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Cécile Mourer-Chauviré¹, Martin Pickford^{2, 3} and Brigitte Senut³

The first Palaeogene Galliform from Africa

1 Université de Lyon, F-69622, Lyon, France ; Université Lyon 1, Villeurbanne; CNRS, UMR 5125, Paléoenvironnements et Paléobiosphère

2 Collège de France, Chaire d'évolution des climats et de l'océan

3 Muséum National d'Histoire Naturelle, Département Histoire de la Terre, CNRS, UMR 7207, Case postale 38, 8, rue Buffon, 75005 Paris

Corresponding author: Cécile Mourer-Chauviré

e-mail: cecile.mourer@univ-lyon1.fr

Tel : 33 (0)6 72 57 04 75

Fax: 33 (0)4 72 44 83 82

Abstract

An almost complete tarsometatarsus from the middle Eocene locality of Silica South, Sperrgebiet, Namibia, is attributed to the order Galliformes. This is the earliest record of the order in Africa. It belongs to a stem group galliform and differs from the Recent families. It is compared with Mesozoic birds from America, and Gallinuloididae, Quercymegapodiidae and Paraortygidae from Europe and the Americas. Because the specimen is an isolated bone, damaged proximally, we do not attribute it to a family, but it is clear that it represents a new genus and species of galliform bird, which we name *Namaortyx sperrgebietensis*.

Keywords Fossil bird, Galliform, Eocene, Namibia, stem lineage, *Namaortyx sperrgebietensis*

Zusammenfassung

Der erste paläogene Hühnervogel aus Afrika

Ein nahezu vollständiger Tarsometatarsus aus der lutetischen Fundstelle Silica South, Sperrgebiet, Namibia, wird der Ordnung Galliformes zugeordnet. Das Fossil ist der älteste Nachweis dieser Ordnung in Afrika. Das Material wird mit mesozoischen Vögeln von Amerika verglichen sowie mit den Gallinuloididae, Quercymegapodiidae und Paraortygidae aus Europa und Amerika. Weil das Exemplar ein isolierter, proximal beschädigter Knochen ist, ordnen wir ihn nicht einer Familie zu, aber es ist offensichtlich, dass es eine neue Gattung und Art galliformer Vögel repräsentiert, die wir *Namaortyx sperrgebietiae* nennen.

Introduction

During the Palaeogene the order Galliformes is represented in the Northern hemisphere, as well as in South America, by several extinct families which belong to stem group galliforms, while the recent families, the crown group galliforms, are unambiguously known only from the Late Oligocene for the Phasianidae and Megapodiidae, and later for the other families (Mayr 2009). Until now no galliform had ever been recorded for the Palaeogene of Africa, and the earliest galliforms known so far from this continent were the Early Miocene phasianids from the localities of Elisabethfeld and Grillental, Northern Sperrgebiet, Namibia (Mourer-Chauviré 2008).

The tarsometatarsus discovered at Silica South can be attributed to the order Galliformes because it presents on the plantar face two well developed fossae, on both sides of the hypotarsus, and because on the plantar face of trochlea met. III the lateral ridge protrudes farther proximally than the medial ridge, which is a characteristic feature of the Galliformes (Mayr 2000).

The locality of Silica South was discovered in 2008 by the Namibia Palaeontology Expedition. It is situated in the Sperrgebiet, in the southwest of Namibia, at approximately 27° 16' S and 15° 25' E (Pickford et al. 2008a). It is an almost circular outcrop of well bedded freshwater limestone. The basal layers of carbonates have been partly silicified and have yielded vertebrate fossils. The dating of this locality is founded on the mammalian fauna which includes hyracoids and rodents. Its age is probably Early Lutetian (Pickford et al. 2008b).

Methods

Osteological terminology follows Baumel and Witmer (1993) and when necessary Howard (1929). The fossil specimen is deposited in the Geological Survey of Namibia, Windhoek, Namibia.

Results

Systematic paleontology

Order Galliformes TEMMINCK 1820

Family incertae sedis

Genus *Namaortyx* nov.

Type species. *Namaortyx sperrgebietensis*

Diagnosis. Tarsometatarsus with splayed trochleae. Trochlea met. II slightly shorter than trochlea met. IV. Crista medianoplantaris reaching the wing of trochlea met. IV and not forked at its distal end. Shaft wide and flattened in section. In distal view trochleae disposed along an asymmetrical curve and trochlea met. III obliquely oriented compared to the dorsal surface of the shaft.

Derivatio nominis. *Nama*, from the region of discovery, and *ortyx*, Greek name for a quail.

Species *Namaortyx sperrgebietensis* nov.

Fig. 1a-c

Holotype. n° SS 8'08, right tarsometatarsus, almost complete.

Type locality. Silica South, Sperrgebiet, Namibia

Age. Middle Eocene, probably Early Lutetian, about 47-49 million years ago.

Diagnosis. As for the genus

Derivatio nominis. For the Sperrgebiet, German name meaning "Forbidden Area"

Description and Comparisons

Right tarsometatarsus. The proximal articular surface and a part of the shaft, which is obliquely broken, are missing. The lateral side is more completely preserved than the medial side. The shaft is wide and flattened. At the distal part trochleae met. II and IV are splayed. On the dorsal surface the outer extensor groove (Howard 1929) is weakly expressed. The opening of the distal vascular foramen is large and situated just proximally to the lateral intertrochlear notch. The dorsal surfaces of trochleae met. II and III are slightly eroded. Trochlea met. IV is incompletely preserved but its wing is present, while the wing of trochlea met. II is missing. Trochlea met. III is the longest, then comes trochlea met. IV, while trochlea met. II is slightly shorter than trochlea met. IV.

On the plantar surface, the hypotarsus is not preserved. The two fossae parahypotarsales, characteristic of the Galliformes, are present on each side of the crista medianoplantaris. Only the lateral proximal vascular foramen can be seen. At the distal part, the crista medianoplantaris reaches the wing of trochlea met. IV and does not fork. The crista plantaris medialis reaches the level of fossa metatarsi I, then follows the medial border of this fossa, then reaches the wing of trochlea met. II. The fossa supratrochlearis plantaris is wide and shallow, and does not show any ridge, but only a small groove which joins the distal vascular foramen. Fossa met. I is very proximodistally elongated, which indicates that the processus articularis tarsometatarsalis was elongated. The lateral rim of trochlea met. III protrudes farther proximally than the medial rim. In distal view, the trochleae are not disposed along an arc, but along an asymmetrical curve, the apex of which corresponds to the dorsolateral angle of the bone. Dorsoplantarly trochlea met. III is oriented not perpendicularly to the dorsal surface of the shaft, but obliquely.

Comparison with the Recent galliform families

The tarsometatarsus from Silica South differs from the Recent families Numididae, Odontophoridae, and Phasianidae (including the Arborophilinae, Phasianinae, Tetraoninae, Meleagridinae, Coturnicinae, Pavoninae, and Gallininae) because in these families trochleae met. II and met. IV are not splayed. In addition trochlea met. II is distinctly shorter than trochlea met. IV and is plantarly displaced (Ksepka 2009). It also differs from the Cracidae because in the Cracidae the trochleae are not splayed but situated close together (Ksepka 2009). It is more similar to the Megapodiidae because it is the only Recent galliform family in

which the trochleae are splayed, and in which trochlea met. II is almost the same length as trochlea met. IV (Ksepka 2009). However it differs from it because in distal view the trochleae are disposed along an asymmetrical curve, and because trochlea met. III is oriented obliquely compared to the dorsal surface of the shaft. By comparison with Eocene stem group Galliformes, the characters “splayed trochleae” and “trochlea met. II almost the same length as trochlea met. IV” present in the Namibian fossil can be identified as the plesiomorphic condition for Galliformes.

Comparison with Mesozoic and early Tertiary forms

In the late Cretaceous of North America the genus *Palintropus* has been tentatively assigned to Galliformes (Hope 2002) but Longrich (2009) has described further material of this genus and assumed that it does not belong to the Neornithes. The tarsometatarsus of this genus is unknown. Clarke (2004) has attributed to the Pangalliformes a distal tarsometatarsus which was the holotype of the species *Ichthyornis lentus* (Marsh 1877), from the Upper Cretaceous of Texas. This tarsometatarsus is attributed to the new taxon *Austinornis*. Unfortunately the provenance of this material is not accurately known. In *Austinornis* the lateral rim of trochlea met. III extends farther proximally than the medial rim. On the plantar surface there are two intermuscular lines. One runs along the lateral edge of the shaft; the second, situated more medially, corresponds to the crista medianoplantaris. It seems that it does not fork (see Clarke 2004, fig. 17). It differs from *Namaortyx* because its trochlea met. II is much shorter and more plantarly displaced. Hwang et al. (2010) have reported a very small galliform from the late Palaeocene or early Eocene of Mongolia, but it is only known by a fragment of humerus. Lindow and Dyke (2007) have attributed to Galliformes incertae sedis a pair of fossilized imprints of feet, from the Lower Eocene Fur Formation of Denmark. The authors write that the trochleae “for digits II and III are approximately equally extended distally” (p. 62) but it is unlikely and they probably intended to write “for digits II and IV”. These tarsometatarsi differ from *Namaortyx* by their very elongate and slender shapes.

Comparison with the Gallinuloididae

Gallinuloididae are known from the early and middle Eocene, with *Gallinuloides wyomingensis* from the early Eocene of the United States, *Paraortygoides radagasti*, from the early Eocene of England, and *P. messelensis*, from the middle Eocene of Germany (Mayr 2000, 2006, 2008, 2009; Mayr and Weidig 2004; Dyke and Gulas 2002; Ksepka 2009; Weidig 2010).

In both specimens of *Gallinuloides wyomingensis* it is not possible to see the plantar surface of the tarsometatarsi, but in distal view the trochleae are disposed along a curved line, and trochlea met. II is considerably shorter than trochlea met. IV (Weidig 2010) while in *Paraortygoides messelensis* trochlea met. II is slightly shorter than trochlea met. IV (Mayr 2000). In *Paraortygoides messelensis* three ridges are present on the plantar surface of the tarsometatarsus, a medial one, a lateral one, and a crista medianoplantaris which forks at the level of fossa met. I. It forks and reaches both wings of trochleae met. II and IV, while in *Namaortyx* it does not fork and reaches only the wing of trochlea met. IV. On the distal part

of tarsometatarsus attributed to *P. radagasti*, the crista medianoplantaris is not visible (see Dyke and Gulas 2002, fig. 2, F and fig. 4, B, and Mayr 2009, fig. 6.4, i).

In the genera *Gallinuloides* and *Paraortygoides* the processus articularis of os metacarpale I is very short.

The genus *Namaortyx* differs from the Gallinuloididae by the wide and flattened shape of the shaft, the disposition of the trochleae along an asymmetrical curve, the presence of an unforked crista medianoplantaris, and the presence of a very elongated fossa articularis met. I.

Comparison with the Quercymegapodiidae

Quercymegapodiidae have been known from the Middle Eocene (localities of Le Bretou and Lavergne, Phosphorites du Quercy, France), to the late Oligocene or early Miocene of Brazil, and the early Miocene of France, with the genera *Quercymegapodius* and *Ameripodius* (Mourer-Chauviré 1988, 1992, 2000, 2006; Alvarenga 1988, 1995). In the locality of Le Bretou a very small galliform was referred to the family Gallinuloididae and tentatively attributed to the genus *Taoperdix* (Mourer-Chauviré 1988, 1992, 2006), because the genus *Taoperdix* was then considered to be a Gallinuloididae (Brodkorb 1964; Ballmann 1969). More recently Mayr and Weidig (2004) have shown that the type species of *Taoperdix*, *T. pessieti*, is not a Gallinuloididae and Mayr (2009) suggests that it may be a Paraortygidae. The descriptions of new specimens of Gallinuloididae (Mayr 2000; Mayr and Weidig 2004) show that this very small galliform from Quercy does not correspond to a Gallinuloididae but to a Quercymegapodiidae. The form from Le Bretou cannot be compared directly to the small species *Q. brodkorbi*, as the tarsometatarsus of the latter species is not known. When compared to the large species *Q. depereti*, for which the tarsometatarsus is known, the form from Le Bretou is metrically slightly smaller than *Q. brodkorbi*. It is designated here as *Quercymegapodius cf. brodkorbi*.

In *Quercymegapodius*, as in *Namaortyx*, the distal trochleae are splayed. *Quercymegapodius* shows the same disposition of the crista medianoplantaris, which does not fork, and of the medial plantar ridge. The fossa supratrochlearis plantaris is wide and shallow. The distal vascular foramen has a wide opening, fossa met. I is very elongate. *Namaortyx* differs from *Quercymegapodius* by the wide and flattened shape of the shaft, and by the disposition of the trochleae in distal view.

Few morphological details are visible on the tarsometatarsus of *Ameripodius granivora* (Alvarenga 1988), and the tarsometatarsus is not preserved in *A. silvasantosi* (Alvarenga 1995), both from Taubaté, Brazil, but the tarsometatarsus is known in *A. alexis*, from the early Miocene of Saint-Gérand-le-Puy, France (Mourer-Chauviré 2000). On the plantar surface the crista medianoplantaris is well marked and reaches the wing of trochlea met. II. On adult specimens it shows a very slight bifurcation, laterally directed, at the level of the distal part of fossa met. I, but this bifurcation is absent on a subadult specimens. The *Namaortyx* tarsometatarsus differs from that of *Ameripodius* by its short and wide shaft, while it is long and slender in *Ameripodius*, and by the disposition of the trochleae.

Comparison with the Paraortygidae

The Paraortygidae are known in the middle and late Eocene of the Phosphorites du Quercy, France, and the early Oligocene of Germany (Mourer-Chauviré 1992; Fischer 1990, 2003). They are also probably present in the late Eocene and the early Oligocene of the United States (Mayr 2009). *Namaortyx* differs from the Paraortygidae because in the latter, trochlea met. II is situated farther in the proximal direction, and it is strongly plantarly displaced. On the dorsal surface, the distal vascular foramen is situated at the end of a deep outer extensor groove, while this groove is weakly indicated in *Namaortyx*. On the plantar side, the displacement of trochlea met. II leads to a narrowing of the fossa supratrochlearis plantaris, a large part of which is occupied by the wide opening of the distal vascular foramen. Fossa met. I extends distally onto the proximal part of the wing of trochlea met. II. The crista medianoplantaris is situated closer to the lateral plantar ridge than to the medial plantar ridge, and it forks at its distal end.

Discussion

Namaortyx shows some similarities with the extinct genus *Quercymegapodius*, and the recent genus *Megapodius*, but these similarities are probably plesiomorphic characteristics for the Galliformes. Some of them are also present in *Austinornis*, a probable galliform from the late Cretaceous of Texas (Clarke 2004). It would be very interesting to have other skeletal elements which could be associated with this tarsometatarsus, such as the coracoid or the humerus. In the absence of these elements we prefer to leave the genus *Namaortyx* in Family incertae sedis. Cracraft (2001) put forward the hypothesis that the galliforms would have diversified on the southern supercontinent Gondwana (South America, Africa, India, and Australia). This hypothesis is founded on the fact that, amongst the Recent crown group galliforms, the two most primitive families, i. e. the Megapodiidae and the Cracidae, are predominantly distributed in the southern Hemisphere. However galliforms are not present in the Palaeocene and early Eocene fossiliferous localities known in India, Australia, and South America (Mayr et al. 2007; Mayr 2009). In Africa the only fossil birds described so far in the Palaeocene and early Eocene belong to marine families (Bourdon 2006, Bourdon et al. 2005, 2008a, 2008b). The occurrence of a galliform in the early middle Eocene of Namibia does not bring an argument in favour of Cracraft's hypothesis because primitive stem group galliforms were present in the Northern Hemisphere as early as the Cretaceous (*Austinornis*), the late Palaeocene or early Eocene of Mongolia (Hwang et al. 2010), and the early Eocene of Europe and North America (Gallinuloididae) (Mayr 2009). The fossil record of the galliforms is still considerably older in the Northern Hemisphere than it is in Gondwana. Crowe et al. (2006) from morphological and molecular data of the Recent forms provided strong arguments for an African origin of the Numididae, Odontophoridae, and Phasianidae, but, again, the Namibian form does not bring an argument in favour of this hypothesis because it belongs to a stem group galliform and cannot be considered as an early representative of a crown group galliform.

Measurements (in mm) of the n° SS 8'08, right tarsometatarsus, type specimen of *Namaortyx sperrgebietensis*.

Total length (as preserved), 54.2; total length estimated, ca. 56; width of shaft in the middle, 6.2; maximum depth on the lateral side, 4.2; maximum depth of the medial side, 3.4; distal width as preserved, 11.9; depth of the lateral rim of the trochlea met. III, 6.7; depth of the trochlea met. IV including the wing, 8.0

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Caption of figure

Fig. 1a-c *Namaortyx sperrgebietensis*, nov. gen. nov. sp. **a** Right tarsometatarsus, n° SS 8'08, holotype, dorsal view. **b** Idem, plantar view. **c** Idem, distal view. Scale bars equal 1 cm