliocene of the Yorktown Fm. of the Lee Creek Mine (Olson & Rasmussen, 2001: pl. 11, p-t et q-u). In this form the collum femoris is also weakly contracted but the trochanter femoris seems to be more caudally projecting. The distal part is also very flattened on the cranial face, with a wide, shallow sulcus patellaris. The caudal face of the distal part is eroded but it seems that the sulcus fibularis, between the lateral and fibular condyles, was also very weakly indicated.

CONCLUSIONS

Although this study only concerns two families from the Ahl al Oughlam avifauna, it provides interesting systematic and paleobiogeographical information.

The ostrich is referred to the species *Struthio asiaticus*, which was widespread in a large part of Eurasia during the Pliocene. This does not mean, however, that the ostriches originated in Eurasia and reached Africa at a recent period, as has sometimes been proposed, e. g. by Mikhailov (1992), or Rasmussen *et al.* (2001). Ostriches have a long evolutionary history in Africa, as evidenced by the occurrence of the oldest representative of the genus *Struthio*, *S. coppensi*, in the Early Miocene of Namibia (Mourer-Chauviré *et al.*, 1996), and by the presence of several eggshell species of the genus *Struthio* in the Late Miocene and Pliocene of Southern and Eastern Africa.

Among the Odontopterygiformes, the genus *Pelagornis* was previously known only by humeri and by a small number of other remains from the locality of Lee Creek (Olson & Rasmussen, 2001). The material found at Ahl al Oughlam made it possible to associate it with the humeri and to describe a large part of the mandible and pseudoteeth, and other elements of the postcranial skeleton. It is possible that some of the other genera of Odontopterygiformes will turn out to be synonymous with the genus *Pelagornis*, which was the first genus to be described in this order.

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	Ph. 1 D III AaO 836	Ph. 2 D III AaO 2219	Ph. 3 D III AaO 2973	Ph. 4 D III AaO 877
Total length	-	74.0	35.3	-
Length as preserved	87.4	-	-	67.0
Proximal width	-	47.7	35.8	31.7
Proximal depth	-	38.5	26.4	27.2
Width in the middle	32.3	31.0	37.2	-
Depth in the middle	25.0	24.0	18.0	-
Width of the distal art. surf.	47.4	ca. 44.5	39.0	-
Depth of the distal art. surf.	ca. 39.7	28.3	19.5	-

Table 1 - *Struthio asiaticus*, from Ahl al Oughlam, dimensions (mm) of the phalanges of the posterior digit III.

Phalanx 1 of post. digit III	Proximal width (1)	Minimum width of shaft (2)	Ratio (1):(2)	Distal width (3)	Ratio (3):(2)
S. cf. *brachydactylus*	41.2	25.3	1.63	-	-
S. cf. *karatheodoris*	48.0	28.5	1.68	44.0	1.54
S. *brachydactylus*	40.0	25.0	1.60	39.5	1.58
S. sp. Maragha	-	29.0	-	45.0	1.55
S. *asiaticus*	41.9	25.0	1.67	-	-
S. *pannonicus*	55.0	est. 35.0	ca. 1.57	ca. 48.0	ca. 1.37
AaO 836	-	31.2	-	47.4	1.52
Mean of fossil *Sruthio*			1.63 (n=5)		1.51 (n=5)
Recent *S. camelus*					
	43.8	23.8	1.84	41.5	1.74
	41.3	21.5	1.92	40.0	1.86
	42.5	22.3	1.90	40.4	1.81
	38.3	21.6	1.77	35.8	1.66
	37.8	21.2	1.78	36.0	1.70
	40.9	23.3	1.76	37.5	1.61
	40.6	24.1	1.68	37.2	1.54
	32.9	19.2	1.71	30.6	1.59
	33.5	19.0	1.76	30.7	1.62
	43.6	22.8	1.91	39.4	1.73
Mean of recent *S. camelus*			1.80 (n=10)		1.69 (n=10)

Table 2 - Comparisons of the dimensions (mm) and ratios of the phalanx 1 of the posterior digit III in fossil and recent species of *Struthio*.

Humerus	Pelagornis miocaenus			
	Holotype Armagnac Paris MNHN (a)	Léognan BMNH cast n° A 167 (b)	Léognan Bordeaux Museum	Condom Bordeaux Museum
Total length	sup. to 580	591	sup. to 625	est. 710
Proximal width	61 as preserved	61.5 as preserved	59.3 as preserved	-
Width at the level of the bicipital surface	40	-	-	-
Largest diameter of shaft in the middle	22	-	24.6	28.0
Smallest diameter of shaft in the middle	19	-	19.8	25.0
Distal width distally to proc. suprac. dorsalis	50	-	-	-
Maximum width at distal end	-	53.7	-	-
Distal depth	39	37.6 *	-	-
Length from tuberc. dors. to the dist. end of deltoid crest	168	174	est. 195	est. 210

Table 3 - Comparisons of the dimensions (mm) of the humeri of *Pelagornis miocaenus* from the French Miocene localities
(a) after the text and illustrations of Milne-Edwards (1867-71).
(b) after Harrison & Walker (1976).
*: "anterior to posterior width at internal condyle" (Harrison & Walker, 1976, p. 33).

	Pelagornis mauretanicus n. sp.		Pelagornis miocaenus		
			Holotype Armagnac Paris MNHN	Léognan BMNH Cast n° A 167 (a)	Léognan Bordeaux Museum
Humerus, proximal part	AaO 895	AaO 710			
Depth of caput humeri	26.5	26.2 as preserved	22.0	21.2	23.3
Humerus, distal part	AaO 705 Holotype	AaO 706 Paratype			
Distal width from the proc. supracond. dors. to the ventral side of cond. ventr. (fig. 5, A)	52 as preserved	51.2 as preserved	43.0	-	-
Distal width of the two condyles measured on the dist. art. surf. (fig. 5, B)	46 as preserved	-	40.0	-	-
Distal width from the most dorsal part of cond. dors. to the protuberance on the ventral face (fig. 5, C)	55 as preserved	-	49.0	-	-
Distal depth from the cranial face of cond. ventr. to the most caudal part of epicond. ventr. (fig. 5, D)	51.5 as preserved	-	39.0	-	-
Distal depth at the level of cond. dors. (fig. 5, E)	39.4	-	31.5	32.5	-
Proximodistal length of cond. ventr. (fig. 5, F)	18.6	18.6 as preserved	17.5	-	-
Proximodistal length of cond. ventr. (fig. 5, G)	32.0	30.5 as preserved	28.0	-	-

Table 4 - Comparisons of the dimensions (mm) of the humeri of *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, with those of *Pelagornis miocaenus*.
(a) after Harrison & Walker (1976).

Quadrate	P. mauretanicus n. sp. AoO 707	Pelagornis sp. 1 or sp. 2 Lee Creek (a)	Indetermined Pelagornithidae Calvert Fm.	Osteodontornis sp. Chichibu Basin (b)
Maximum height	48.4	45.6	44.1	44.6
Maximum depth, measured on the medial face, from cond. pter. to the caudalmost edge of cot. quadrat.	31.7	-	-	33.0
Maximum depth at the top of proc. otic.	18.0	-	-	16.8
Maximum depth at the level of the surf. artic. mand.	ca. 26	-	-	27.2
Pterygoid	Pelagornis n. sp. AaO 708	mauretanicus AaO 878	Pelagornis sp. 1 or sp. 2 Lee Creek (a)	
Total length	42.9	sup. to 48	40.1	
Greatest cranial width	14.6	16.9	17.2	

Table 5 - Comparisons of the dimensions (mm) of the quadrate and pterygoids of *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, with those of other Pelagornithidae
(a) after Olson & Rasmussen (2001).
(b) after the text and illustrations of Ono (1989).

Pelagornis mauretanicus n. sp.	mandible	AaO 884		
Right ramus			**Left ramus**	
Axis of pseudotooth order 2	0			
Axis of needle	6 mm			
Axis of pseudotooth order 3	12 mm			
Trace of needle	17 mm			
Axis of pseudtooth order 1	24 mm		Axis of pseudtooth order 1	0
Trace of needle	30.5 mm		Trace of the needle	7 mm
Axis of pseudotooth order 3	35 mm		Axis of pseudotooth order 3	12 mm
Axis of needle	39 mm		Axis of needle	16 mm
Axis of pseudotooth order 2	45 mm		Axis of pseudotooth order 2	22 mm
Axis of needle	50 mm		Axis of needle	27 mm
Axis of pseudotooth order 3	54 mm		Axis of pseudotooth order 3	31 mm
Axis of needle	58 mm		Axis of needle	36 mm
Axis of pseudotooth order 1	66 mm		Axis of pseudotooth order 1	42 mm
Break of the right ramus			Break of the right ramus	
Axis of needle	72 mm		missing part	
Axis of pseudotooth order 3	76 mm		missing part	
Axis of needle	81 mm		Axis of needle	59 mm
Axis of pseudotooth order 2	86 mm		Axis of pseudotooth order 2	64 mm
Axis of needle	90 mm		Trace of needle	68.5 mm
Axis of pseudotooth order 3	94 mm		Axis of pseudotooth order 3	72 mm
Axis of needle	98 mm		Trace of needle	74.5 mm
Axis of pseudotooth order 1	103 mm		Axis of pseudotooth order 1	80 mm
Axis of needle	109 mm		Axis of needle	87 mm
Axis of pseudotooth order 3	114 mm		Axis of pseudotooth order 3	92 mm
Axis of needle	119 mm		Trace of needle	95.5mm
Axis of pseudotooth order 2	123 mm		Axis of pseudotooth order 2	100 mm
Axis of needle	129 mm		Axis of needle	107 mm
Intraramal joint			Axis of pseudotooth order 3	112 mm
Axis of pseudotooth order 3	136 mm		Intraramal joint	

Table 6 - *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, distance from the median axis of the pseudoteeth to that of the first preserved pseudotooth on the two rami of the mandible AaO 884.

Pelagornis mauretanicus n. sp.	Height	Craniocaudal length at the base
Mandible AaO 884		
Pseudoteeth of order 1	20	9
Pseudoteeth of order 2	11	5
Pseudoteeth of order 3	7	2.5
Needles	3	1

Table 7 - *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, dimensions (mm) of the pseudoteeth on the mandible AaO 884.

Pelagornis mauretanicus n. sp.				
Fragments of rostrum	AaO 881		AaO 882	
	Height	Craniocaudal length at the base	Height	Craniocaudal length at the base
Pseudoteeth of order 1	est. 16	8	-	7.4
Pseudoteeth of order 2	-	-	-	5
Pseudoteeth of order 3	-	3	-	2.7
Needles	-	1	-	0.9

Table 8 - *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, dimensions (mm) of the pseudoteeth on the fragments of rostrum.

Radius		*Pelagornis*	*mauretanicus*	n. sp.
	AaO 885	AaO 894	AaO 899	AaO 709
Proximal width	25.2	-	-	-
Proximal depth	24.6	-	-	-
Distal width	-	28.7	26.5 as preserved	26.4 as preserved
Distal depth	-	21.5	-	-

Table 9 - *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, dimensions (mm) of the fragments of radius.

Femur	*Pelagornis mauretanicus* n. sp. AaO 897	*Pelagornis* sp. 1 Lee Creek (a)	*Pelagornis* sp. 2 Lee Creek (a)	*Palaeochenoides miocaenus* (b)
Total length as preserved	133	-	-	-
Proximal width	32.4	29.0-30.0	-	-
Proximal depth	ca. 18	-	-	-
Depth of caput femori	16.0	-	-	-
Distal width	34.5	29.6-30.6-30.9-32.7	sup. to 33	40
Depth at the level of condylus medialis	18.2	-	-	ca. 25
Depth at the level of condylus lateralis	24.5	-	-	25

Table 10 - Comparisons of the dimensions (mm) of the femur of *Pelagornis mauretanicus* n. sp., from Ahl al Oughlam, with those of other Pelagornithidae. (a) after Olson & Rasmussen (2001); (b) after Shufeldt (1916).