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# A new taxon of stem group Galliformes and the earliest record for stem group Cuculidae from the Eocene of Djebel Chambi, Tunisia

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**Abstract** — A distal tarsometatarsus and a fragment of carpometacarpus of a small galliform, the size of a recent quail, have been found in the late Early or early Middle Eocene of Chambi, in Tunisia. Although a large number of stem group representatives of Galliformes are known from the Eocene of the Northern Hemisphere, and one from the middle Eocene of Namibia, the taxon from Chambi differs from them and is described as a new genus and species. A very small zygodactyl form, represented by three distal tarsometatarsi, is also present in the same locality. This form, described as a new genus and species, is a stem group representative of the recent family Cuculidae. It shows a plesiomorphic morphology compared to the recent members of the Cuculidae, but it is, however, more derived than the younger genus *Eocuculus*. It is the earliest Cuculidae known so far.

**Key words:** fossil bird, Eocene, Djebel Chambi, Tunisia, Galliformes, Cuculiformes

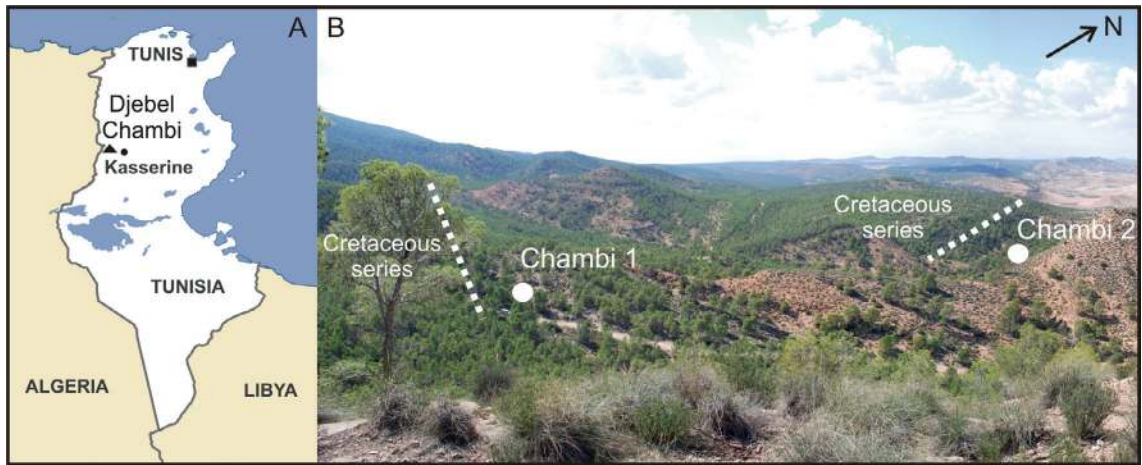
## Introduction

The Djebel Chambi in central Tunisia is famous for having yielded a rich faunal and floral assemblage (HARTENBERGER *et al.* 2001), including indeterminate amphibians and squamates, a paradedtid marsupial, and several eutherians among which there are chiropterans, a putative erinaceomorph, a strepsirrhine primate, a zegdoumyid rodent, a stem macroscelidid, a hyracoid, and charophytes. HARTENBERGER *et al.* (2001) have proposed that the fauna is Early Eocene in age, roughly contemporaneous with that of the Glib Zegdou in Algeria. However, the age of Chambi and Glib Zegdou faunas have long remained a matter of discussion, and current data rather indicate a late Early or early Middle Eocene age,

unfortunately without more precision (e. g. ADACI *et al.* 2007; SEIFFERT 2010). Recent fieldwork on the Djebel Chambi has led us to the recovery of a new vertebrate locality (Chambi 2) in the same lacustrine limestone strata as the former site (here named Chambi 1) (Fig. 1). Careful acid etching of the fossiliferous limestone from Chambi 1 and 2 has yielded numerous vertebrate elements, among them the few avian elements described here.

## Material and methods

The anatomical terminology follows BAUMEL & WITMER (1993), and when necessary HOWARD (1929). The fossil material is deposited in the



**FIGURE 1.** A, Map of Tunisia, showing the location of the Djebel Chambi Mountain near the city of Kasserine. B, Northern flank of the Djebel Chambi outcrops, section to the northwest, showing the sites of Chambi 1 and Chambi 2. The site of Chambi 1 corresponds to the locality of HARTEN-BERGER *et al.* (2001, and references therein) (see also RAVEL *et al.* 2013, and BENOIT *et al.* 2013); Chambi 2 was discovered in 2009. Only 650 m separate the two sites; both are located in the same stratigraphic position and have delivered the same mammalian assemblage, indicating a late Early or early Middle Eocene age.

collection of the “*Office National des Mines de Tunis*”, Tunisia. Acronyms: UCBL, Université Claude Bernard, Lyon 1, France; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.; ONM, Office National des Mines de Tunis, Tunisia.

### Systematic Paleontology

**Aves** LINNAEUS, 1758

**Order Galliformes** TEMMINCK, 1820

**Family incertae sedis**

***Chambiortyx* nov. gen.**

**Type species:** *Chambiortyx cristata* nov. spec.

**Diagnosis:** Distal part of tarsometatarsus with trochlea met. IV extending distally to about the half of trochlea met. III; trochlea met. II slightly shorter than trochlea met. IV; presence of a ridge starting from trochlea met. II and extending proximally along the boundary between the dorsal and medial sides of the shaft; foramen vasculare distale wide and not situated at the end of an outer extensor groove; trochlea met. II slightly plantarly deflected; trochleae arranged along a weakly arched curve in distal view.

**Derivatio nominis:** Chambi, from Djebel

Chambi in Tunisia, and *ortyx*, Greek word for a quail.

***Chambiortyx cristata* nov. spec.**

(Figs 2A–D)

**Holotype:** CB1-548 left tarsometatarsus, distal part.

**Paratype:** CB1-549 left carpometacarpus, fragment of distal part.

**Type locality:** Chambi 1, Central Tunisia, Kasserine district.

**Age:** Late Early or early Middle Eocene.

**Diagnosis:** As for the genus.

**Derivatio nominis:** *cristata*, Latin word indicating the presence of a characteristic ridge.

**Measurements:** Tarsometatarsus, holotype: Length as preserved, 7.6 mm; width of shaft at the level of the break, 2.8 mm; depth of shaft at the same level, 1.3 mm; distal width, 5.3 mm; distal depth, 3.7 mm; width of tr. met. III, 2.0 mm; depth of tr. met. III, 2.3 mm. Carpometacarpus, paratype: Length as preserved, 8.7 mm; dorsoventral dimension of the major metacarpal at the level of the break, 1.8 mm; craniocaudal dimensions of the major metacarpal at the same level, 1.5 mm; dorsoventral dimension of the distal end, 1.8 mm; craniocaudal dimension of the distal end, 3.1 mm.

**Description and comparisons — Tarsometatarsus** (Fig. 2A–C)

On the distal part of the tarsometatarsus, trochlea met. III is relatively elongate, trochlea met. IV extends distally to a little less than the middle of trochlea met. III, and trochlea met. II is slightly shorter than trochlea met. IV. Trochlea met. II is slightly plantarly displaced. The foramen vasculare distale is wide and elongate. There is no visible outer extensor groove (HOWARD 1929). Proximally compared to the opening of the distal foramen, the dorsal face of the shaft is practically flat. On the medial side of the shaft, proximally compared to trochlea met. II, there is a longitudinal ridge situated at the boundary between the cranial and the medial faces.

On the plantar side, although the lateral rim of trochlea met. III is incomplete; it is possible to see that it extends proximally farther than the medial rim. The fossa supratrochlearis plantaris is relatively narrow and shallow. It is included between two ridges, a medial one which prolongs the proximal part of trochlea met. II, and a lateral one which prolongs the proximal part of trochlea met. IV. The wings of both trochleae met. II and IV are incompletely preserved. The distal vascular foramen is widely open and is situated close to the incisura intertrochlearis lateralis. The canalis interosseus distalis is absent.

In distal view the trochleae are arranged along a weakly arched curve. The medial rim of trochlea met. III advances more dorsally than the lateral rim, and the lateral rim advances more plantarly than the medial rim.

**Comparisons with recent galliforms**

*Chambiortyx* differs from the Phasianidae because in this family trochlea met. II is always more strongly plantarly displaced. In the Megapodiidae, the trochleae are more splayed. In *Megapodius* there are also two ridges on the plantar face, but it differs in the morphology of trochlea met. II, which appears very globular on the dorsal face and extends farther distally than trochlea met. IV. In the Cracidae, trochlea met. II extends slightly farther distally than trochlea met. IV; the distal part of the tarsometatarsus is rather flat; on the plantar face, the two ridges, medial and lateral, are present but they are only slightly

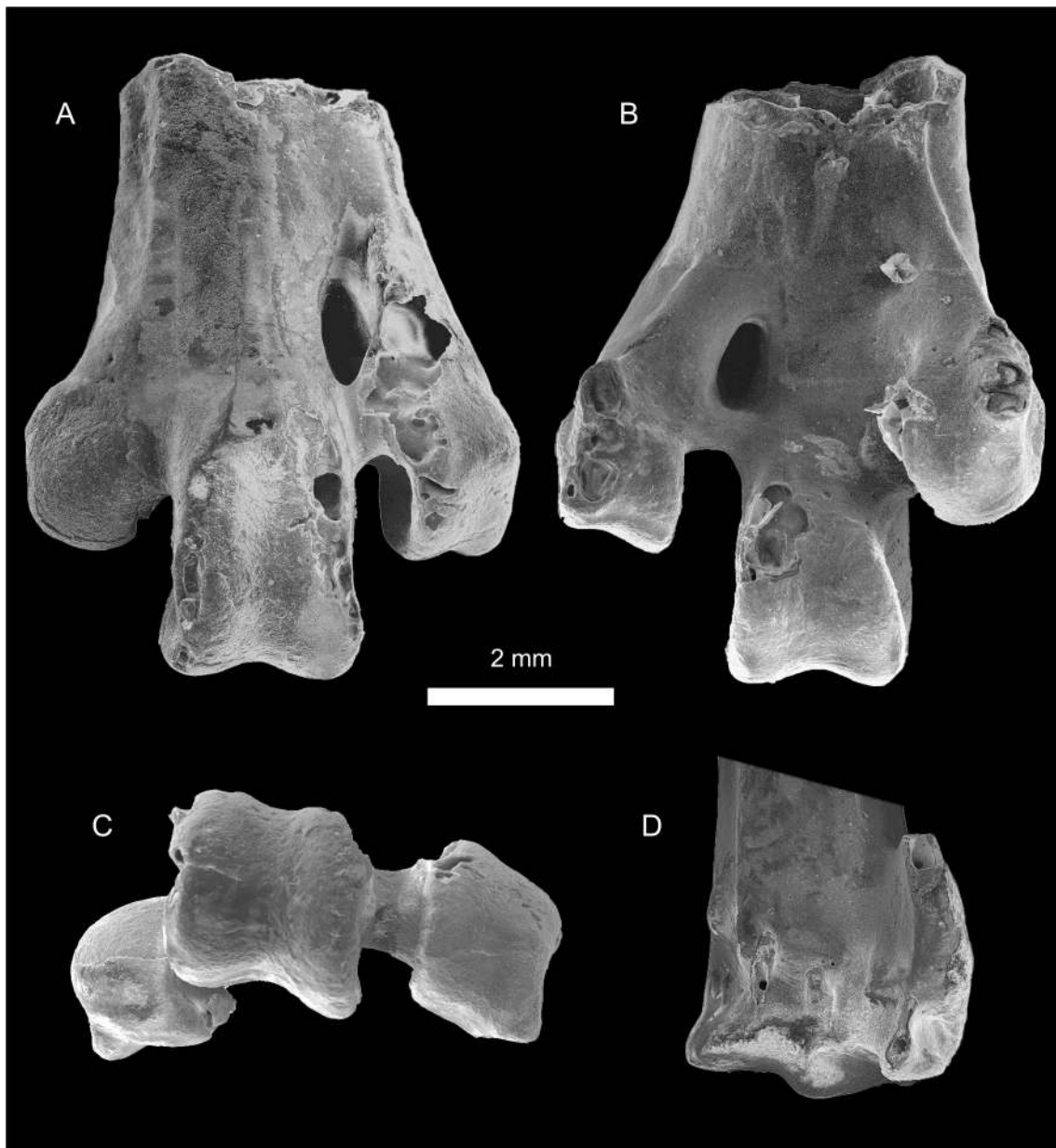
raised; the fossa supratrochlearis plantaris is wide and shallow; the distal vascular foramen is small.

**Comparisons with fossil galliforms**

1. *Austinornis* — CLARKE (2004) has attributed to the “Pan-Galliformes” a distal tarsometatarsus from the upper Cretaceous of Texas, which was the holotype of the species *Ichthyornis lentus* (MARSH, 1877), and created for it the new generic name *Austinornis*. This genus differs from *Chambiortyx* in having the distal vascular foramen very small and situated at the distal extremity of a distinct outer extensor groove. In *Austinornis* a “slight groove extends proximally from the juncture of metatarsals II and III on the dorsal surface of the tarsometatarsus” (CLARKE 2004: p. 53). This groove is very short in *Chambiortyx* and its characteristic ridge, on the cranial face, medial side, proximal to trochlea met. II, does not exist in *Austinornis*. Lastly, in *Austinornis*, trochlea met. II is more plantarly displaced than in *Chambiortyx*.

2. *Gallinuloididae* — The Gallinuloididae were present in the early Eocene of North America and in the Early and Middle Eocene of Europe, with the two genera *Gallinuloides* and *Paraortygoides* (MAYR 2009). In both genera the metatarsal trochleae are splayed (MAYR & WEIDIG 2004). The relative extension of trochleae met. II and IV compared to trochlea met. III is different in these two genera (MAYR 2000a; WEIDIG 2010). In *Paraortygoides messelensis* MAYR, 2000a the crista medianoplantaris forks and splits into two ridges which reach the wings of trochleae met. II and IV (see MAYR 2000a: fig. 9A). In *Chambiortyx* the two ridges do not meet. In *Paraortygoides radagasti* DYKE & GULAS, 2002 from the Early Eocene of England, there are two ridges on the plantar face, and these two ridges do not meet. These two ridges are not situated on the medial and lateral borders of the bone, but closer to its median axis. There is no ridge on the dorsal surface, proximal to trochlea met. II, and this trochlea is more plantarly displaced than in *Chambiortyx* (see DYKE & GULAS 2002: fig. 2B and F; MAYR 2009: fig. 6.4i).

3. *Paraortygidae* — The Paraortygidae are known in the Late Eocene and Early Oligocene of the Phosphorites du Quercy, France, and in the



**FIGURE 2.** *Chambiortyx cristata* nov. gen., nov. spec. from the late Early or early Middle Eocene of the locality Chambi 1, Central Tunisia. **A–C**, holotype, left tarsometatarsus (CB1-548), distal part, dorsal view (**A**), plantar view (**B**), distal view (**C**). **D**, paratype, left carpometacarpus (CB1-549), fragment of distal part, dorsal view.

Early Oligocene of Germany (MOURER-CHAUVIRÉ 1992a; FISCHER 1990, 2003). They were also probably present in the Late Eocene and Early Oligocene of the United States (MAYR 2009). In this family trochlea met. IV extends farther distally than in *Chambiortyx* and reaches the middle of trochlea met. III. Trochlea met. II is more plantarily displaced and, in distal view, the trochleae are more dorsoplantarly elongate. The dorsal surface is more convex, the outer extensor groove

is well marked, and there is no ridge proximal to trochlea met. II. However, on the plantar face, there are two well marked ridges, one starting from trochlea met. II, and the other one starting from trochlea met. IV. These two ridges run in proximal direction along the plantar surface and do not meet.

4. *Quercymegapodiidae* — The Quercymegapodiidae are known in the Middle Eocene (Le



Bretou, see MOURER-CHAUVIRÉ *et al.* 2011a) and the Late Eocene of the Phosphorites du Quercy, France, with the genus *Quercymegapodius*, in the Late Oligocene or Early Miocene of Brazil, and finally in the Early Miocene of France, with the genus *Ameripodius* (ALVARENGA 1988, 1995; MOURER-CHAUVIRÉ 1992a, 2000). In *Quercymegapodius* trochleae met. II and IV are splayed, and trochlea met. II is very globular on the dorsal face. The relative length of the trochleae is the same as in *Chambiortyx*, but in *Quercymegapodius* the dorsal surface of the shaft, proximal of the trochleae, is convex, and the outer extensor groove is deeper. The ridge starting from trochlea met. II and situated on the boundary between the dorsal and medial faces is absent. On the plantar face the ridge starting from trochlea met. IV is present but not the ridge starting from trochlea met. II. In *Ameripodius* the trochleae are less splayed than in *Quercymegapodius*, and, in distal view, trochleae met. II and IV are more plantarly displaced than in *Chambiortyx*. In *Ameripodius*, the dorsal face, proximally to the trochleae, is strongly convex, thus differing from *Chambiortyx*, but the ridge starting from trochlea met. II is present. This ridge first follows the boundary between the dorsal and medial faces, then continues on the dorsal face and finally merges into the surface of the shaft. On the plantar face, the ridge starting from trochlea met. II is absent in *Ameripodius*, while it is present in *Chambiortyx*.

5. *Megapodiidae* — A small fossil megapode, *Ngawupodius minya* has been described from the Late Oligocene of Australia (BOLES & IVISON 1999). It differs from *Chambiortyx* by the following characteristics: trochleae met. more splayed; trochleae met. II and IV with the same distal extension; trochlea met. II more plantarly displaced; on the dorsal face no ridge starting from trochlea met. II.

6. *Namaortyx* — *Namaortyx sperrgebietensis*, from the Middle Eocene, (probably early Lutetian, about 47 to 49 million years ago), of Namibia, was described as the first Paleogene galliform from Africa (MOURER-CHAUVIRÉ *et al.* 2011a). It is only known by a tarsometatarsus and has been left in family incertae sedis. *Namaortyx* resembles *Chambiortyx* by the relative length

of the trochleae, and their arrangement along a weakly arched curve in distal view. But it differs from it by its wide and flattened shaft, the strongly developed wing of trochlea met. IV, and the oblique orientation of the trochlea met. III in distal view, compared to the dorsal surface of the shaft. On the dorsal face there is no ridge starting from trochlea met. II.

7. *Nanortyx* — *Nanortyx inexpectatus* WEIGEL, 1963, from the Late Eocene (Chadronian) of Canada, is a very small form, described from a distal part of a tarsometatarsus and an omal part of a coracoid. This genus has been attributed to the family Odontophoridae, which itself is part of the family Phasianidae s. l. (MAYR 2009: fig. 6.1). Although it is poorly preserved, the coracoid is more similar to the Quercymegapodiidae than to the Phasianidae (MOURER-CHAUVIRÉ 1992a). These elements, as well as a distal tarsometatarsus from the early Oligocene of Colorado, assigned to the Odontophorinae by TORDOFF (1951), are insufficient to confirm the presence of crown group Galliformes in the Eocene (MAYR 2009). The *Nanortyx* tarsometatarsus differs from that of *Chambiortyx* in the following characteristics: trochlea met. IV extending farther distally; trochlea met. II extending less far distally and more plantarly deflected; presence of an outer extensor groove; on the dorsal surface, absence of the ridge starting from trochlea met. II.

8. *Comparisons with members of other orders* — The genus *Coturnipes* HARRISON & WALKER, 1977 was described from a distal tarsometatarsus from the Early Eocene of the London Clay, England. This taxon was classified in the order Galliformes, and included in the family Phasianidae, but MAYR (2006a) suggested that this genus could be closely related to the genus *Masillaraptor* from the Middle Eocene of Messel, which is classified in the “Falconiformes”. The genus *Coturnipes* has also been reported from the Early Eocene of the Nanjemoy Formation, Virginia, United States (OLSON 1999), and from the Middle Eocene of the Geiseltal, Germany (MAYR 2002a). The different distal parts of tarsometatarsus of *Coturnipes* differ from that of *Chambiortyx* by the following characteristics: large and elongate distal vascular foramen; well defined outer exten-

sor groove; dorsal surface of the shaft proximal to the trochleae convex; trochlea met. II strongly plantarly deflected (see HARRISON & WALKER 1977: pl. 8, fig. T); no ridge starting from trochlea met. II; trochleae met. III and IV dorsoplantarily elongate in distal view. Among the buttonquails (Order Charadriiformes, family Turnicidae), the tarsometatarsus of the genus *Turnix* looks very similar to that of the galliforms. On the plantar face of this tarsometatarsus, the lateral rim of trochlea met. III extends farther proximally than the medial rim. This feature is present in all Galliformes, but occurs also in other avian clades (MAYR 2000a; KSEPKA 2009). Compared to *Chambiortyx* the tarsometatarsus of *Turnix* differs in the following characteristics: articular parts of the trochleae shorter; dorsal surface of the shaft, proximally to the trochleae, strongly convex; distal vascular foramen situated at the end of a well marked outer extensor groove; trochlea met. II more plantarly displaced (BOCK & McEVEY 1969). In the genus *Ortyxelos*, the tarsometatarsus is more different from that of galliforms, because its trochleae are strongly splayed, and the articular parts of these trochleae are very short. Fossil Turnicidae have been described from the Middle Eocene of Germany, and from the Early Oligocene of France and Germany, but when this detail can be observed, trochlea met. II is more plantarly deflected than in *Chambiortyx* (MAYR 2000b; MAYR & KNOPF 2007).

#### **Description and comparisons — Carpometacarpus (Fig. 2D)**

The fragment of left carpometacarpus only includes the os metacarpale majus. It shows a well marked sulcus tendineus on the dorsal face. At the level of the symphysis metacarpalis distalis, on the dorsal face, there is a small groove for the tendon of the musculus interosseus distalis, but no osseous arch. This osseous arch is present in *Paraortygoides messelensis* (MAYR 2000a: text-fig. 5E). The morphology of this fragment resembles that observed in Gallinuloididae, Paraortygidae, and Quercymegapodiidae by the fact that the articular surface for the minor digit of the wing is situated at the same level as the articular surface for the major digit, while in the recent

galliforms this articular surface extends farther distally. The size of this fragment of bone is compatible with the size of the tarsometatarsus.

#### **Remarks concerning the size of *Chambiortyx cristata* nov. spec.**

The size of *Chambiortyx cristata* nov. spec. (distal width of tarsometatarsus 5.3 mm) is slightly larger than that of the recent Common Quail (*Coturnix coturnix*, distal width 4.8 mm) and larger than that of the smallest recent galliform, the Asian Blue Quail (*Coturnix chinensis*, distal width 3.7–3.8 mm). Among the stem group fossil galliforms the smallest known so far are *Quercymegapodius* cf. *brodkorbi*, Middle Eocene (distal width 3.8 mm) (MOURER-CHAUVIRÉ 1992a; MOURER-CHAUVIRÉ *et al.* 2011), and *Nanortyx inexpectatus*, Late Eocene (distal width 5.2 mm) (WEIGEL 1963). The other fossil stem galliforms are larger: *Austinornis lentus*, Late Cretaceous, distal width ca. 10 mm (CLARKE 2004); *Gallinuloides wyomingensis*, Early Eocene, distal width ca. 7.1 mm (WEIDIG 2000); *Paraortygoides messelensis*, Middle Eocene, distal width ca. 7.6 mm (MAYR 2000a); *Namaortyx sperrgebietensis*, Middle Eocene, distal width 11.9 mm (MOURER-CHAUVIRÉ *et al.* 2011); *Quercymegapodius depereti*, Late Eocene, distal width 5.5–6.1 mm (MOURER-CHAUVIRÉ 1992a).

#### **Order Cuculiformes WAGLER, 1830**

##### **Family Cuculidae LEACH, 1820**

#### ***Chambicuculus* nov. gen.**

**Type species:** *Chambicuculus pusillus* nov. spec.

**Diagnosis:** Small zygodactyl form with a well-developed trochlea accessoria, separated from the condylus of trochlea metatarsi IV by a clearly expressed notch. Distal extension of trochlea metatarsi IV situated more proximally than the incisura intertrochlearis lateralis. Presence of a canalis interosseus distalis dorsally roofed by an osseous bridge. Trochlea accessoria oriented plantarly and slightly medially.

**Derivatio nominis:** Chambi from the Djebel Chambi, in Tunisia, and *cuculus*, Latin word for a cuckoo.

***Chambicuculus pusillus* nov. spec.**

(Figs 3, 4, 5B, 6A–B)

**Holotype:** CB1-541, distal part of right tarsometatarsus, well preserved with the exception of a slight erosion of the crest which is situated on the dorsal side of trochlea met. IV.

**Paratypes:** CB2-1001, distal part of right tarsometatarsus, incompletely preserved on its dorsal side. Trochlea met. IV is incomplete but the sehnenhalter is well preserved and separated from the condylus by a well expressed notch. On this specimen the sehnenhalter is slightly more bulging than on the Chambi 1 specimen. CB1-560, fragment of a left tarsometatarsus, distal part, with only trochlea met. III preserved.

**Type locality:** Chambi 1, Central Tunisia, Kasserine district.

**Age:** Late Early or early Middle Eocene.

**Diagnosis:** As for the genus.

**Derivatio nominis:** *pusillus*, Latin word meaning tiny, quite small.

**Measurements:** Holotype, CB1-541, distal width, 2.66 mm; distal depth, 1.60 mm. Paratype, CB2-1001, distal width, 2.70 mm; distal depth, 1.72 mm. Paratype CB1-560, width of trochlea met. III, 1.00 mm.

**Description and comparisons**

This taxon is characterized by the presence of a sehnenhalter, or trochlea accessoria, on trochlea met. IV, with the shape of a wing-like flange. Trochleae met. II and IV are slightly plantarly deflected. Trochlea met. III shows two parallel rims, which are clearly separated by a deep groove, well visible in distal view. The lateral rim is slightly wider and more developed plantarly than the medial rim. This trochlea is proximodistally short. It bears a protuberance at the base of its lateral face, on the dorsal side. Trochlea met. II is shorter than trochlea met. III and it reaches distally about the mid-length of this trochlea. It is globular on its dorsal face and shows a slight groove and a short wing on its plantar face. Trochlea met. IV is much shorter and its distal end is situated slightly proximally compared to the incisura intertrochlearis. It shows a prominent crest on its dorsal side. On its lateral side it shows a

bulging condyle and a thin and elongate sehnenhalter, plantarly and slightly medially oriented. The condyle is separated from the sehnenhalter by a distinct notch. The articular surface of the condyle does not extend on the sehnenhalter. The distal vascular foramen is very large. This is not clearly visible on Fig. 3A, because the orientation of this canal is oblique and medioplantarly directed, but when it is slightly more medially oriented, this foramen appears extremely wide (Fig. 6A). On the dorsal face this opening is not located at the distal extremity of an outer extensor groove. The canalis interosseus distalis is present. On its dorsal side, a thin osseous bridge joins the lateral side of trochlea met. III to the medial side of trochlea met. IV. Trochlea met. IV also shows a groove on its dorsal face, medial side, clearly visible in distal view. This groove is delimited medially by a protuberance which is situated at the base of trochlea met. III, and laterally by the dorsal crest of trochlea met. IV. On the plantar face, there is a short and shallow groove, proximodistally oriented, which ends in the medial intertrochlear notch. The fossa metatarsi I is situated entirely on the plantar face. It is elongate and made up of two lobes.

**Comparison with crown group Cuculidae (Cuckoos)** (Figs 5A, 6C–D): The morphological characteristics of the recent Cuculidae have been indicated by HUGUES (2000). On the distal part of the tarsometatarsus the first characteristic is the distal end of trochlea met. IV which is situated proximally compared to the incisura intertrochlearis lateralis. In some genera, which are relatively primitive, such as *Geococcyx*, *Morococcyx*, or *Centropus*, the distal end of trochlea met. IV is slightly proximal, whereas in some more derived genera, such as *Cuculus*, *Clamator*, or *Coccyzus*, this distal end is highly proximal compared to the incisura intertrochlearis lateralis. The other characteristic is the presence of a prominent sehnenhalter that is strongly inflected medially.

In the recent Cuculidae the canalis interosseus distalis is absent. At its location there is a groove on the dorsal face, between trochleae met. III and IV and the osseous strip (which bridged the canalis interosseus distalis) has disappeared. The condyle of trochlea met. IV is very globular on its lateral side and dorsoplantarly elongate. As in the

Chambi specimens, there is a sharp crest on the dorsal face of trochlea met. IV and a protuberance at the base of trochlea met. III on its lateral side. *Chambicuculus* differs from the recent Cuculidae by the following features: Presence of a canalis interosseus distalis; condylus of trochlea met. IV less globular and less dorsoplantarily elongate; sehnenhalter more distally and plantarly oriented, while it is more medially oriented in the recent Cuculidae (see also STEINBACHER 1935: p. 253, figs 15–16; MAYR 1998: p. 48, fig. 28G; MAYR 2002b: p. 724, fig. 7C); more pronounced notch between the condylus and the sehnenhalter.

**Comparisons with stem group Cuculidae and related forms:** The genus *Eocuculus* CHANDLER, 1999, has been attributed to the Cuculidae by CHANDLER (1999) and to ?Cuculidae by MAYR (2006b). It is known by the species *Eocuculus cherpinae*, described from the Late Eocene of the United States (CHANDLER 1999), and by *Eocuculus* cf. *cherpinae*, from the Early Oligocene of France (MAYR 2006b). The skeleton exhibits some derived characteristics of the recent Cuculidae but the tarsometatarsus is quite different. The foot is not zygodactyl but probably only semi-zygodactyl, and does not show a large trochlea accessoria. Both trochleae met. II and IV are more plantarly deflected than in *Chambicuculus*. Unlike *Chambicuculus*, the foramen vasculare distale is small, the canalis interosseus distalis is absent, and it is replaced by a narrow sulcus. In addition trochlea met. IV extends as far distally as trochlea met. II and it reaches the mid-section of trochlea met. III. Lastly trochlea met. II is wider than in *Chambicuculus*. The presence of a well-developed sehnenhalter in *Chambicuculus* indicates that this new taxon is different from the genus *Eocuculus*.

The other fossil Cuculidae are *Neococcyx mccorquodalei* and *Cursoriococcyx geraldinae*. *Neococcyx mccorquodalei* has been described from the Late Eocene (MAYR 2009) of Canada (WEIGEL 1963). It is represented by a distal part of

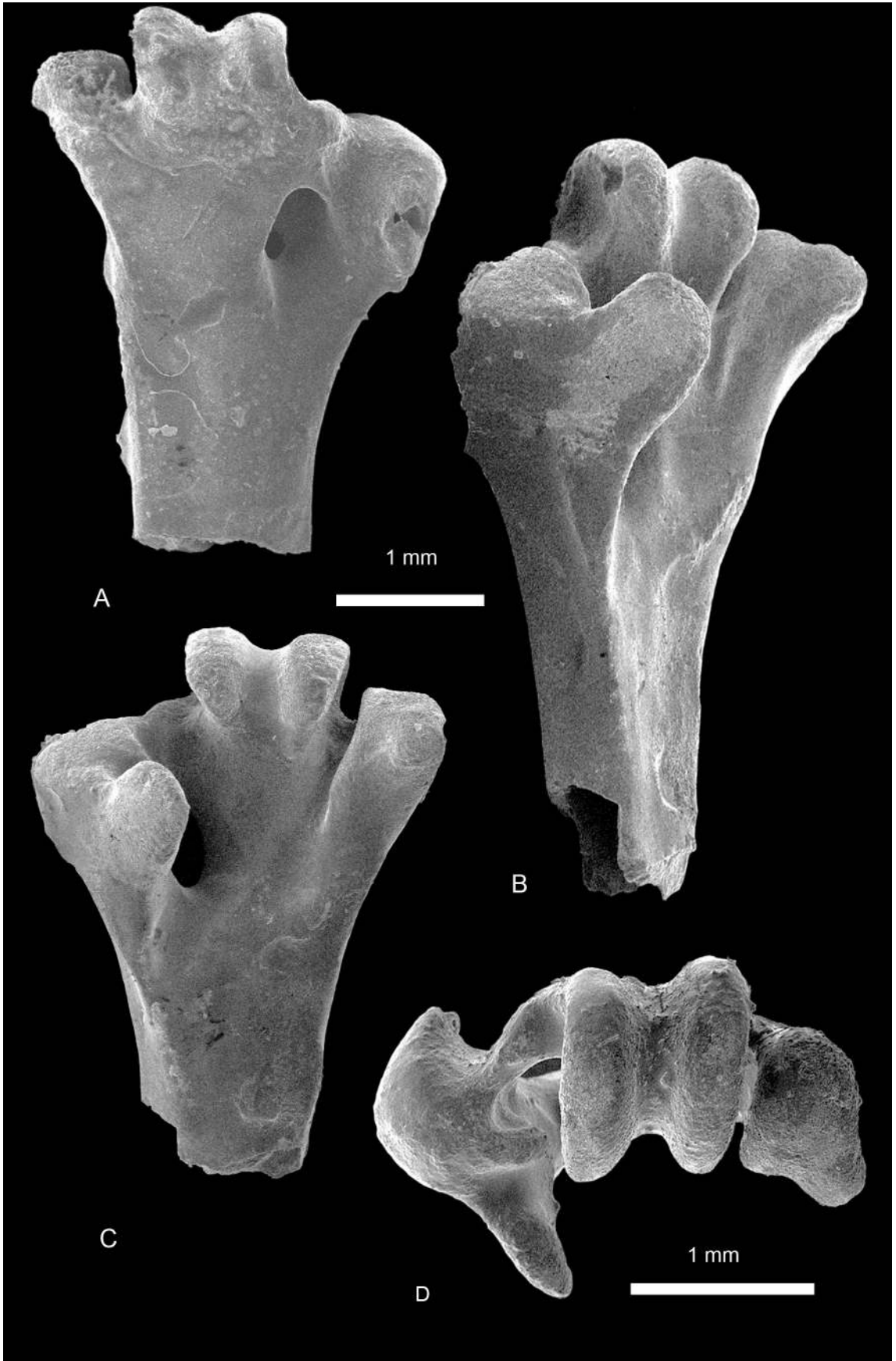
humerus, which presents morphological characteristics close to those found in the recent genus *Coccyzus*. *Cursoriococcyx geraldinae* has been described from the Early Miocene of Colorado (MARTIN & MENGEL 1984). It is known by several bone fragments which do not include any distal tarsometatarsus. This fossil is close to the recent genus *Geococcyx* and is placed in the subfamily Neomorphae.

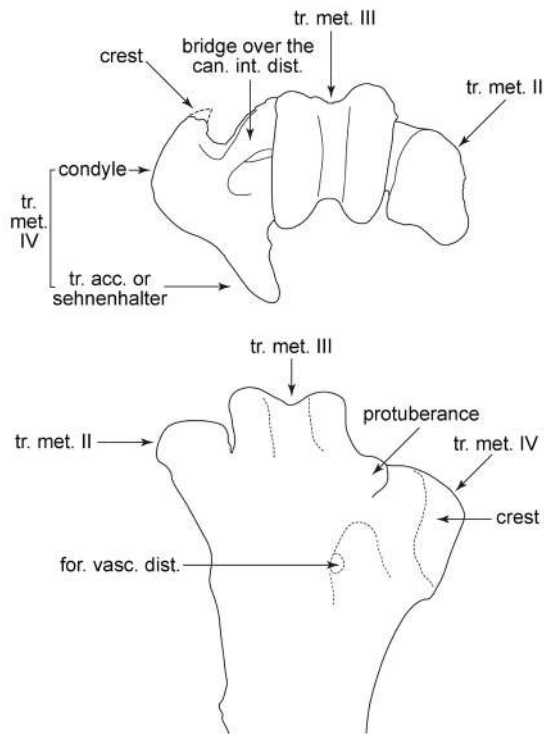
*Pumiliornis tessellatus* MAYR, 1999, is a very tiny form, known by two skeletons from the Middle Eocene of Messel, Germany (MAYR 1999; 2008). Its morphological characteristics remind those of *Eocuculus* (MAYR 2008). In *Pumiliornis* trochlea met. IV is oriented plantarly but it lacks a well-developed trochlea accessoria. In addition trochleae met. II and IV have approximately the same length. Both end distally at the level of the base of trochlea met. III. Trochlea met. III shows a well-developed trochlear furrow on its dorsal side and there is a depression at its base. The foramen vasculare distale is small. According to MAYR (2008: p. 251), its foot was at least semizygodactyl. These characteristics are different from those of *Chambicuculus*.

In the Early Eocene of Fur Fm., in Denmark, the partial skeleton of *Morsoravis sedilis* BERTELLI *et al.*, 2010, attributed to the Charadriiformes, has been described. A phylogenetic analysis performed by MAYR (2011) has shown the existence of close relationships between the Early and Middle Eocene *Morsoravis* and *Pumiliornis*, and the Late Eocene and Early Oligocene *Eocuculus*. In *Pumiliornis* and *Morsoravis*, the short and wide proximal phalanx of the fourth toe suggests the presence of a semizygodactyl foot. In *Morsoravis* trochleae met. II and IV have almost the same distal extension and reach about the middle of trochlea met. III (see BERTELLI *et al.* 2010: fig. 12), and the foramen vasculare distale is very small. In addition trochlea met. II bears a distinct groove on its medial surface, and it is bilobed (see MAYR 2011: fig. 7D). These morphological characteristics are different from those of *Chambicuculus*.

**FIGURE 3.** *Chambicuculus pusillus* nov. gen., nov. spec. from the late Early or early Middle Eocene of the locality Chambi I, Central Tunisia. **A** and **D**, holotype, right tarsometatarsus (CB1-541), dorsal view (A), distal view (D). **B** and **C**, paratype, right tarsometatarsus (CB2-1001), lateral view, slightly plantarly oriented (B), plantar view (C). For figure B the bone has been slightly obliquely oriented in the scanning electron microscope, which gives to the bone a more elongated shape than in figure C.



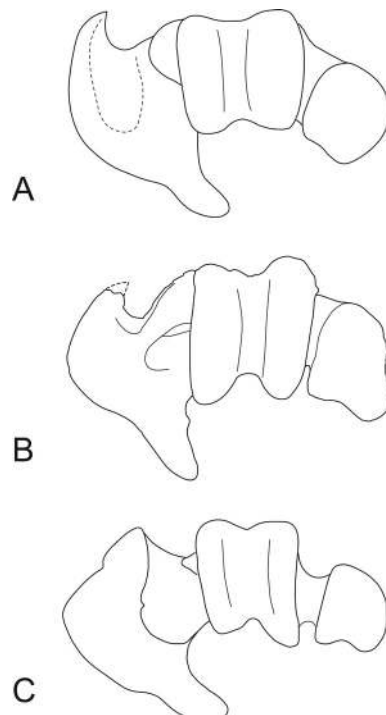




**FIGURE 4.** Diagrams showing the different parts of the distal tarsometatarsus in *Chambicuculus pusillus* nov. gen., nov. spec., in distal (above) and plantar (below) views. Abbreviations: Bridge over the can. int. dist.: bridge over the canalis interosseus distalis; For. vasc. dist.: foramen vasculare distale; tr. met. II-IV, trochlea metatarsi II-IV; tr. acc. or sehnenhalter: trochlea accessoria or sehnenhalter.

*Eutreptodactylus itaboraiensis*, from the Late Paleocene of Brazil, was initially attributed to the Cuculidae (BAIRD & VICKERS-RICH 1997), but its morphological characteristics are different from those of the Cuculidae. MAYR (2005) has placed the genus *Eutreptodactylus* in the extinct family Gracilitarsidae that he considers related to the Piciformes. *Eutreptodactylus* differs from *Chambicuculus* by the following characteristics: trochlea met. II strongly projecting medially; trochlea met. IV ending more distally than incisura intertrochlearis lateralis; trochlea met. IV with a wide and short, plantarly directed, sehnenhalter; canalis interosseus distalis absent; foramen vasculare distale situated at the distal end of the outer extensor groove.

**Comparison with crown group Galbulae (Jacamars and Puffbirds)** (Figs 5C, 6E–F): Both Chambi specimens show similarities with the tar-



**FIGURE 5.** Distal views of the right tarsometatarsus (not to scale). **A**, Recent Cuculidae, *Centropus senegalensis*, coll. UCBL. **B**, *Chambicuculus pusillus* nov. gen., nov. spec., Eocene of Tunisia, coll. ONM, CB1-541. **C**, Recent Bucconidae, *Monasa nigrifrons*, coll. USNM 612064.

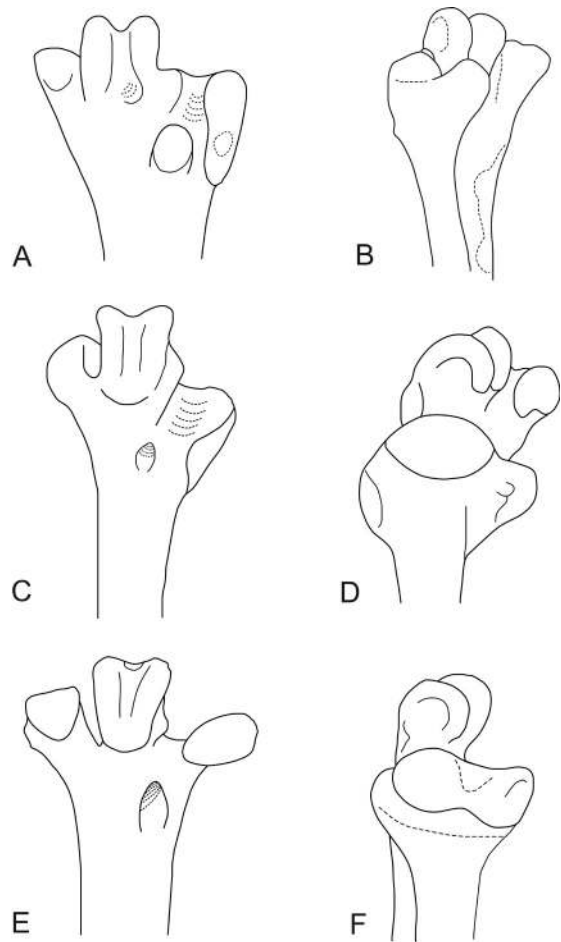
sometatarsus of the recent Galbulae, particularly in distal view. The Galbulae belong to the order Piciformes and include two families, the Galbulidae (Jacamars) and the Bucconidae (Puffbirds). Their distribution is restricted to the Neotropical zone, ranging from Southern Mexico to Southern Brazil for the Galbulidae (TOBIAS 2002), and from Southern Mexico to Northern Argentina for the Bucconidae (RASMUSSEN & COLLAR 2002). The distal extremity of the tarsometatarsus has been described in detail by STEINBACHER (1935). In these two families the foot is zygodactyl and trochlea met. IV bears a trochlea accessoria or sehnenhalter. In the Galbulidae, trochlea met. IV shows two articular facets for phalanx 1 of posterior digit IV. The first one is found only on the condylus itself of the trochlea, and the second one is on the sehnenhalter. Both articular facets are equivalent in size and are separated by a well marked groove (see STEINBACHER 1935: p. 256,

fig. 18–19; SIMPSON & CRACRAFT 1981: p. 484, fig. 2B; MAYR 1998: p. 48, fig. 28E; MANEGOLD 2005: p. 124, fig. 39C–D).

In the Bucconidae, the articular facet for phalanx 1 of posterior digit I extends also on the sehnenhalter, but the two parts are not so clearly separated. In *Notharchus* the two articular surfaces are separated by a clearly expressed groove, visible in both lateral and distal views of the tarsometatarsus. In *Hypnelus* the articular surface situated on the condylus is larger than that situated on the sehnenhalter, and both surfaces are separated by a faintly visible groove. In *Monasa* and *Chelidoptera* both parts form an inflated and elongate surface, which is perpendicular to the long axis of the bone, and there is no visible groove between them. In the Bucconidae trochlea met. IV is very broad dorsoplantarily and the sehnenhalter is relatively short and thick (see also FEDUCCIA & MARTIN 1976: p. 103, figs 2g–l; HOUDE & OLSON 1992: p. 145, figs 15–16; MAYR 1998: p. 48, fig. 28F; MAYR 2002b: p. 724, fig. 7E).

*Chambicuculus* differs from the Galbulae by the fact that the articular surface for phalanx 1 of posterior digit IV is situated only on the condyle and not on the sehnenhalter. In addition the distal end of trochlea met. IV is situated slightly proximally compared to the incisura intertrochlearis, while in the Galbulae it is situated slightly distally. *Chambicuculus* also differs from the Galbulae in the strong development of a crest on the dorsal face of trochlea met. IV. This strongly prominent crest seems to be characteristic of the Cuculidae (see STEINBACHER 1935: fig. 16 for *Centropus*, and MAYR 2002b: fig. 7C for *Coua*).

**Comparison with putative stem group Galbulae:** A large number of small forms from the Early Eocene of North America and Europe were attributed first to the family Bucconidae, then to the family Primobucconidae, but these Primobucconidae are now considered as ancestral forms of the Coraciiformes sensu stricto (MAYR 2009). Other forms previously attributed to Primobucconidae have been transferred to the family Sandcoleidae (HOUDE & OLSON 1992), which are stem group representatives of the Coliiformes. The only Paleogene form which can be attrib-



**FIGURE 6.** Dorsal and lateral views of the right tarsometatarsus (not to scale). **A–B**, *Chambicuculus pusillus* nov. gen., nov. spec.; **A**: dorsal view; **B**: lateral view slightly plantarly oriented. **C–D**, Recent Cuculidae, *Centropus senegalensis*, coll. UCBL; **C**: dorsal view; **D**: lateral view slightly plantarly oriented. **E–F**, Recent Bucconidae, *Monasa nigrifrons*, coll. USNM 612064; **E**: dorsal view; **F**: lateral view.

uted to ?Galbulae is “*Neanis*” *kistneri* (FEDUCCIA, 1973), represented by two almost complete skeletons from the Early Eocene of the Green River Formation in the United States (WEIDIG 2010). On the holotype it is possible to see that the foot is zygodactyl and shows a sehnenhalter but no more details are available. However “*Neanis*” *kistneri* shares morphological characteristics with the Galbulae in the skull, the coracoid, and the humerus. *Chambicuculus* is probably different from “*Neanis*” *kistneri* since its morphological characteristics are closer to the Cuculidae than to the Galbulae.

**Comparisons with Quercypsittidae:** The tarsometatarsus of *Chambicuculus* looks superficially similar to that of the Quercypsittidae, stem group representatives of the Psittaciformes (see MOURER-CHAUVIRÉ 1992b and MAYR *et al.* 2010). However it differs from them by the following characteristics: in *Chambicuculus* the distal part of the tarsometatarsus is constricted (more splayed in *Quercypsitta*); trochlea met. II more elongate (it reaches only the basis of trochlea met. III in *Quercypsitta*); trochlea accessoria oriented plantarly and slightly medially (oriented more medially in *Quercypsitta*); distinct notch between trochlea accessoria and trochlea met. IV (more strongly expressed furrow in *Quercypsitta*); canalis interosseus distalis covered by a bony bridge (dorsally open in *Quercypsitta*); groove in the middle of trochlea met. II slightly indicated on the plantar face (present and well visible in distal and plantar views in *Quercypsitta*). In *Chambicuculus* a prominent crest is present on the dorsal face of trochlea met. IV. This part is incompletely preserved on all the specimens of *Quercypsitta*, but it is a characteristic of the Cuculidae and it is absent in the other stem group representatives of the Psittaciformes (MAYR *et al.* 2010).

**Remarks concerning the size of *Chambicuculus pusillus*:** In *Chambicuculus* the only measurement which can be compared with other forms is the distal width of the tarsometatarsus which is about 2.7 mm. In *Pumiliornis tessellatus*, which resembles the genus *Eocuculus*, this distal width can be estimated at 2.3 and 2.4 mm after the illustrations given by MAYR 1999 and MAYR 2008; this form is thus still smaller than *Chambicuculus*. In *Morsoravis sedilis* the distal width is 3.0 mm (BERTELLI *et al.* 2010). In *Eocuculus cherpinae* it is 4.2 mm (CHANDLER 1999) and in *Eocuculus* cf. *cherpinae* it can be estimated at 4.3 mm (MAYR 2006b). Recent Cuculidae are generally middle- to large-sized, but there are a few very small forms, such as *Chrysococcyx minutillus*, the Little Bronze-cuckoo, which measures 15–16 cm and weights 17g (PAYNE 1997). The size of *Chambicuculus* was probably comparable to that of the smallest recent Cuculidae.

## Discussion

The early evolutionary history of birds in Africa is still poorly known. Their Paleogene fossil record is limited to a handful of localities. Marine forms have been described in the Late Paleocene and Early Eocene of Morocco, and also in the Middle Eocene of Nigeria and Togo (BOURDON *et al.* 2010, and references therein). Among the terrestrial birds only a galliform in the early Middle Eocene of Namibia, and a phororhacoid in the early Middle Eocene of Algeria, are known (MOURER-CHAUVIRÉ *et al.* 2011a, 2011b). The other Paleogene African forms come from the Late Eocene and Early Oligocene of the Fayum, in Egypt (RASMUSSEN *et al.* 1987, 2001).

According to the fossil record of the Northern Hemisphere, the Galliformes seem to have been abundant and diversified during the Paleogene. Several stem group families have been found in the Early Eocene (MAYR 2009). However their record is not limited to the Paleogene but it extends back to the Late Cretaceous (HOPE 2002). In the Southern Hemisphere, until recently, they were only known from the Late Oligocene, with a Quercymegapodiidae in South America (ALVARINGA 1995) and a Megapodiidae in Australia (BOLES & IVison 1999). The presence of two galliforms in Africa, one in the late Early or early Middle Eocene of Tunisia, and the other in the Middle Eocene of Namibia, shows that this group was also present and diversified in this landmass during the Paleogene. *Namaortyx*, from Namibia, and *Chambiortyx*, from Tunisia, do not belong to the same families as those recorded in the Northern Hemisphere. They probably belong to stem group families but, for confirmation, it would be necessary to have some other elements of the postcranial skeleton. Recent African galliforms belong to the family Phasianidae s. l., which are crown group representatives of the Galliformes, and which are only known since the second part of the Oligocene (MOURER-CHAUVIRÉ 1992a; MAYR 2009).

Concerning the Cuculiformes, a large number of semizygodactyl or zygodactyl forms have been described in the Paleogene of Eurasia and North America, and also in South America



(MAYR 2009), but for Africa, this group was so far undocumented in the Paleogene. The new taxon described here, *Chambicuculus*, represents therefore the first and oldest occurrence of this group in Africa. Another zygodactyl form, *Miopico benimellalensis* MAYR, 1998, family Miopiconidae, was described from the Middle Miocene of Beni Mellal, Morocco. According to MAYR (1998), the Miopiconidae are the sister-group of the Pici, and thus *Chambicuculus* is not related to it.

*Chambicuculus* is older than the other fossil Cuculidae known so far. In this taxon the presence of a canalis interosseus distalis is a plesiomorphic condition for birds (MAYR *et al.* 2003). By the presence of this canal, *Chambicuculus* could appear somewhat more primitive than *Eocuculus* from the Late Eocene and Early Oligocene. However in *Chambicuculus*, the presence of a well-developed sehnenhalter, which is a derived condition indicating that this taxon was fully zygodactyl, and the lesser distal extension of trochlea met. IV suggests that *Chambicuculus* was morphologically more derived than *Eocuculus*.

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