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Birds (Aves) from the Early Miocene of the Northern Sperrgebiet, Namibia

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Abstract

The avifaunas of the Northern Sperrgebiet are among the richest and the most diversified known from the Early Miocene of Africa. They include *Struthio coppensi*, a small ostrich which is the earliest known representative of the genus *Struthio*, the skeletal remains of which are associated with aepyornithoid type eggshells. They also include representatives of extinct genera, which were widespread in other parts of the world, such as *Megapaloelodus*, *Mionetta* or *Palaeortyx*. The majority of these forms are waterbirds. Although the sediments have been carefully washed and sorted, the only small avian fossil is a fragment of tarsometatarsus of a Coliidae. No passeriform remains has been recovered, as was also the case for the more recent Middle Miocene locality of Arrisdrift in Namibia.

Résumé

Les avifaunes de la Northern Sperrgebiet font partie des plus riches et des plus diversifiées connues pour le moment dans le Miocène inférieur d'Afrique. Elles comportent *Struthio coppensi*, une petite autruche qui est le plus ancien représentant du genre *Struthio* et dont les restes osseux sont associés à de coquilles d'œufs de type aepyornithoïde. Elles comportent aussi des représentants de genres éteints qui étaient largement répandus dans d'autres parties du monde, telles que *Megapaloelodus*, *Mionetta*, ou *Palaeortyx*. La majorité des ces oiseaux sont aquatiques. Bien que les sédiments aient été soigneusement lavés et triés, le seul reste de petite taille est un fragment de tarsométatarse de Coliidae. Aucun Passériforme n'a été trouvé, ce qui était également le cas pour le gisement du Miocène plus récent d'Arrisdrift en Namibie.

Introduction

This study concerns the fossil birds collected by Brigitte Senut and Martin Pickford from the localities of Elisabethfeld, Grillental, Langental and Fiskus, in the Northern Sperrgebiet, Namibia. The age of these localities is Early Miocene, approximately 21 Ma for Elisabethfeld, 20 Ma for Grillental and Fiskus, and 19 Ma for Langental (Pickford and Senut, 2003). These avifaunas are among the richest and the most diversified known so far from the Early Miocene of Africa. The only avifaunas of comparable age previously described were those of Songhor and Rusinga Island, in Kenya (Harrison and Walker, 1976; Harrison, 1980; Pickford, 1986), Arrisdrift, in Namibia (age 17 Ma, MN 4b) (Pickford and Senut, 2003; Mourer-Chauviré, 2003) and Gebel Zelten, in Libya (age MN 4) (Mlíkovsky, 2003). The material is deposited in the collection of the Geological Survey of Namibia, Ministry of Mines and Energy, Windhoek, Namibia. The anatomical terminology follows Baumel and Witmer (1993) and when necessary Howard (1929). The measurements are in mm.

Systematic description

Elisabethfeld locality

Order Struthioniformes

Family Struthionidae

Struthio Linné, 1758

Struthio coppensi Mourer-Chauviré *et al.*, 1996a

Figures 1-3

distal part and shaft, EF 3'94, holotype; left femur, proximal part, EF 9'93; left tarsometatarsus, distal part, EF 1'94; left tarsometatarsus, incomplete distal part, EF 2'94; right tarsometatarsus, shaft, EF 83'94; left fibula, EF 7'94; cost, EF 12'94, paratypes (figure 1 and figure 3, D).

New material: Three dorsal vertebrae, incompletely preserved, articulated, the XXIIIrd, EF 1a'05, the XXIVth, EF 1b'05, and the XXVth, EF 1c'05; left tarsometatarsus, distal part, EF 172'01; right tarsometatarsus, distal part, EF 35'96; phalanx 2 of posterior digit III, juvenile, EF 240'01; phalanx 3 of posterior digit III, proximal part, EF 6'03 (figure 3, A-C and E-F).

The species *Struthio coppensi* was originally described from the locality of Elisabethfeld (Mourer-Chauviré *et al.*, 1996a). It is the known representative of the genus *Struthio*. It has been found associated with aepyornithoid eggshells (Senut *et al.*, 1995) (figure 2). It is a small ostrich the known elements of which show primitive characteristics compared to recent ostriches, but the tarsometatarsus is already typically didactylous, with a vestigial trochlea metatarsi II. The fact of having skeletal remains of the genus *Struthio* associated with aepyornithoid-type eggshells shows that these eggs were not necessarily laid by birds belonging to the family Aepyornithidae (Elephant-birds). In the absence of skeletal remains and based only on eggshells it is thus not possible to write that « This record confirms that elephant birds survived in mainland Africa until at least the late Miocene » (Harrison and Msuya, 2005, p. 313).

Material previously described: Left tibiotarsus,

Description and comparisons: *Struthio coppensi* is a

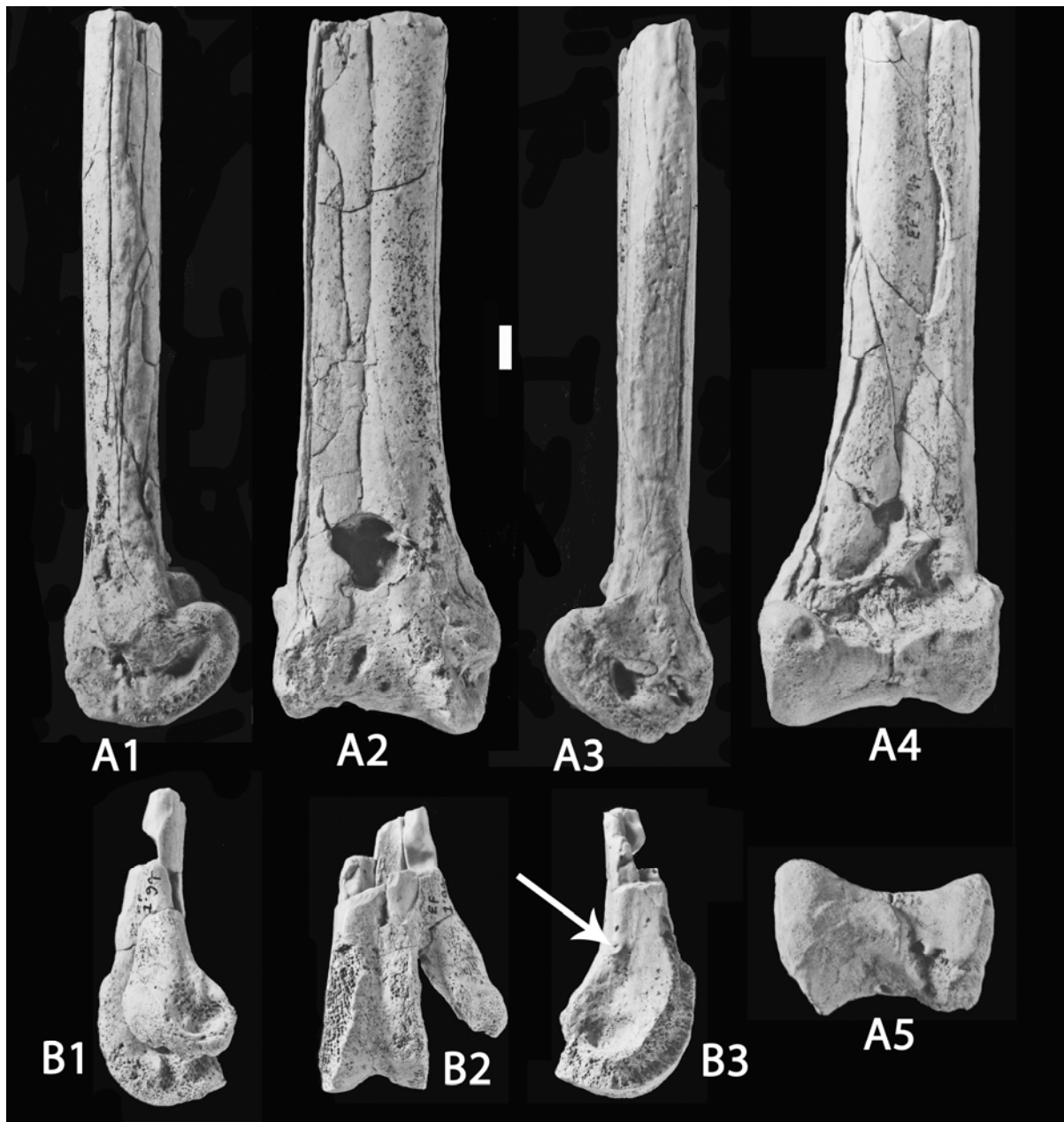


Figure 1 (Struthionidae 1)

Struthio coppersi, Elisabethfeld.

A, left tibiotarsus, holotype, EF 3'94: A1, medial surface; A2, caudal surface; A3, lateral surface; A4, cranial surface; A5, distal surface.

B, left tarsometatarsus, distal part, paratype, EF 1'94: B1, lateral surface; B2, dorsal surface; B3, medial surface. The arrow shows the vestigial trochlea II (scale bar 10 mm).

much smaller form than the recent *S. camelus* and shows different morphological characteristics. In *S. camelus*, the width and the depth of the distal part of the tibiotarsus are almost equal. In *S. coppersi* (EF 3'94) the width is greater than the depth and in cranial view the incisura intercondylaris is much more pronounced. In the Struthionidae, in the middle of the area situated proximally to the condyles, there is a flattened tubercle, called the tuberculum supra-trochlearis (Tsa). The shape of this tubercle is vari-

able in the recent *S. camelus* but in general it is a large rectangular plate. In *S. coppersi* this tubercle is slightly eroded but is constituted of two parts, a lateral one and a medial one. In the Struthionidae there is an oval fossa on the lateral side of the Tsa. In *S. coppersi* this fossa is shallower and situated more proximally than is generally the case in *S. camelus*. The sulcus extensorius, absent in *S. camelus*, is still visible in *S. coppersi* and is limited on its lateral side by the Tsa. The condylus medialis does not project as



Figure 2 (Aepyornithoid)
Struthio coppensi, Elisabethfeld.
Aepyornithoid-type egg shell associated with skeletal remains of *Struthio coppensi* (scale bar 10 mm).

far cranially in *S. coppensi* as in *S. camelus*, and its distal outline is rounded, while it is flattened in *S. camelus*.

Measurements of the holotype tibiotarsus (EF 3'94): Length from the foramen of the medullary

artery to the distal end, 255; maximal distal width at the level of condyles, on the cranial face, 54.6; depth of condylus medialis, 40.5; depth of condylus lateralis, ca. 35; depth of incisura intercondylaris, 26.

The femur EF 9'93 shows a pneumatic foramen distal to the proximal articular surface. This foramen is small, narrow and obliquely elongated. Compared to *S. camelus* the trochanter is craniocaudally narrower and the collum femoris is much more expressed. The caput femoris is more projecting in the proximal direction. At the end of the caput femoris, the fovea ligamenti capitis is wide and shallow, while it is narrow and deep in the recent ostrich.

Measurements of the paratype femur (EF 9'93): Maximal proximal width, 83; depth of caput femoris, 34.7; depth of collum femoris, 22.

The tarsometatarsus EF 1'94 shows the trochleae metatarsorum III and IV and a vestigial trochlea met. II. The tarsometatarsus EF 172'01 has the trochleae metatarsorum III and IV and a fragment of shaft. The vestigial trochlea met. II is just visible. The two trochleae are eroded on the plantar side. The tarsometatarsus EF 35'96 also shows the trochleae met. III and IV but it is strongly compressed and the distal part of the trochlea met. III is missing. On these tarsometatarsi the trochlea met. III is not so mediolaterally widened as in *S. camelus* and its two foveae lig. collateralium are shallower than in the ostrich.

Measurements: Table 1

The phalanx 2 of posterior digit III, EF 240'01, is juvenile and it is strongly eroded. The phalanx 3 of posterior digit III only has its proximal part and it is extremely small. Its dimensions are: width and depth of the proximal articular surface, 22.0 and 16.8; width and depth of the shaft in the middle, 16.1 and 9.7

The XXIIIrd vertebra EF 1a'05 has the corpus vertebrae and two caudal zygapophyses, the XXIVth,

Table 1 : *Struthio coppensi* from Elisabethfeld, measurements of the tarsometatarsi (1) from the vestigial trochlea met. II to the distal extremity.

Tarsometatarsus	EF 1'94 paratype	EF 172'01 new material	EF 95'96 new material
Distal width	ca. 49.3	ca. 46	-
Length of the trochlea met. III (1)	32.2	ca. 32	-
Width of the trochlea met. III	ca. 28	27.3	-
Maximum depth of the trochlea met. IV	ca. 28	-	25.5 as preserved
Length of the dorsal articular surface of trochlea met. III, internal side	ca. 37.5	ca. 36	-
Idem, external side	ca. 32	ca. 32	-

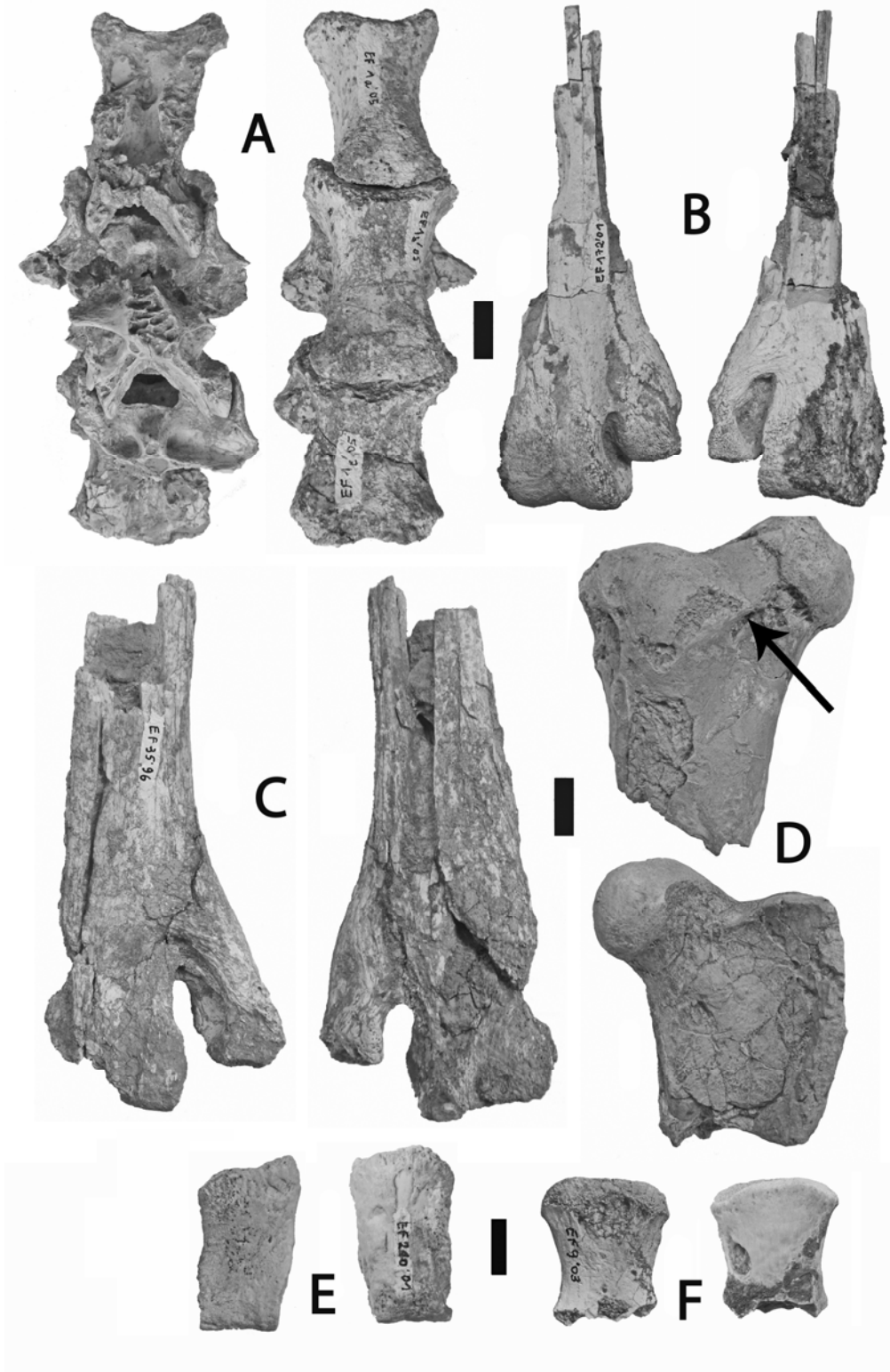


Figure 3 (Struthionidae 2)

Struthio coppensi, Elisabethfeld.

A, XXIIIrd, XXIVth, and XXVth dorsal vertebrae, EF 1a'05, EF 1b'05, and EF 1c'05. Left, dorsal surface; right, ventral surface; B, left tarsometatarsus, distal part, EF 172'01. Left, dorsal surface; right, plantar surface; C, right tarsometatarsus, distal part, EF 35'96. Left, plantar surface; right, dorsal surface; D, cast of the left femur, proximal part, paratype, EF 9'93. Top, caudal surface; bottom, cranial surface. The arrow shows the position of a small pneumatic foramen distal to the proximal articular surface; E, phalanx 2 of posterior digit III, juvenile, EF 240'01. Left, plantar surface; right, dorsal surface; F, phalanx 3 of posterior digit III, proximal part, EF 6'03. Left, plantar surface; right, dorsal surface (scale bar 10 mm).

EF 1b'05, has the corpus vertebrae, two cranial zygapophyses and the caudal part of the arcus vertebrae with the two caudal zygapophyses, and the XXVth, EF 1c'05, has the corpus vertebrae and the cranial part of the arcus vertebrae with the two cranial zygapophyses. On the three vertebrae the processus spinosus is absent or broken but it can be seen that it was strongly developed. On the dorsal face of the arcus vertebrae of the XXIVth vertebra one can see two lateral fossae (f2 of Mivart, 1874, fig. 57) situated either side of the processus spinosus, and one posterior fossa (f3 of Mivart), which is not subdivided. On the dorsal surface of the arcus vertebrae of the XXVth vertebra one can see two anterolateral fossae (f1 of Mivart). On the ventral face of the corpus vertebrae there is no crista ventralis corporis. The ventral surface of the XXIIIrd vertebra is concave in the craniocaudal direction. The ventral surface of the centrum of the XXIVth and XXVth vertebrae is very flat. The centrum of the XXIVth vertebra has its caudal articular surface very concave dorsoventrally. The caudal articular surface of the centrum of the XXVth vertebra has its transverse extent nearly two times its dorsoventral dimension. It has a bilobed shape, with a narrowing in the middle in the dorsoventral direction.

Measurements: Table 2

Compared to the recent *S. camelus* the proportions of the bones of *S. coppensi* are more slender. This Early Miocene ostrich is very different from the larger *Struthio* sp. reported in the Middle Miocene of Fort Ternan (13.7 Ma), Kadianga West (ca. 14 Ma), and Ngorora (12.5 Ma), in Kenya (Leonard *et al.*, 2006). In this *Struthio* the trochlea met. III is wider, the trochlea met. IV is very short and not so splayed as in *S. coppensi*, there is no sulcus extensorius on the distal tibiotarsus, and the cranial surface proximal to the condyles is much less excavated.

Table 2: *Struthio coppensi* from Elisabethfeld, measurements of the dorsal vertebrae from the cranialmost part of the facies articularis cranialis to the caudalmost part of the facies articularis caudalis.

Dorsal vertebrae	XXIIIrd EF 1a'05	XXIVth EF 1b'05	XXVth EF 1c'05
Maximum length of the corpus vertebrae (1)	46.3	49.2	44.6
Width of the corpus vertebrae in the middle	21.8	19.3	22.8
	as preserved		
Maximum width of the facies articularis caudalis	23.0	27.2	31.6
		as preserved	as preserved
Maximum dorsoventral length of the facies articularis caudalis	19.0	20.4	16.3
			as preserved

Order Pelecaniformes
Family Phalacrocoracidae
***Oligocorax* Lambrecht, 1933**
cf. *Oligocorax littoralis* (Milne-Edwards, 1871)
 Figure 4

Material: Left femur, proximal part and shaft, very eroded, EF 10'96.

Description and comparisons: This proximal part of femur corresponds to a Phalacrocoracidae and differs from the Anhingidae because its articular part is mediolaterally wider and its femoral head is more medially protruding than in the Anhingidae. The Phalacrocoracidae of the Late Oligocene and of the Miocene include several extinct genera, namely *Borvocarbo* from the Latest Oligocene of France (Mourer-Chauviré *et al.*, 2004), *Oligocorax* from the Late Oligocene of Germany (Mayr, 2001) and the Early Miocene of France (Milne-Edwards, 1867-71; Cheneval, 1984), and *Nectornis* from the Early Miocene of France, Germany (Cheneval, 1984), Czech Republic (Mlíkovský, 1998), and from the Middle Miocene of Turkey (Paicheler *et al.*, 1978; Mlíkovský, 1998). The recent genus *Phalacrocorax* is also present in the Early Miocene with the species *P. intermedius* from France and the Czech Republic (Milne-Edwards, 1867-71; Cheneval, 1984; Mlíkovský, 1998), and *P. marinavis* from North America (Shufeldt, 1915; Brodkorb, 1963; Mayr, 2001). In the genus *Borvocarbo* only the coracoid is known so far and this coracoid presents primitive characteristics. In the genus *Nectornis* the femoral head is not so medially protruding as in the Elisabethfeld form.

Although it is poorly preserved, the Elisabethfeld form is more closely related to *Oligocorax littoralis*. It seems that in this species the femur is less curved and its proximal part less projecting medially than in the genus *Phalacrocorax*. By its dimensions the EF form is very close to *O. littoralis*. It is slightly smaller

Table 3: cf. *Oligocorax littoralis* from Elisabethfeld and *Oligocorax littoralis* from Saint-Gérard-le-Puy, measurements of the femur from the cranialmost part of the crista trochanteris to the medio-caudal part of the caput femoris after the illustrations in Milne-Edwards, 1867-71, pl. 43, fig. 1-4.

Femur	Elisabethfeld EF 10'96	St-Gérard-le-Puy MNHN Av 9431
Maximum width of the proximal part (1)	14.6	15.3 (2)
Width of the shaft in the middle	5.3	6.0 (2)
Depth of the shaft in the middle	6.4	-



Figure 4 (Phalacrocoracidae)
cf. *Oligocorax littoralis*, Elisabethfeld.
Left femur, proximal part and shaft, EF 10'96. Left, caudal surface; right, cranial surface (scale bar 10 mm).

than the recent species *P. aristotelis*, the Shag, and clearly smaller than the extinct species *P. intermedius* and *P. marinavis*. *Oligocorax* cf. *littoralis* (syn. *Phalacrocorax* cf. *littoralis*) has been reported in Tunisia, in the Beglia Fm., Lower faunal level, dating from the latest Middle Miocene or the beginning of the Late Miocene (Rich, 1972). In this locality it is represented only by a carpometacarpus, so it is not possible to compare the EF form with it.
Measurements: Table 3

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate, small size
Figure 5, D

Material: Terminal phalanx of a posterior digit, EF 39'01.

Description and comparisons: The proximal part of the phalanx is not preserved. This phalanx is very thin and flattened, it shows a processus flexorius also

strongly flattened and strongly protruding on the plantar surface, as is seen in the genus *Pandion*. However in the genus *Pandion* the plantar surface of the claws is rounded while in the EF form the plantar surface is flat. The shape of this claw resembles that of the claws in the genus *Haliaeetus* but its processus flexorius is clearly more projecting than in *Haliaeetus*.

A small Accipitridae has been reported in the Middle Miocene of Arrisdrift, Namibia (Mourer-Chauviré, 2003).

Measurement in mm: Length, as preserved, 15.3

Order Galliformes
Family Phasianidae
cf. *Palaeortyx* Milne-Edwards, 1869
Figure 6, A

Material: Right carpometacarpus, proximal part, EF 4'06

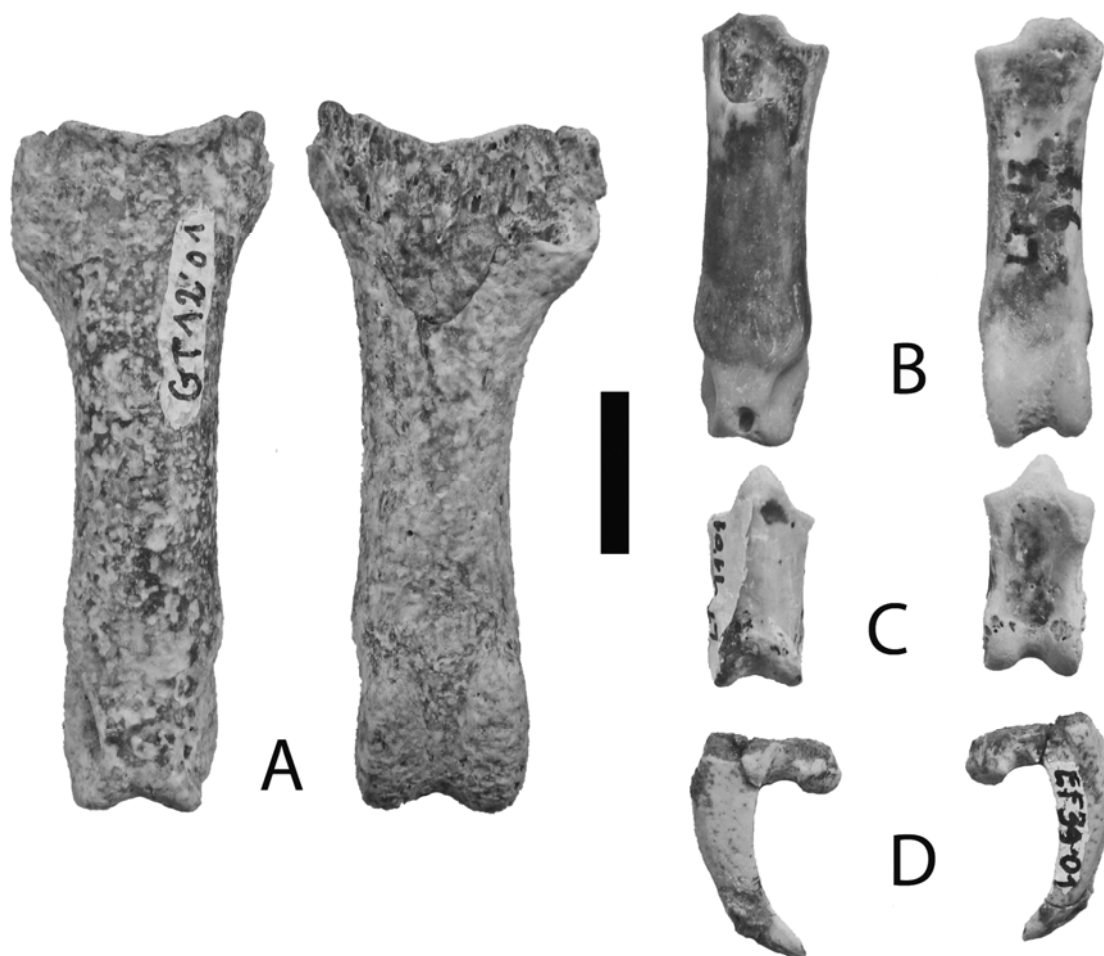


Figure 5 (Accipitridae)

Accipitridae indeterminate, Grillental, Langental, and Elisabethfeld.

A, phalanx 1 of posterior digit I, Grillental, Langental, GT 12'01. Left, dorsal surface; right, plantar surface; B, phalanx 3 of posterior digit III, or phalanx 4 of posterior digit IV, Langental, LT 13'94. Left dorsal surface; right, plantar surface; C, phalanx 2 of posterior digit III, Langental, LT 11'01. Left, dorsal surface; right, plantar surface; D, terminal phalanx of a posterior digit, Elisabethfeld, EF 39'01. Medial and lateral surfaces (scale bar 10 mm).

Description and comparisons: This proximal part of carpometaarpus shows the morphological characteristics of the genus *Palaeortyx*, as they have been described by Mourer-Chauviré *et al.* (2004) for a specimen from the locality of Créchy, France. In the different specimens of the Quercy species *P. brevipes*, *P. gallica*, and *P. prisca*, on the dorsal face, in the fossa supratrochlearis, there is a ridge which ends distally in a tubercle. In the Créchy form the ridge is not very pronounced and the most conspicuous character is a flattened tubercle in the middle of the fossa supratrochlearis. In the EF specimen the ridge is not very strongly expressed but it is present.

The genus *Palaeocryptonyx* is also present as early as the Early Miocene of Petersbuch 2, Germany, (Göhlich and Mourer-Chauviré, 2005). The type species of this genus is *Palaeocryptonyx donzani* from the Pliocene of Perpignan, France. The carpometaarpus of *Palaeocryptonyx* differs from that of

Palaeortyx by the following characteristics: processus pisiformis much less projecting and less cranially elongated; ventral ledge of the trochlea carpalis showing a pronounced notch; dorsal ledge of the trochlea carpalis also showing a notch, this dorsal ledge is much shorter than the ventral ledge and does not extend distally. In addition, in *Palaeocryptonyx* the processus intermetacarpalis is situated much farther distally than in *Palaeortyx*, but this is not visible on the EF form.

A proximal humerus which possesses all the hallmarks of the genus *Palaeortyx* is present in the Middle Miocene of Arrisdrift, Namibia, and has been reported as Phasianidae, form 4 (Mourer-Chauviré, 2003). Its size corresponds to that of *P. gallica* while the carpometaarpus of the EF form corresponds to a slightly larger form. The Galliformes are very diversified at Arrisdrift, but all the other forms correspond to larger species.

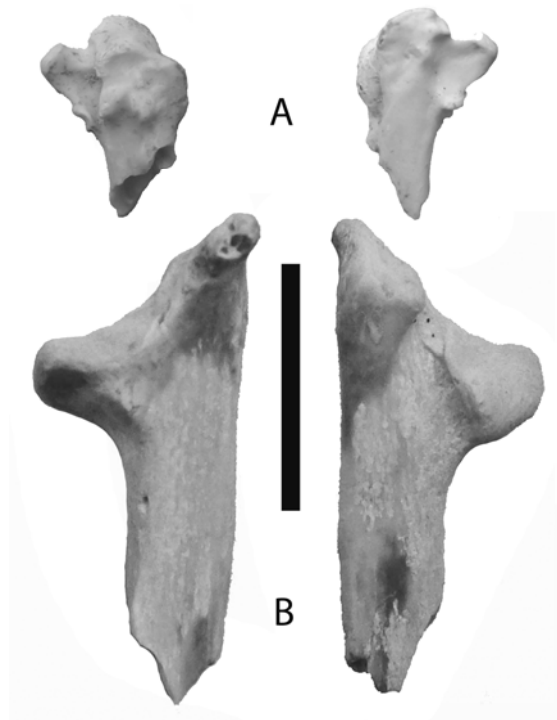


Figure 6 (Phasianidae)
cf. *Palaeortyx*, Elisabethfeld. A, right carpometacarpus, proximal part, EF 4'06. Left, ventral surface; right, dorsal surface: Phasianinae indeterminate, Grilental; B, right scapula, cranial part, GT 110'06. Left, costal surface; right, lateral surface (scale bar 10 mm).

The size of the EF specimen is intermediate between *P. gallica* and *P. prisca* (syn. of *P. intermedia*, Göhlich and Mourer-Chauviré, 2005). At the present time the genus *Palaeortyx* is known from the Late Oligocene of France to the Late Miocene of Spain (Cheneval and Adrover, 1995).

Measurements: Table 4

Table 4: *Palaeortyx* sp. from Elisabethfeld, comparisons of the measurements of the carpometacarpus with *Palaeortyx brevipes*, *P. gallica*, and *P. prisca* from the Phosphorites du Quercy (Mourer-Chauviré, 1992). The species *P. intermedia*, reported in the Phosphorites du Quercy, has been placed in synonymy with *P. prisca* by Göhlich & Mourer-Chauviré (2005).

Carpometacarpus	cf. <i>Palaeortyx</i> Elisabethfeld EF 4'06	<i>Palaeortyx</i> <i>brevipes</i> mean	<i>Palaeortyx</i> <i>gallica</i> mean	<i>Palaeortyx</i> <i>prisca</i> mean
Proximal depth	6.5	5.25	5.85	7.30
Width of carpal trochlea	3.2	2.67	3.05	3.55
Ratio Depth/Width	2.03	1.97	1.92	2.06

Order Charadriiformes
Charadriiform indeterminate, small size

Material: Left tibiotarsus, distal part, EF 21'05, and right tarsometatarsus, distal part, EF 22'05.

Description and comparisons: The morphological details of these distal tibiotarsus and tarsometatarsus correspond to a Charadriidae, such as *Tringa totanus*, the Redshank, but they are slightly smaller. They correspond to a smaller form than the indeterminate charadriiform reported at Arrisdrift (Mourer-Chauviré, 2003).

Measurements: Tibiotarsus, distal width, 3.9; distal depth, 3.6; tarsometatarsus, distal width, 4.2; distal depth, 2.8.

Aves indeterminate

Material: Left femur, distal part, very eroded, EF 9'96; Phalanx 1 of the major digit of the wing, EF 157'01.

Grilental locality

Order Phoenicopteriformes
Family Palaelodidae
***Megapaloelodus* A. H. Miller, 1944**
***Megapaloelodus* sp.**

Figure 7

Material: Right humerus, distal part, GT 44'00.

Description and comparisons: This humerus consists in the distal end and a part of the shaft comprising several crushed fragments. The condylus ventralis is incompletely preserved and the epicondylus ventralis is missing. This humerus shows the morphological characteristics of the Palaelodidae, with a condylus dorsalis which ends proximally in a ventrally recurved point. The attachment of the anterior articular ligament (Howard, 1929) forms a flattened



Figure 7 (Palaelodidae)
Megapaloelodus sp., Grillental.
Right humerus, distal part, GT 44'00. Left, cranial surface; right, caudal surface (scale bar 10 mm).

surface, very elongated in the proximodistal direction and situated in same plane as the surface of the cranial surface. The ectepicondylar prominence (Howard, 1929) is well developed and projects dorsally. Inside the fossa m. brachialis, the impressio of the m. brachialis anticus extends obliquely and its distalmost and ventralmost part forms an oval, very deep fossa. In the genus *Palaelodus* the impressio of the m. brachialis anticus has a variable shape but it is always deep and some individuals show a very deep depression on the distal and ventral side, as in the Grillental fossil.

The Palaelodidae range from the Lowermost Oligocene of Europe (Mayr and Smith, 2002) to the Middle Pleistocene of Australia (Baird and Vickers-Rich, 1998). They are present in numerous localities, generally in the Late Oligocene, the Early Miocene, and the Middle Miocene. In Europe they are represented by *Palaelodus ambiguus* Milne-Edwards, 1863, *P. gracilipes* Milne-Edwards, 1863, *P. crassipes* Milne-Edwards, 1863, and *Megapaloelodus goliath* (Milne-Edwards, 1871) (Cheneval, 1983a; Heizmann and Hesse, 1995; Mourer-Chauviré *et al.*, 2004). In North America is found only the genus *Megapaloelodus*, represented by two species, *M. connectens* A. H. Miller, 1944, from the Early and Middle Miocene, and *M. opsionus* Brodkorb, 1961, from the Late Miocene (Becker, 1987). In South America, *Palaelodus* aff. *ambiguus* has been reported in the Tremembé Fm., Taubaté Basin, age Late Oligocene or Early Miocene (Alvarenga, 1990), and *Megapaloelodus* sp. in the Late Miocene of Argentina (Noriega, 1995). In Africa, two forms related to the genus *Palaelodus*, one the size of *P. gracilipes*, the other the size of *P. crassipes*, have been reported from the Early Oligocene of Jebel Qatrani, Fayum Province, Egypt (Rasmussen *et al.*, 1987). Lastly in Australia two species of the genus *Palaelodus* are known, a small one, *P. pledgei*, only in the Middle Miocene, and a large one, *P. wilsoni*, from the Middle Miocene to the Middle Pleistocene (Baird and Vickers-Rich, 1998). It appears, thus, that the family Palaelodidae had a worldwide distribution and it is not surprising to find one of its representatives in the Early Miocene of Southwest Africa.

The genus *Megapaloelodus* differs from *Palaelodus* by its larger size and by some distinctive morphological characteristics. Unfortunately the distal part of the humerus is unknown in any of the species attributed to this genus. In the Grillental specimen the minimal distal width of the humerus is 29.0 mm. According to the measurements given by Cheneval (1983a) on a large sample of *Palaelodus* and *Megapaloelodus* ssp. the ratio between the mean dimensions of *P. ambiguus* and *M. goliath* is on average 1.36, with extreme values of 1.21 and 1.51. The mean value of the distal width of the humerus of *P. ambiguus* being 18.40 mm, the mean value of the distal width of the humerus of *M. goliath* should be ca. 25.02 mm, with extremes values of 22.26 mm and

27.78 mm. The Grillental humerus is thus slightly larger than the presumed value of the *M. goliath* humerus.

In the species *M. connectens*, some elements are from 15% to 23% larger than the corresponding elements of *M. goliath*, but other elements are quite equivalent in size (A. H. Miller, 1944; L. Miller, 1950; 1952). In the species *M. opsionus* the measurements given by Brodkorb (1961) for the proximal width of the tarsometatarsus fall within the variation range of *M. goliath*, and for the distal part of the tarsometatarsus attributed by Howard (1971) to ?*M. opsionus*, they are only slightly larger than those of *M. goliath*. In the *Megapaloelodus* sp. from the Miocene of Argentina, the dimensions of the distal part of tibiotarsus also fall in the range of variation of *M. goliath*.

Lastly Olson (1985) reports that a form still larger than *M. goliath*, *M. connectens*, and *M. opsionus* is present in the Early Miocene of France and the Middle Miocene of Texas (see below, about the genus *Cygnopterus*).

In conclusion it is not possible to attribute the Grillental specimen to any of the species previously described in the genus *Megapaloelodus*. One may simply write that large forms of Palaelodidae were present almost everywhere in the world throughout the Miocene, and that some of them survived in Australia until the Pleistocene.

Order Anseriformes
Family Anatidae
Subfamily Oxyurinae

The subfamily Dendrocheninae had been described by Livezey and Martin (1988) to include the extinct genera *Dendrochen* and *Mionetta*. Worthy *et al.* (2007) have included in this subfamily the extinct genus, *Manuherikia*, from the Early-Middle Miocene of New Zealand. However in a more recent work Worthy and Lee (2008) have placed the Dendrocheninae into synonymy with the recent subfamily Oxyurinae and have placed the extinct genera *Mionetta*, *Dendrochen*, *Manuherikia* and *Dunstanetta* in this expanded subfamily.

***Mionetta* Livezey and Martin, 1988**
***Mionetta* sp.**
Figure 8, B

Material: Left humerus, distal part, GT 133'06.

Description and comparisons: On this humerus, on the cranial face, the proximal part of the dorsal and ventral condyles is eroded, and on the caudal face, the epicondylus ventralis is incompletely preserved. This specimen shows the morphological characteristics of the genus *Mionetta*, as they have been defined by Livezey and Martin (1988) and modified by Worthy *et al.* (2007). The facet for the anterior articular

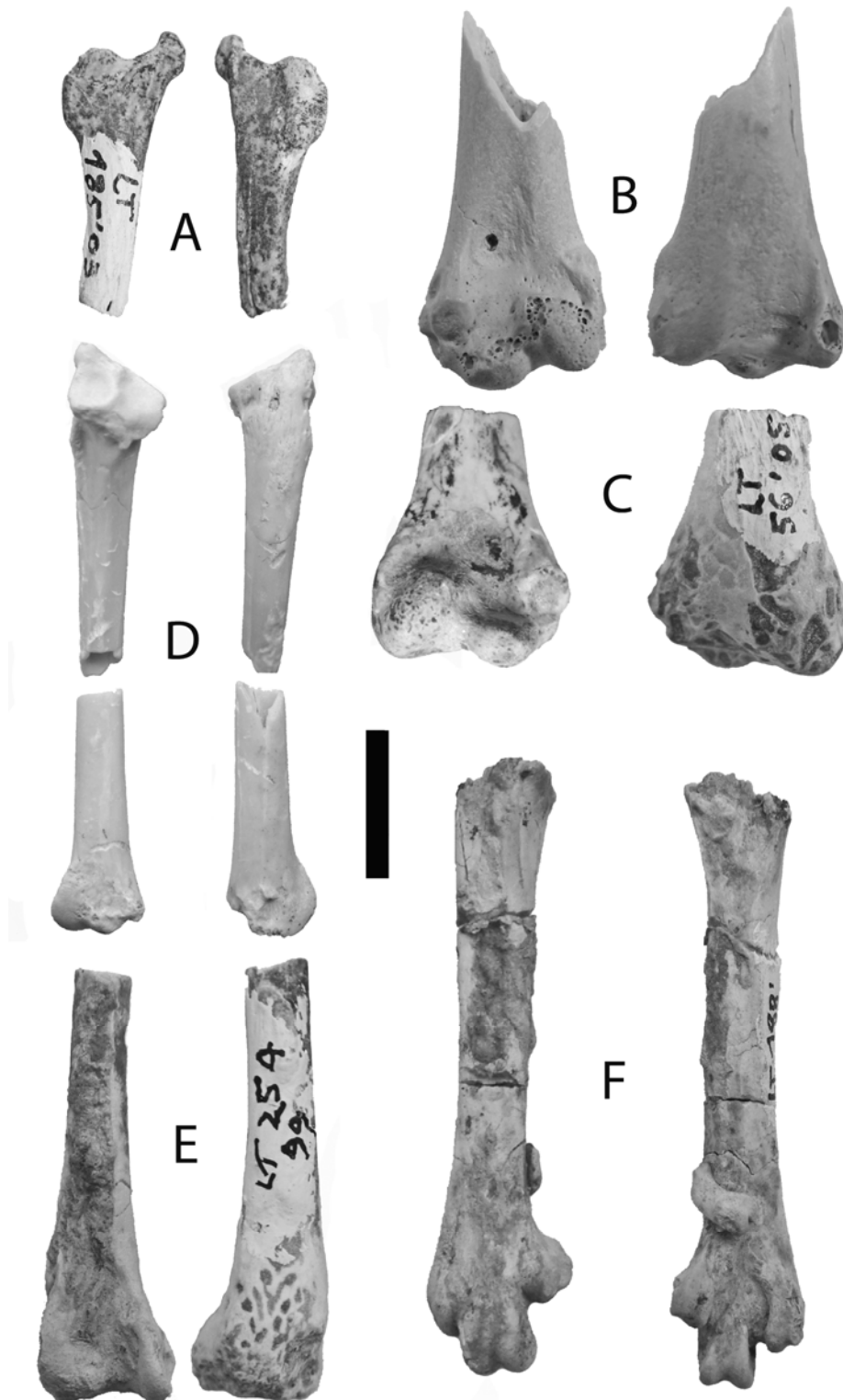


Figure 8 (Oxyurinae)

Mionetta sp. and Dendrocheninae., Langental. A, right scapula, cranial part, LT 185'03. Left, costal surface; right, lateral surface.

Mionetta sp., Grillental. B, left humerus, distal part, GT 133'06. Left, cranial surface; right, caudal surface.

Mionetta sp., Langental. C, right humerus, distal part, LT 56'05. Left, cranial surface; right, caudal surface.

Oxyurinae indeterminate, Grillental. D, left ulna, proximal and distal parts, GT 46'05. Proximal part, left, cranial surface; right, caudal surface. Distal part, left, ventral surface; right, caudal surface.

Mionetta sp., Langental. E, right tibiotarsus, distal part, LT 254'99. Left cranial surface; right, caudal surface.

Mionetta sp., Langental. F, right tarsometatarsus, almost complete, LT 188'03. Left, cranial surface; right, plantar surface (notice adhering nodule) (scale bar 10 mm).

ligament is not situated in a plane parallel to the surface of the cranial face but it is raised and rotated (tilted) distally. It differs from *Mionetta blanchardi* and from *Manuherikia* because, in these forms, on the ventral face, the attachment point for the m. pronator brevis (Howard, 1929) is at the same level as the top of the facet for attachment of the anterior articular ligament, while in the Grillental form, and in *Mionetta consobrina*, it is situated slightly more proximally. The Grillental form differs from *Manuherikia* because, in the later, the fossa m. brachialis is deep and bounded by a sharp ridge ventrally, whereas in *Mionetta* the fossa m. brachialis is shallow and bounded ventrally by a more rounded ridge.

Measurements: Distal width, 13.7; distal depth, 7.9

Oxyurinae indeterminate
Figure 8, D

Material: Left ulna, proximal and distal part, GT 46'05.

Description and comparisons: This ulna shows the morphological characteristics of the Oxyurinae. The cotyla ventralis has a rounded outline and is very deep. The olecranon is slightly ventrally oriented. The tuberculum lig. collateralis has an oval shape, it is well delimited and proximodistally elongated. On the ventral side, the rim of the cotyla ventralis forms a projecting ledge above the tuberculum lig. coll. The impressio brachialis is very wide at its proximal side. It takes up almost all the ventral side and extends very far distally. At the distal part it is not possible to see any difference from the genus *Dendrocygna*.

This form is different from *Mionetta* because, in ventral view, the cotyla ventralis is more perpendicularly oriented compared to the axis of the shaft, while in *Mionetta* it is more obliquely oriented. As part of the shaft missing it is not possible to know the total length of the bone. The other measurements show that this form is almost the same size as *Mionetta natator*, the smallest species of *Mionetta*.

Table 5: Oxyurinae indet. from Grillental, comparison of the measurements of the ulna with *Mionetta natator* from Saint-Gérard-le-Puy, after Cheneval (1983b). (1) Distal diagonal after Bacher (1967).

Ulna	Oxyurinae indet. GT 46'05	<i>Mionetta natator</i> , mean Saint-Gérard-le-Puy
Proximal width	6.3	6.6
Proximal depth	7.0	5.7
Depth of condylus dorsalis	5.5	-
Distal diagonal (1)	6.3	5.2

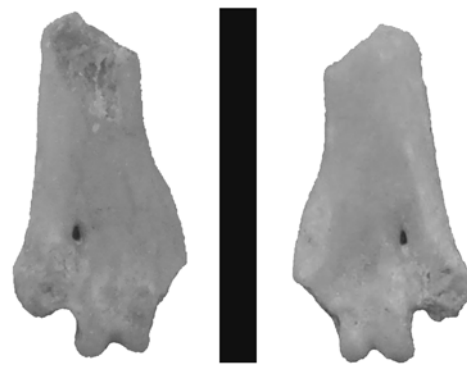


Figure 9 (Coliidae)
Coliidae indeterminate, Grillental.
Right tarsometatarsus, distal part, GT 120'06. Left, cranial surface; right, plantar surface (scale bar 5 mm).

Measurements: Table 5

Early representatives of the subfamily Oxyurinae were widely distributed in the world. They are known from the Late Oligocene of Kazakhstan (Mlíkovsky and Svec, 1986: *Anas oligocaena* has been transferred to the genus *Dendrochen* by Mlíkovsky and Svec, 1986), and the Latest Oligocene of Créchy, France (Mourer-Chauviré *et al.*, 2004). They are very abundant in the Early Miocene of France, Germany (Cheneval, 1983b; Livezey and Martin, 1988), and the Czech Republic (Svec, 1981), and persist into the Middle Miocene of Hungary (Mlíkovsky, 2002), Romania (Kessler, 1992) and maybe also of Sansan, France (Worthy *et al.*, 2007). The genus *Dendrochen* is known in the Early Miocene of the United States (Miller, 1944) and the genus *Manuherikia* in the Early-Middle Miocene of New Zealand (Worthy *et al.*, 2007). A "Dendrocheninae" gen. and sp. indet. is also present in the Late Miocene of Argentina (Noriega, 1995).

Finally, in Namibia, the species *Anas luederitzensis* Lambrecht, 1929, has been found in the E-Bay Fm., dated from the Early Miocene on the basis of a micromammalian fauna (Pickford, pers. comm. 6. 03. 2007). This species is known by a proximal part of humerus which does not present a pneumatic foramen in the ventral pneumotricipital fossa. For this reason it cannot belong to the genus *Anas* (Worthy *et al.*, 2007). By this characteristic "*Anas*" *luederitzensis* is similar to *Mionetta* and also differs from the Dendrocygnae which have a pneumatic foramen in the pneumotricipital fossa.

In conclusion the occurrence of Oxyurinae in the Early Miocene of the Northern Sperrgebiet makes it possible to complete the biogeographical distribution of this subfamily which was probably already represented in Africa by "*Anas*" *luederitzensis*.

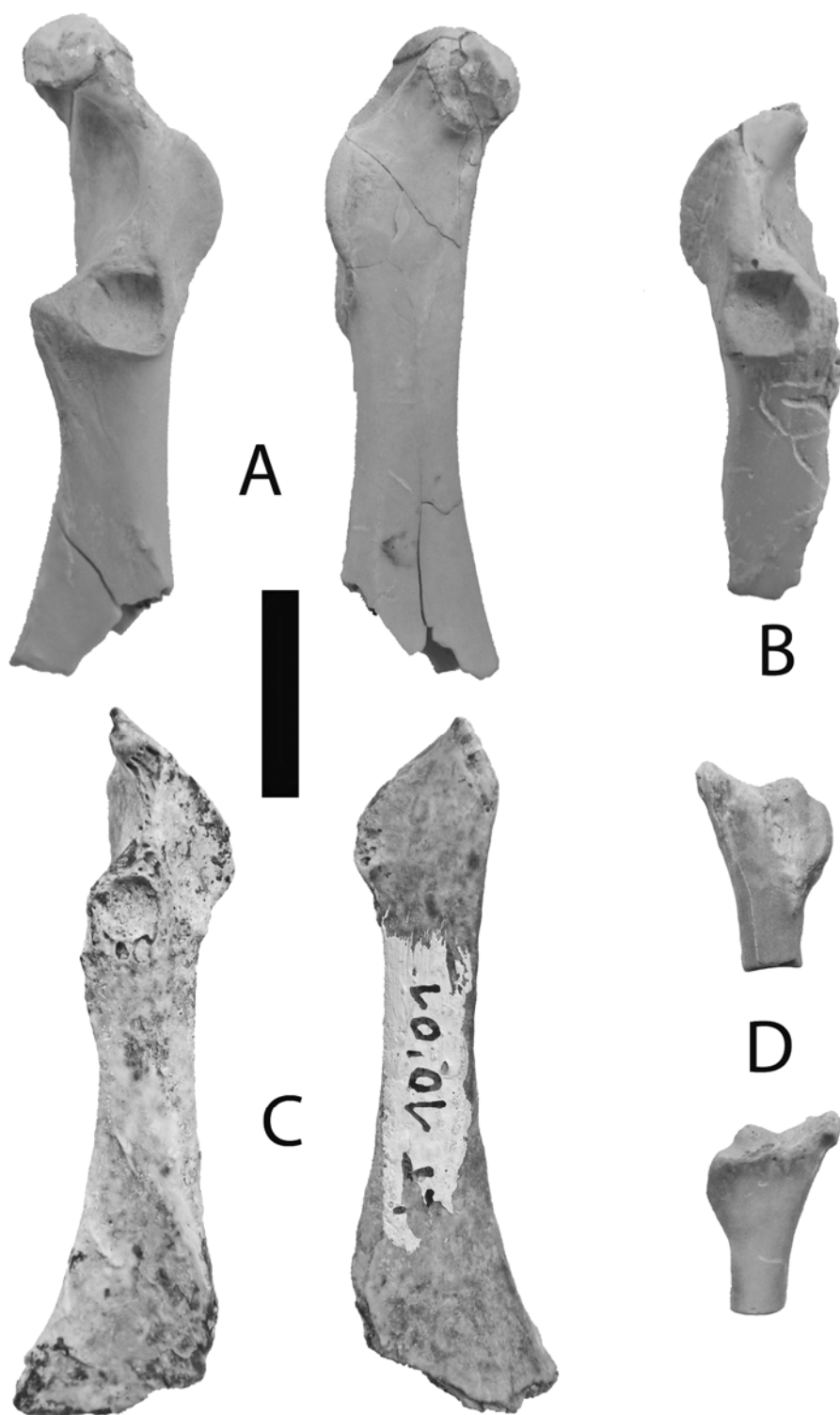


Figure 10 (Anserinae)

Anserinae indeterminate, Grillental; A, left coracoid, omal part and shaft, GT 10'03 GT6. Left, dorsal surface; right, ventral surface; B, right coracoid, middle part, GT 11'06 GT6, dorsal surface; Anserinae indeterminate, Langental; C, right coracoid, LT 10'01. Left, dorsal surface; right, ventral surface; Anatidae indeterminate, Fiskus; D, right scapula, FS 32'01. Top, lateral surface; bottom, costal surface (scale bar 10 mm).

Subfamily Anserinae
Anserinae indeterminate
Figure 10, A-B

Material: Left coracoid, pars omalis and shaft, GT 10'03 GT6; right coracoid, middle part, GT 11'06 GT6. On the left coracoid the pars omalis is complete. It shows the facies articularis scapularis, the facies articularis humeralis, and a part corresponding to two thirds of the shaft. On the right coracoid the pars omalis is absent. It shows mainly the facies art. scapularis and the facies art. humeralis. This right element is quite similar in size to the left element, thus it seems that these two specimens come from the same individual, although they were found three years apart.

Description and comparisons: The pars omalis is strongly developed in the dorsoventral direction. The processus acroracoideus is very globular and projects ventrally. The facies art. clavicularis is dorsoventrally elongated and omalosternally narrow. There is no pneumatic foramina under the caudal ledge of the facies articularis clavicularis. There is an oblique ridge which divides into two parts the fossa situated in the sulcus m. coracoidei, a cranioventral part, under the ledge of the facies art. clavicularis, and a caudodorsal part. The facies art. scapularis has a rounded shape and is very deep. The processus procoracoideus is present but poorly developed in the medial direction and it ends in a blunt point. There is no hint of foramen n. supracoracoidei, or of incisura n. supracoracoidei. The shaft is robust.

This coracoid differs from the Dendrocygninae and Oxyurinae because in both of these subfamilies the pars omalis is much narrower dorsoventrally, the facies art. clavicularis is elongated in the omalosternal direction and narrow in the dorsoventral direction, and the shaft is much thinner. It looks similar to the Anserinae by the shape of the pars omalis, but it differs from the recent Anserinae by the absence of pneumatic foramina under the ledge of the facies art. clavicularis.

Among the recent Anserinae, it is closer to the genus *Branta* than to the genus *Anser* by the shape of the processus procoracoideus which is not strongly developed and not ventrally incurved. In the genus *Branta* there are numerous pneumatic foramina under the facies art. clavicularis, and a small pneumatic foramen on the dorsal face, cranially to the facies art. scapularis, on the medial side of the facies art. humeralis. All these foramina are absent in the Grillental form.

The absence of pneumatic foramina under the facies art. clavicularis is a primitive characteristic among the Anseriformes (Livezey, 1996). The Grillental form probably corresponds to a primitive form of Anserinae, not included in the crown-group Anserinae.

Measurements of the coracoid GT 10'03: Me-

diolateral width of processus acroracoideus, 5.5; dorsoventral depth of processus acroracoideus, 8.2; width of the omal part from the lateral edge of facies articularis humeralis to tip of processus procoracoideus, 10.3; width of shaft in the middle, 5.5; depth of shaft in the middle, 4.2

The oldest known Anserinae known at present is *Cygnavus formosus* from the Early Oligocene of Kazakhstan, only represented by a tibiotarsus (Kurochkin, 1968; Mlíkovsky and Svec, 1986). The genus *Cygnopterus* was described by Lambrecht (1931) in the Early Oligocene of Belgium, with the species *Cygnopterus affinis* (van Beneden, 1883), and two other species have been attributed to this genus, *C. lambrechtii* Kurochkin, 1968, from the Middle Oligocene of Kazakhstan, and *C. alphonsi* Cheneval, 1984, from the Early Miocene of France.

The species *Cygnopterus affinis* was described on the basis of several elements from the same individual (Lambrecht, 1931; 1933), and the coracoid shows a fossa under the facies articularis clavicularis which is devoid of pneumatic foramina, so this species does not belong to the crown-group Anserinae. Mayr (2005) even suggests that this taxon does not belong to the Anatidae.

The species *Cygnopterus lambrechtii* was placed into synonymy with the Phoenicopteridae "*Agnopterus*" *turgaiensis* (Mlíkovsky and Svec, 1986).

The species *Cygnopterus alphonsi* is known by several skeletal elements, including coracoids (Cheneval, 1984). However my opinion is that these coracoids actually belong to very large Palaelodidae. Indeed the shaft is proportionally shorter than in the Anserinae, the processus acroracoideus and the angulus medialis are much more projecting medially, the facies articularis scapularis is proportionally larger and deeper, and there is a foramen n. supracoracoidei situated very close to the facies articularis scapularis, on its sternal and medial side. This foramen only exists in the primitive Anseriformes and is absent in the Anatidae (Livezey, 1997). In addition the pars omalis of the coracoids attributed to *C. alphonsi* is different from that of *C. affinis*.

Compared to *Palaelodus ambiguus*, the dimensions of the coracoids attributed to *Cygnopterus alphonsi* are on average 1.82 times larger, and compared to *Megapaloelodus goliath* on average 1.39 times larger.

The species *Aminornis excavatus*, described by Ameghino from the Middle Oligocene of Patagonia has been recently revised and transferred to the Anseriformes, family Anatidae, subfamily Anserinae (Agnolin, 2004). This species is only known by a coracoid which does not show any pneumatic foramen under the facies articularis clavicularis (Ameghino, 1899). So this taxon also corresponds to a primitive form, not included in the crown-group Anserinae.

In conclusion the Grillental form corresponds to

a primitive Anserinae but cannot be attributed to any known form. scapulae, 2.5

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate
Figure 5, A

Material: Phalanx 1 of posterior digit I, GT 12'01.

Description and comparisons: This phalanx is slightly incomplete, a part of the proximal articular surface is missing. Its proportions recall that of the genus *Hieraaetus*, but it is larger than that of *Hieraaetus fasciatus*, which is the largest species in the genus (del Hoyo *et al.*, 1994). It is more elongate than the corresponding phalanx of the genus *Aquila*. At the distal part, on the dorsal surface, the trochlea articularis is narrow, and the foveae lig. collateralium are very deep, as in *Hieraaetus*, while the trochlea is wide and the foveae shallow in *Aquila*. It also differs from the genus *Haliaeetus* where the proximal part of the phalanx is very wide.

Measurements: Total length, as preserved, 45.6; Proximal width, as preserved, 18.4; Maximal distal width, on the plantar face, 11.0; Width between the two foveae, on the dorsal face, 5.6; Width in the middle, 9.6; Depth in the middle, 7.4

Order Galliformes
Family Phasianidae
Subfamily Phasianinae
Phasianinae indeterminate
Figure 6, B

Material: Right scapula, cranial part, GT 110'06

Description and comparisons: In this scapula the acromion is strongly curved costally. There is no pneumatic foramen between the facies art. clavicu-laris and the facies art. humeralis. It is different from the genus *Palaeortyx* because in this genus the acromion is almost rectilinear and only very slightly curved at its tip (Göhlich and Mourer-Chauviré, 2005). It differs from the recent genera *Afropavo*, *Numida* and *Phasianus*, which have an acromion which is either rectilinear or is less curved than the Grillental form. The form which is the most similar is a wild specimen of *Gallus gallus*. Forms related to the recent genera *Gallus* and *Phasianus* are present at Arrisdrift (Phasianidae, forms 1 and 3, Mourer-Chauviré, 2003). A *Gallus* sp. has been reported from the Middle Miocene of Beni Mellal, in Morocco (Brunet, 1961) and cf. *Phasianus* in the Late Miocene of Lemudong'o, in Kenya (Stidham, 2007).

Measurements: Length from base of facies articularis humeralis to tip of acromion, 10.8; width of corpus scapulae, 4.4; dorsoventral depth of corpus

Order Coliiformes
Family Coliidae
Coliidae indeterminate
Figure 9

Material: Right tarsometatarsus, distal part, GT 120'06

Description and comparisons: The trochleae metatarsi II and IV are missing. The trochlea met. III is proximodistally short. On the dorsal side, the two rims of this trochlea are slightly eroded. The dorsal surface of this distal part is very flat. There is no longitudinal ridge and the outer extensor groove is poorly indicated. The plantar surface is also very flat. There is a weak ridge which prolongs proximally the wing of the trochlea met. IV. The fossa metatarsi I is present but it does not seem that there has been a ridge connecting the wing of the trochlea met. II with this fossa met. I. In plantar view the two rims of the trochlea met. III are parallel.

This form differs from the two recent mouse-birds *Colius* and *Urocolius*, because in both genera the trochlea met. III is raised compared to the surface of the shaft and its two rims are divergent in the distal direction. The outer extensor groove is wide and well marked; the plantar surface of the distal part is concave, it is bordered by two ridges which prolong in proximal direction the wings of the trochleae met. II and IV.

This form differs from the extinct genus *Primocolius*, from the Late Eocene of Quercy and Montmartre, France (Mourer-Chauviré *et al.*, 1988; Mayr 1998) because *Primocolius* has a strong longitudinal ridge on the dorsal surface of the shaft, and this ridge extends onto the trochlea met. III, the distal vascular foramen is situated in a deep outer extensor groove, the two wings of trochleae met. II and IV are prolonged by a ridge on each side of the shaft on the plantar surface. It is difficult to compare the Grillental form with the genus *Oligocolius*, from the Early Oligocene of Germany (Mayr, 2000) because an important morphological characteristic of this genus lies in the relative length of trochlea met. III compared to trochleae met. II and IV and these latter are not preserved in the Grillental specimen.

In the Early Miocene of Saint-Gérard-le-Puy, France, is known the genus *Limnatornis*, with the two species *L. paludicola* and *L. archiaci* (Milne-Edwards, 1867-71). The tarsometatarsus of the genus *Limnatornis* has not been described but two specimens are present in the collection of the Université Claude Bernard, Lyon 1. On these two specimens the trochlea met. IV is missing. In *Limnatornis* the distal part is also flat, both on the dorsal and plantar faces. The outer extensor groove is weakly indicated and the trochlea met. III is proximodistally short. The main difference between the Grillental form and *Lim-*

natornis is that in *Limnatornis* the two rims of the trochlea met. III are divergent in the distal direction, while they are almost parallel in GT 120'06.

In the Middle Miocene of La Grive-Saint-Alban and Sansan, France, is found the genus *Necrornis* with the species *N. palustris* (Milne-Edwards, 1867-71; Ballmann, 1969, Cheneval, 2000). From Sansan is known a distal part of a tarsometatarsus which has been illustrated by Milne-Edwards (1871, pl. 187, fig. 6-10) and by Cheneval (2000, fig. 24). This distal part is very flat and the trochlea met. III is short, but the outer extensor groove is long and deep (Cheneval, 2000, p. 370).

In conclusion it is not possible to ascribe the Grillental mousebird to one of the recent or fossil genera of Coliidae.

In Africa fossil Coliidae have been reported only from the Pliocene and belong to the recent genera *Colius* and *Urocolius* (Rich and Haarhoff, 1985; Haarhoff, 1993).

Measurements: Estimated distal width, 2.6; Width of shaft, 1.5; Depth of shaft, 0.7; Width trochlea met. III, 1.1.

Langental locality

Order Anseriformes

Family Anatidae

Subfamily Oxyurinae

Mionetta Livezey and Martin, 1988

Mionetta sp.

Figure 8, A, C, E-F

Material: Almost complete right tarsometatarsus, LT 188'03; right tibiotarsus, distal part, LT 254'99; cranial part of right scapula, LT 185'03; right humerus, distal part, LT 56'05.

Description and comparisons: The tarsometatarsus shows the morphological characteristics of the genus *Mionetta* as they have been described by Livezey and Martin (1988). The trochlea met. II does not show a groove in dorsal and medial views, and the groove is only visible in plantar view. In medial view this trochlea is globular and is prolonged plantarly by a wing. The proximal part is incompletely preserved and the calcaneal ridges are missing. In the genus *Dendrocygna*, there is a median ridge on the plantar surface of the proximal part of the shaft. This ridge starts from the third calcaneal ridge. In the genus *Mionetta* there is no median ridge but only a weakly indicated ridge starting from the first calcaneal ridge and following the medioplantar border of the shaft. In the Langental specimen, the surface of the shaft situated distally to the calcaneal ridges is flattened as in the genus *Mionetta*. If one estimates the missing part of the bone, the Langental tarsometatarsus was longer than that of *Mionetta blanchardi*.

Table 6: *Mionetta* sp. from Langental, comparison of the measurements of the tarsometatarsus with *Mionetta blanchardi* from Saint-Gérard-le-Puy, after Cheneval (1983b). (1) Distal diagonal after Bacher (1967).

Tarsometatarsus	<i>Mionetta</i> sp. LT 188'03	<i>Mionetta blanchardi</i> , mean Saint-Gérard-le-Puy
Total length	49 (estimated)	43.8
Width of shaft in the middle	4.9	4.5
Distal width	10.6	9.7
Distal depth	9.1	-
Width of trochlea met. III	4.3	-
Distal diagonal (1)	11.5	9.8

Measurements: Table 6

On the tibiotarsus, the condylus medialis has been eroded on the medial face, which makes it appear very thin and slightly oblique compared to the axis of the shaft. The cranial face is still covered of a very hard deposit and it is not possible to see the sulcus extensorius and the pons supratendineus. As indicated by Livezey and Martin (1988) for *M. blanchardi*, the condylus medialis extends farther anteriorly than the condylus lateralis and the distal end of the tibiotarsus is less centered on the shaft than in the genus *Dendrocygna*. It is not possible to take measurements but the size is very similar to that of *Mionetta blanchardi*.

The cranial part of the scapula is also very similar to the scapulae of *Mionetta blanchardi* from Saint-Gérard-le-Puy, France. The acromion is strongly projecting cranially and dorsally. It shows a small ridge on the facies lateralis. The tuberculum coracoideum has a hemispherical shape, it is distinctly visible on the facies costalis, and it is distinctly distal to the acromion.

Measurements: From the top of the acromion to the caudal part of the facies art. humeralis, 10.3

The humerus is strongly eroded and the two epicondyles, dorsalis and ventralis, have disappeared. The condylus ventralis is also very eroded, mainly on the caudal face. However the shape of the entepicondylar prominence (Howard, 1929) corresponds well to an Anseriform. In *Mionetta* the condylus ventralis has a flattened shape on the cranial face, on the proximal side, and it is very globular on the distal face. In cranial view the condylus ventralis is much more globular in the genus *Dendrocygna* than in the genus *Mionetta*. In the Langental specimen the shape corresponds well to *Mionetta*.

Measurements: Distal width, estimated, 14.5

Subfamily Anserinae
Anserinae indeterminate

Figure 10, C

Material: Right coracoid, LT 10'01

Description and comparisons: On this coracoid the processus acrocoracoideus is incompletely preserved, and the processus procoracoideus as well as the processus lateralis of the sternal part are missing. It can be ascribed to an Anatidae because the facies art. humeralis is very protruding laterally, the foramen n. supracoracoidei is absent, and on the dorsal face of the shaft there are two oblique intermuscular lines. It differs from the genera *Anas*, *Dendrocygna*, and *Mionetta*, because the shaft is proportionally much wider and dorsoventrally deeper, and because the intermuscular lines are much more oblique. It recalls the Anserinae coracoid found at Grillental but it is smaller.

Measurements: Total length measured on the medial side, estimated, 35; Width of the shaft in the middle, 4.6; Depth of the shaft in the middle, 3.4

Order Accipitriformes
Family Accipitridae
Accipitridae indeterminate

Figure 5, B-C

Material: Phalanx 2 of posterior digit III, LT 11'01; Phalanx 3 of posterior digit III or phalanx 4 of posterior digit IV, LT 13'94.

Description and comparisons: The phalanx 2 of posterior digit III differs from the recent genera *Aquila*, *Haliaeetus* and *Hieraetus* because at its proximal part the processus extensorius is very sharp while it is more rounded in these genera. By the general morphology of its distal articulation and by its measurements, it is more similar to the recent species *Hieraetus fasciatus*. The other phalanx is incom-

Table 7: Accipitridae indet. from Langental, measurements of the phalanx 2 of posterior digit III (LT 11'01) and of the phalanx 3 of posterior digit III or phalanx 4 of posterior digit IV (LT 13'94).

Posterior phalanges	LT 11'01	LT 13'94
Total length	14.1	27.5 (estimated)
Proximal width	6.9	8.1
Proximal depth	7.1	-
Distal width	6.1	6.4
Distal depth	5.2	6.2
Width in the middle	5.6	6.0
Depth in the middle	3.8	5.3

plete, its proximal articular surface is lacking. Its morphological characteristics are the small width of the distal articular surface in dorsal view (this part of the surface seems pinched) and the deep foveae lig. collateralium. By these characters it looks more similar to the genus *Hieraetus* than to the other genera.

Measurements: Table 7

Aves indeterminate

Material: Right femur, proximal part, very small, LT 72'97.

Fiskus locality

Order Anseriformes
Family Anatidae
Anatidae indeterminate
Figure 10, D

Material: Right scapula, cranial part, FS 32'01.

Description and comparisons: At its cranialmost part the acromion shows two tubercles, one quite at the top, and a second one more caudal, on the lateral surface. This form is different from the Oxyurinae which show a tubercle at the top and a ridge on the lateral face, and corresponds better to an Anatinae. The tuberculum coracoideum is globular and stands out on the lateral face as well as on the costal face. This scapula corresponds to a form smaller than the scapula from Langental LT 185'03.

Measurements: From the top of the acromion to the caudal part of the facies art. humeralis, 7.9

Palaeoecological significance

From the palaeoecological point of view the ostrich, which only occurs at Elisabethfeld, indicates a savannah environment, while two other forms, the cormorant and the small charadriiform, indicate an aquatic biotope. In the other localities one finds a very large majority of aquatic forms such as the Palaelodidae, the Oxyurinae, the Anserinae and the Anatinae. The Palaelodidae were birds related to modern flamingos but adapted to diving (Cheneval, 1983a). They were living in relatively deep water expanses (Cheneval, 1989). The presence of an aquatic environment is also attested by the study of other classes of animals which include freshwater snails, a few fishes, Pipidae frogs, and brachyodont mammals (M. Pickford, pers. comm.).

The galliforms are mainly terrestrial birds and for the accipitriforms it is not possible to know whether they preferentially fed on aquatic or terrestrial prey. Finally the present day Coliidae live in wooded areas, with scrub or light woodland, but they avoid dense forests (del Hoyo *et al.*, 2001).

Conclusions

These Northern Sperrgebiet avifaunas are very interesting faunistically. They show the first appearing of the genus *Struthio*, which ultimately spread very widely over the Old World (Mourer-Chauviré *et al.*, 1996b). Representatives of groups are also found which were present at the same time in other parts of the world, and which became extinct, such as the Palaelodidae, the genus *Mionetta*, or the small galliform *Palaeortyx*, which was present mainly in Europe. They include a representative of the Coliidae, which were very diverse and widespread in the European Tertiary, but which disappeared from Europe and survive at the present time only in Africa. They also include a primitive form of Anserinae, and some Phasianinae close to the genera *Gallus* or *Phasianus* which do not occur any longer in Africa.

Although the sediments have been carefully washed and sorted, in order to collect micromammal teeth, no passerine remains have been found and the only small bird remains is a fragment of tarsometatarsus of a Coliidae, or mousebird. This was also the case in the more recent locality of Arrisdrift, Namibia (age ca. 17 Ma, MN 4) (Mourer-Chauviré, 2003). Studies based on DNA imply a very early origin of Passeriformes in the Gondwanan continent (Ericson *et al.*, 2002; 2003). From a central southern origination point some groups would have reached New Zealand, some Australia, some the Old World, and some South America. In Europe, the first known passerines are from the lower part of the Oligocene of Southern France (Roux, 2002) and Germany (Mayr and Manegold, 2004). According to the hypothesis proposed by Ericson *et al.* (2002; 2003) the Old World Suboscines would have reached Africa and Asia through the Kerguelen Plateau and the Indian Plate before 80 Ma ago. Considering their apparent absence in the Early Miocene African localities, one may suppose that they first reached Asia and that they arrived relatively late in Africa. For the moment they are known in Africa only since the Middle Miocene, in the Beni Mellal locality, Morocco (Brunet, 1961; 1971), aged about 13 Ma, MN 7 (Pickford and Senut, 2003).

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References

- Agnolin, F.L. 2004. Revisión sistemática de algunas aves deseádenses (Oligoceno Medio) descritas por Ameghino en 1899. *Rev. Mus. Argentino Cienc. Nat.*, n. s., **6** (2), 239-244.
- Alvarenga, H.M.F. 1990. Flamingos Fósseis da Bacia de Taubaté, Estado de São Paulo, Brasil: Descrição de Nova Espécie. *An. Acad. Bras. Ci.*, **62**(4), 335-345.
- Ameghino, F. 1899. *Sinopsis geológico-paleontológica, en Segundo Censo nacional de la República argentina. Suplemento (Adiciones y Correcciones)*. Imprenta y Encuadernación "La Libertad", La Plata, 13 p.
- Bacher, A. 1967. *Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Schwäne und Gänse*. Inaugural Dissertation, Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin, München, 109 p.
- Baird, R.E. and Vickers-Rich, P. 1998. *Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia. *Alcheringa*, **22** (1/2), 135-152.
- Ballmann, P. 1969. Les oiseaux miocènes de La Grive-Saint-Alban (Isère). *Geobios*, **2**, 157-204.
- Baumel, J.J. and Witmer, L.M. 1993. Osteologia. In: J.J. Baumel (ed.), *Handbook of Avian Anatomy. Nomina Anatomica Avium*, 2nd Edition. Nuttall Ornith. Club, **23**, 45-132.
- Becker, J.J. 1987. Neogene Avian Localities of North America. *Smithsonian Research Monographs*, Smithsonian Instit. Press, Washington and London, 171 p.
- Brodkorb, P. 1961. Birds from the Pliocene of Juntura, Oregon. *Quart. Journ. Florida Acad. Sci.*, **24** (3), 169-184.
- Brodkorb, P. 1963. Catalogue of Fossil Birds: part 1 (Archaeopterygiformes through Ardeiformes). *Bull. Florida State Mus.*, **7** (4), 179-293.
- Brunet, J. 1961. Oiseaux. In: R. Lavocat *et al.*, Le gisement de Vertébrés miocènes de Beni Mellal (Maroc). *Notes et Mém. Serv. Géol. Maroc*, **155**, 105-108.
- Brunet, J. 1971. Oiseaux miocènes de Beni-Mellal (Maroc); un complément à leur étude. *Notes et Mém. Serv. géol. Maroc*, **31** (237), 109-111.
- Cheneval, J. 1983a. Révision du genre *Palaelodus* Milne-Edwards, 1863 (Aves, Phoenicopteriformes) du gisement aquitainien de Saint-Gérand-le-Puy (Allier, France). *Geobios*, **16** (2), 179-191.
- Cheneval, J. 1983b. Les Anatidae (Aves, Anseriformes) du gisement aquitainien de Saint-Gérand-le-Puy (Allier, France). *Symposium international Georges Cuvier* (Montbéliard, 1982), 85-98.
- Cheneval, J. 1984. Les oiseaux aquatiques

- (Gaviiformes à Anseriformes) du gisement aquitain de Saint-Gérard-le-Puy (Allier, France): Révision systématique. *Palaeovertebrata*, **14** (2), 33-115.
- Cheneval, J. 1989. Fossil bird study and paleoecological and paleoenvironmental consequences: Example from the Saint-Gérard-le-Puy deposits (Lower Miocene, Allier, France). *Palaeogeogr., Palaeoclimat., Palaeoecol.*, **73**, 295-309.
- Cheneval, J. 2000. L'avifaune de Sansan. In: L. Ginsburg (ed.). La faune miocène de Sansan et son environnement. *Mém. Mus. natn. Hist. nat.*, **183**, 321-388.
- Cheneval, J. and Adrover, R. 1995. L'Avifaune du Miocène supérieur d'Aljezar B (Los Aljezars, Province de Teruel, Espagne). Systématique et paléoécologie. *Paleontologia i Evolucio*, Sabadell, **26-27** (1993), 133-144.
- Ericson, P.G.P., Christidis, L., Cooper, A., Irested, M., Jackson, J., Johansson, U.S. and Norman, J.A. 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. Royal Soc. London, B* (2002) **269**, 235-241.
- Ericson, P.G.P., Irested, M. and Johansson, U.S. 2003. Evolution, biogeography, and patterns of diversification in passerine birds. *J. Avian Biol.*, **34**, 3-15
- Göhlich, U.B. and Mourer-Chauviré, C. 2005. Revision of the Phasianidae (Aves: Galliformes) from the Lower Miocene of Saint-Gérard-le-Puy (Allier, France). *Palaeontology*, **48** (6), 1331-1350.
- Haarhoff, P.J. 1993. Latest Pliocene Mousebirds (Aves, Coliidae) from Olduvai Gorge, Tanzania. *Annals of the South African Museum*, **103** (4), 191-211.
- Harrison, C.J.O. 1980. Fossil birds from Afrotropical Africa in the collection of the British Museum (Natural History). *Ostrich*, **51**, 92-98.
- Harrison, C.J.O. and Walker, C.A. 1976. Cranial material of Oligocene and Miocene flamingos: with a description of a new species from Africa. *Bull. Brit. Mus. nat. Hist., Geol.*, **27** (4), 305-314.
- Harrison, T. and Msuya, C.P. 2005. Fossil struthionid eggshells from Laetoli, Tanzania: Taxonomic and biostratigraphic significance. *Journal of African Earth Sciences*, **41**, 303-315.
- Heizmann, E.P.J. and Hesse, A. 1995. Die mitelmiozänen Vogel- und Säugetierfaunen des Nördlinger Ries (MN 6) und des Steinheimer Beckens (MN 7) – ein Vergleich. *Courier Forschungsinstitut Senckenberg*, **181**, 171-185.
- Howard, H. 1929. The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool.*, Berkeley Calif., **32** (2), 301-394.
- Howard, H. 1971. Pliocene avian remains from Baja California. *Contributions in Science, Los Angeles County Museum*, **217**, 17 p.
- del Hoyo, J., Elliott, A. and Sargatal, J. eds. 1994. *Handbook of the Birds of the World, vol. 2. New World Vultures to Guinea-fowl*. Lynx Edicions, Barcelona, 638 p.
- del Hoyo, J., Elliott, A. and Sargatal, J. eds. 2001. *Handbook of the Birds of the World, vol. 6. Mousebirds to Hornbills*. Lynx Edicions, Barcelona, 589 p.
- Kessler, E. 1992. Review of the Neogene waterfowl (Aves: Anatidae) of Eastern Paratethys. *Studia Univ. Babeş-Bolyai, Biologica*, **37** (2), 47-54.
- Kurochkin, Ye.N. 1968. New Oligocene birds from Kazakhstan. *Paleontological Journal*, **1**, 83-90.
- Lambrecht, K. 1929. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere. 4. *Stromeria fayumensis* n.g., n.sp., die Kontinentale Stammform der Aepyornithidae, mit einer Übersicht über die fossilen Vögel Madagaskars und Afrikas. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, Neue Folge, **4**, 4-18.
- Lambrecht, K. 1931. Cygnopterus und Cygnavus, zwei fossile Schwäne aus dem Tertiär Europas. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, **7** (31), 6 p.
- Lambrecht, K. 1933. *Handbuch der Palaeornithologie*. Borntraeger Verlag, Berlin, 1029 p.
- Leonard, L.M., Dyke, G.J. and Walker, C.A. 2006. New specimens of a fossil ostrich from the Miocene of Kenya. *Journal of African Earth Sciences*, **45**, 391-394.
- Livezey, B.C. 1996. A phylogenetic analysis of geese and swans (Anseriformes: Anserinae), including selected fossil species. *Systematic Biology*, **45** (4), 415-450.
- Livezey, B.C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. *Zool. Journal of the Linnean Society*, **121**, 361-428.
- Livezey, B.C. and Martin, L.D. 1988. The systematic position of the Miocene anatid *Anas* [?] *blanchardi* Milne-Edwards. *Journ. Vertebr. Paleont.*, **8** (2), 196-211.
- Mayr, G. 1998. "Coraciiforme" und "Piciforme" Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg*, **205**, 101 p.
- Mayr, G. 2000. A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. *Journal für Ornithologie*, **141**, 85-92.
- Mayr, G. 2001. A cormorant from the late Oligocene of Enspel, Germany (Aves, Pelecaniformes, Phalacrocoracidae). *Senckenbergiana lethaea*, **81** (2), 329-333.
- Mayr, G. 2005. The Paleogene fossil record of birds in Europe. *Biological Reviews*, **80**, 515-542.
- Mayr, G. and Manegold, A. 2004. The oldest Euro-

- pean fossil songbird from the early Oligocene of Germany. *Naturwissenschaften*, **91** (4), 173-177.
- Mayr, G. and Smith, R. 2002. Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **72**, 139-150.
- Miller, A.H. 1944. An avifauna from the Lower Miocene of South Dakota. *University of California Publications, Bulletin of the Department of Geological Sciences*, **27** (4), 85-100.
- Miller, L. 1950. A Miocene flamingo from California. *The Condor*, **52**, 69-73.
- Miller, L. 1952. The avifauna of the Barstow Miocene of California. *The Condor*, **54** (5), 296-301.
- Milne-Edwards, A. 1863. Sur la distribution géologique des oiseaux fossiles et description de quelques espèces nouvelles. *C. R. Acad. Sci.*, Paris, **56**, 1219-1222.
- Milne-Edwards, A. 1867-71. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*, Paris, Victor Masson et Fils, t. 1: 474 p., t. 2: 627 p.
- Mivart, St. G. 1874. On the Axial Skeleton of the Ostrich (*Struthio camelus*). *Transactions of the Zoological Society*, VIII, part VII: 385-451.
- Mlíkovský, J. 1998. Early Miocene birds of Brestany, Czech Republic. *Casopis Národního muzea, Radapřírodovědná*, **167** (1-4), 103-109.
- Mlíkovský, J. 2002. *Cenozoic Birds of the World. Part 1: Europe*. Praha, Ninox Press, 406 p.
- Mlíkovský, J. 2003. Early Miocene birds of Djebel Zelten, Libya. *Casopis Národního muzea, Radapřírodovědná*, **172** (1-4), 114-120.
- Mlíkovský, J. and Svec, P. 1986. Review of the Tertiary Waterfowl (Aves: Anseridae) of Asia. *Vestník Československé Společnosti zoologické*, **50**, 249-272.
- Mourer-Chauviré, C. 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. II. Oiseaux. *Palaeontographica*, Abt. A, **205**, 29-50.
- Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and Biostratigraphy. *Natural History Museum of Los Angeles County, Science Series*, **36**, 67-95.
- Mourer-Chauviré, C. 2003. Birds (Aves) from the Middle Miocene of Arrisdrift (Namibia). Preliminary study with description of two new genera: *Amanuensis* (Accipitriiformes, Sagittariidae) and *Namibiavis* (Gruiformes, Idiornithidae). *In: Geology and Palaeobiology of the Central and Southern Namib. Vol. 2: Palaeontology of the Orange River Valley, Namibia* (M. Pickford and B. Senut Eds.). *Memoirs of the Geological Survey of Namibia*, **19**, 103-113.
- Mourer-Chauviré, C., Berthet, D. and Huguency, M. 2004. The late Oligocene birds of the Créchy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). *Senckenbergiana lethaea*, **84** (1/2), 303-315.
- Mourer-Chauviré, C., Senut, B., Pickford, M. and Mein, P. 1996a. Le plus ancien représentant du genre *Struthio* (Aves, Struthionidae), *Struthio coppensi* n. sp., du Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, série II a, **322**, 325-332.
- Mourer-Chauviré, C., Senut, B., Pickford, M., Mein, P. and Dauphin, Y. 1996b. Ostrich legs, eggs and phylogenies. *South Afr. J. Sci.*, **92**, 492-495.
- Noriega, J.I. 1995. The avifauna from the "Mesopotamian" (Ituzaingó Formation; Upper Miocene) of Entre Rios Province, Argentina. *Courier Forschungsinstitut Senckenberg*, **181**, 141-148.
- Olson, S.L. 1985. The fossil record of birds. *Avian Biology*, **8**, 79-252.
- Paicheler, J.C., Broin, F.de, Gaudant, J., Mourer-Chauviré, C., Rage, J.C. and Vergnaud-Grazzini C. 1978. Le bassin lacustre miocène de Beskonak (Anatolie, Turquie) : Géologie et introduction à la paléontologie des Vertébrés. *Geobios*, **11** (1), 43-65.
- Pickford, M. 1986. Cainozoic Palaeontological Sites of Western Kenya. *Münchner Geowiss. Abh.*, **8**, 151 p.
- Pickford, M. and Senut, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. *In: Geology and Palaeobiology of the Central and Southern Namib. Vol. 2: Palaeontology of the Orange River Valley, Namibia* (M. Pickford and B. Senut Eds.). *Memoirs of the Geological Survey of Namibia*, **19**, 1-22.
- Rasmussen, D.T., Olson, S.L. and Simons, E.L. 1987. Fossil birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *Smiths. Contrib. Paleobiol.*, **62**, IV + 20 p.
- Rich, P.V. 1972. A fossil avifauna from the Upper Miocene Beglia formation of Tunisia. *Notes Serv. géol. Tunis*, **35** (5), 29-66.
- Rich, P.V. and Haarhoff, P.J. 1985. Early Pliocene Coliidae (Aves, Coliiformes) from Langebaanweg, South Africa. *Ostrich*, **56**, 20-41.
- Roux, T. 2002. Deux fossiles d'oiseaux de l'Oligocène inférieur du Luberon. *Courier scient. Parc natur. Région. Luberon*, **6**, 38-57.
- Senut, B., Pickford, M. and Dauphin, Y. 1995. Découverte d'œufs de type "Aepyornithoïde" dans le Miocène inférieur de Namibie. *C. R. Acad. Sci. Paris*, série II a, **320**, 71-76.
- Shufeldt, R.W. 1915. Fossil birds in the Marsh collection of Yale University. *Trans. Connec. Acad. Arts Sci.*, **19**, 1-110.
- Stidham, T.A. 2007. Preliminary assessment of the Late Miocene avifauna from Lemudong'o, Kenya. *In: Monography of the Late Miocene*

- mammalian-dominated fossil site of Lemudong'o, Southern Kenya. *Kirtlandia*, **56**, 173-176.
- Svec, P. 1981. Lower Miocene birds from Dolnice (Cheb Basin), western Bohemia, part II. *Casopis pro mineralogii a geologii*, **26** (1), 45-56.
- Worthy T.H. and Lee M.S.Y. 2008. Affinities of the Miocene waterfowl (Anatidae: *Manuherikia*, *Dunstanetta* and *Miotadorna*) from the St Bathans fauna, New Zealand. *Palaeontology*, 2008, 1-32.
- Worthy, T.H., Tennyson, A.J.D., Jones, C., McNamara, J.A. and Douglas, B.J. 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology*, **5** (1), 1-39.