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The Sarmatian (late Middle Miocene) avian fauna from Gratkorn, Austria

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Abstract Among the rich late Middle Miocene vertebrate fauna from Gratkorn [MN(7+)8] in Styria, Austria, birds are among the rarest of vertebrate fossils. Only isolated elements—13 bones and two claws—have been recorded, most of which are fragmentary, thereby hampering systematic determinations. However, four different taxa have been identified as representing at least three different species of galliforms (*Miogallus altus*, cf. *Palaeocryptonyx edwardsi*, cf. *Palaeocryptonyx* sp.) and the mousebird *Necrornis* cf. *palustris*. All of these taxa have been known to be present before from Middle Miocene deposits in Europe, but there existence has been proven for the first time in Austria.

Keywords *Miogallus* · *Palaeocryptonyx* · Phasianidae · *Necrornis* · Coliidae · Aves · Middle Miocene

Introduction

The locality Gratkorn (clay pit St. Stefan, 15°20′56″E, 47°08′14″N) is located 0.7 km east of the market town Gratkorn and 10 km northeast of the city of Graz in south-eastern Austria (federal state of Styria) (Fig. 1). It is situated in an Eastern Alpine intramontane basin (Gratkorn basin), beyond the north-western margin of the Styrian basin. [For detailed geological, biostratigraphical and palaeoenvironmental information on the locality and its deposits, the reader is referred to Gross et al. (2011) and Harzhauser et al. (2008)]. The locality has yielded one of the richest vertebrate faunas of the late Middle Miocene (approx. 12.2–12.0 Ma) of Central Europe (Gross et al. 2011), dominated by fossils of mammals, reptiles and subordinate amphibians. Fossils of fishes and birds are only sparsely represented.

This article is a contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin."

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Material and methods

Thirteen bone fragments and two claws of fossil birds have been discovered to date from the Gratkorn locality and housed in the Universalmuseum Joanneum (UMJGP) in Graz, Austria. The osteological terminology for the descriptions of the bones follows Baumel et al. (1993) and occasionally Ballmann (1969a, b). Measurements were taken after von den Driesch (1976). In terms of the genus *Palaeocryptonyx* and their species, we follow the systematics proposed by Göhlich and Mourer-Chauviré (2005) and Pavia et al. (2012).

Measurements of comparative material were taken by UBG in the following collections: NHMW: Naturhistorisches Museum, Vienna (Ornithological Dept. for extant taxa); FSL: Faculté de la Science de la Terre, Université Lyon 1, Lyon; ML: Muséum Lyon, Lyon; MNHN: Muséum National d'Histoire Naturelle, Paris; SMNS: Staatliches Museum für Naturkunde, Stuttgart; BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

Osteological abbreviations used in this work are: cmc: carpometacarpus; tmt: tarsometatarsus; tt: tarsometatarsus.

Measurement abbreviations used in Tables 1–5 are: Dp: proximal depth (in coracoid: of proc. acrocoracoideus; in cmc: over processus extensorius and caudalmost edge of trochlea carpalis); Dd: distal depth; dWfas: distal width of facies art. sternalis; Lm: medial length; GL: greatest length; Wc: width

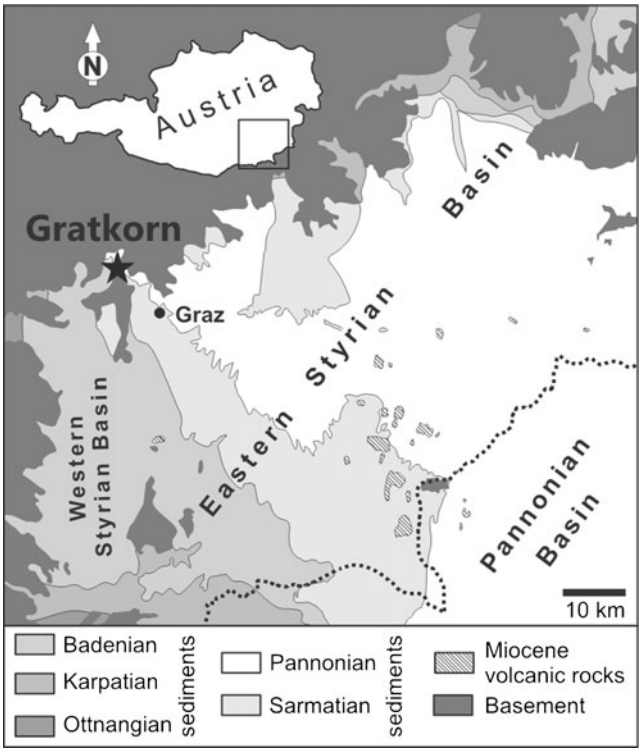

Fig. 1 Geographic position of the locality Gratkorn in Austria (modified after Harzhauser et al. 2008, fig. 1b)

Fig. 2 *Miogallus altus* from the late Middle Miocene of Gratkorn (Austria). Left coracoid (UMJGP 204698a), ventral view (**a**), dorsal view (**b**); cranial end of left scapula (UMJGP204698b), lateral view (**c**)

of collum; Wd: distal width; Wp: proximal width (in scapula: diagonal over acromion and facies art. humeralis); Ws: smallest width of shaft.

Systematic palaeontology

Galliformes Temminck, 1820

At least three different taxa of galliformes can be distinguished in the Gratkorn avifauna due to the different dimensions of the skeletal remains.

Phasianidae Vigors, 1825
Miogallus Lambrecht, 1933
Miogallus altus (Milne-Edwards, 1869)
(Fig. 2)

Type locality: Sansan (Gers, France), Middle Miocene, Astaracian, biozone MN6.
Stratigraphical and geographical distribution: Late Early to early Late Miocene (MN4-MN9) from France, Germany, Slovakia, and Spain (Sánchez Marco 2006).
Material: Left coracoid (UMJGP 204698a); cranial end of left scapula (UMJGP 204698b). Both specimens were found in loose articulation and thus are supposed to represent one individual.
Remarks: *Miogallus altus* is better known as *Miophasianus altus*. It was Mlíkovský (2002) who recognised the genus *Miophasianus* Lambrecht, 1933 to be a nomen nudum. Even if the genus name *Miophasianus* was made available later by Brodkorb (1952), we agree with Mlikovský (2002) that *Miogallus longaevus* Lambrecht, 1933 is very probably a junior synonym of *M. altus*. As a consequence of the priority of *Miogallus* Lambrecht, 1933 over *Miophasianus* Brodkorb, 1952, the species must be named *Miogallus altus*.

The genus *Miogallus* is monospecific comprising only *M. altus* (see Cheneval 2000). *M. altus* is the largest phasianid in the Miocene of Europe and is closest related to peafowl (*Pavo cristatus*) (Ballmann 1969a); in size, *M. altus* was most similar to the females of extant black grouse (*Tetrao urogallus*) (see Erbersdobler 1968).

Description and comparison

Coracoid (Fig. 2a, b): The coracoid is almost complete, only its processus lateralis is broken off and its distal (sternal) blade is somewhat crushed. The shape of the processus acrocoracoideus, the knob-like processus procoracoideus, the large and flat facies articularis humeralis and cotyla scapularis and the overall shape of the distal (sternal) blade are typically galliform. The distal (sternal) edge of the facies articularis clavicularis is straight in medial view, as in extant *Pavo cristatus* (Tomek and Bocheński 2009). No pneumatic foramen is traceable on the dorsal surface of the distal (sternal) blade. The facies articularis sternalis is somewhat more concave than in the extant *Pavo cristatus*.

Scapula (Fig. 2c): Only the cranial end of the scapula up to the collum is preserved. The facies articularis humeralis is rounded triangular and its ventral angle bends cranially; as typical for galliforms its mediolateral extension is wider than its dorsoventral one. The acromion bends slightly medially, but its craniomedial margin is broken off. There is neither a pneumatic foramen on the lateral side of the cranial end, nor cranially between facies articularis humeralis and acromion.

Coracoid and scapula represent a quite large-sized individual of *M. altus* compared to material from the type locality Sansan (France) and other Middle Miocene European localities (Table 1).

Palaeocryptonyx Depéret, 1892
cf. *Palaeocryptonyx edwardsi* (Fig. 3a–g)

Type locality: La Grive-Saint-Alban (Isère, France), Middle Miocene, Astaracian, biozone MN7+8.
Stratigraphical and geographical distribution: Middle Miocene (MN7+8) from France. *P. edwardsi* has also been reported from the late Early Miocene (Can Mas, MN4) and the transition Middle/Late Miocene (Hostalets de Pierola, MN8-9) of Spain (Villalta and Crusafont Pairó 1950; Villalta 1963; Sanchez Marco 1999, 2006).
Material: Left humerus (UMJGP 204727), damaged, preserved in situ in a sediment chunk; proximal end of a right carpometacarpus (UMJGP 204680); fragmentary furcula (UMJGP 204072), preserved in situ in a sediment chunk; fragmentary cranial portion of sternum (UMJGP 204042).
Remarks: Five species are known of *Palaeocryptonyx* during the Neogene and Pleistocene of Europe (Sanchez Marco 2009; Pavia et al. 2012), *P. edwardsi* being the largest one; it is intermediate in size between *Palaeortyx gallica* and *Palaeortyx prisca*, but corresponds in some bones more to *P. prisca*. (Göhlich and Mourer-Chauviré 2005).

Description and comparison

Humerus (Fig. 3a): The left humerus is embedded with its caudal side up in a small sediment chunk. Its proximal end is crushed, the diaphysis is broken and partly missing and the ventral half of the distal end is missing. Despite its damage, by means of its shallow dorsal fossa pneumotricipitalis, which proceeds smoothly slightly oblique distoventrally, the bone can be identified as *Palaeocryptonyx*. In the contemporary and more frequent genus *Palaeortyx* this dorsal fossa is deeper (Göhlich and Mourer-Chauviré 2005; Göhlich and Pavia 2008). An additional distinguishing feature, the non-pneumatisation of the ventral fossa pneumotricipitalis (which is pneumatized in *Palaeortyx*) (Göhlich and Mourer-Chauviré 2005; Göhlich and Pavia 2008) is not verifiable due to complete sediment filling in this fragile fossa.

In dimension (Table 2), the humerus—even if its measurements are approximations due to its damages—falls well in the size range of *P. edwardsi* from its type locality La Grive-Saint-Alban (see also Göhlich and Mourer-Chauviré 2005, text, fig. 3).
Carpometacarpus (Fig. 3e–g): Only the proximal end with a portion of the os metacapale majus is preserved. The shape of the trochlea carpalis and of the processus extensorius and alularis, and the distict processus pisiformis are typically galliform. Unfortunately, the caudal wall of the os metacarpale majus is missing, and therefore also the processus intermetacarpalis is not preserved, which is another typical galliform feature. So far, for the cmc, no distinguishing morphological characters are known between the taxa *Palaeocryptonyx* and *Palaeortyx* (Göhlich and Mourer-

Table 1 Measurements[a] of the coracoid and scapula of *Miogallus altus* from Gratkorn and additional Middle Miocene localities[b]

Coracoid/scapula	Locality	Age	GL	Lm	dWfas	Ws	Wp	Dp
Coracoid								
Miogallus altus	Gratkorn	MN(7+)8	~70	66.6	15	6.7	12.3	8.4
M. altus	Sansan[c]	MN6	-	-	-	6.5	-	
M. altus	La Grive-Staint-Alban	MN7+8	~63	-	14.2	5.8–6.5 (n=4)	-	
M. altus	Steinheim	MN7	66.1	63.2	~14	6.5	-	
M. altus	Toril 3A	MN7+8	60.5	-	-	-	12.5	7.9
Scapula						Wc	Wp	
M. altus	Gratkorn	MN(7+)8	-			6.6	~15.5	
M. altus	Steinheim	MN7	-			-	15.2–15.4 (n=2)	
M. altus	Sandelzhausen	MN5	-			6.5	16.1	

[a] Measurements are given in millimetres and definitions of measurement abbreviations are given in the Material and methods section

[b] Measurements of comparative material from Sansan (France), La Grive-Saint-Alban (France), Steinheim and Sandelzhausen (both Germany) by UBG in the collections of FSL, MNHN, SMNS, and BSPG; measurements for Toril 3A (Spain) from Sánchez Marco (2006)

[c] Type locality

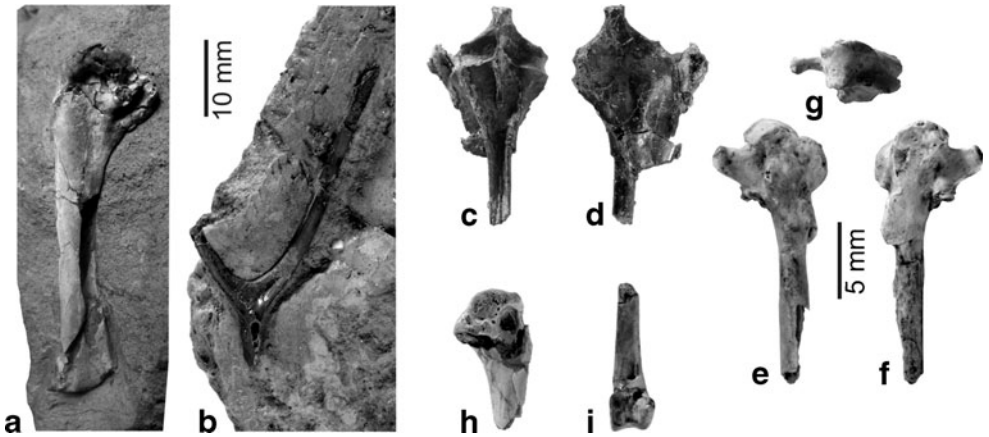

Fig. 3 cf. *Palaeocryptonyx edwardsi* (**a**–**g**), cf. *Palaeocryptonyx* sp. (**h**) and Galliformes indet. (**I**) from the late Middle Miocene of Gratkorn (Austria). Cf. *P. edwardsi*: Left humerus (UMJGP 204727), caudal view (**a**); furcula (UMJGP 204072), caudal view (**b**); cranial fragment of sternum (UMJGP 204042), ventral view (**c**), dorsal view (**d**); proximal end of right carpometacarpus (UMJGP 204680), ventral view (**e**), dorsal view (**f**), proximal view (**g**). cf. *Palaeocryptonyx* sp.: proximal end of right humerus (UMJGP 210965), caudal view (**h**). **I** Galliformes indet.: distal end of right tibiotarsus (UMJPG 210963) cranial view

Chauviré 2005). However, the cmc-fragment from Gratkorn falls perfectly in the size range of the cmc of *P. edwardsi* from its type locality (see Table 2).

Furcula (Fig. 3b): The incomplete furcula is preserved with its caudal side up in situ in a small sediment chunk. As typical for galliforms, the furcula is v-shaped and ends ventrally in a sagittal blade-like hypocleidium (apophysis furculae), which is partly broken. The scapi claviculae are thin, and both extremitates omales claviculae (epicleidia) are broken off. The caudal side of the ventral most part of both clavicles (extremitates sternales clavicularum) is concave.

Because of the lack of fossil galliform furculae in the Miocene record of Europe, no comparisons are possible. One very fragmentary furcula from Sansan (Milne-Edwards 1869–1871, pl.131, figs. 9, 10) referred to *Palaeortyx prisca* (Milne-Edwards, 1869) is untraceable (Göhlich and Mourer-Chauviré 2005: 1341), but based on Milne-Edwards' above-mentioned figures, the Sansan furcula is of a similar size to the present furcula from Gratkorn. This fits well with Göhlich and Mourer-Chauviré's (2005) observation, that *P. edwardsi* is "… middle-sized between *Palaeortyx gallica* and *Palaeortyx prisca*, but corresponds in some bones more to *P. prisca*."

Sternum (Fig. 3c, d): Preserved is the cranial-most portion of the sternum (corpus sterni), including a part of the cranial edge of the carina. The shape of the spina interna rostri and of the sulci articulares coracoidei, the ventrally extended, blade-like spina externa (partly broken) pierced by a small foramen, the strongly caudoventrally receding cranial edge of the spina, the deep sulcus carina bordered by two distinct ridges diverging towards cranial are typically galliform. No sternum has been described of *Palaeocryptonyx* so far. In size, the sternum corresponds best to those of the extant *Perdix perdix*. However, the shape of the ventral margins of the sulci articulares coracoidei are more similar to those of the slightly larger extant *Alectoris rufa*, whereas in *Perdix perdix* they are more rounded, convex cranially. Also, the lengths (in cranial direction) of the diverging ridges bordering the sulcus carina, the small size of the foramen piercing the base of the blade-like spina externa and the two dents on the dorsal surface of the corpus sterni correspond more with the morphology in *A. rufa* than in *P. perdix*.

Table 2 Measurements[a] of the humerus and carpometacarpus of cf. *Palaeocryptonyx edwardsi* from Gratkorn (Austria) and the type locality La Grive-Saint-Alban (France)[b]

Humerus/carpometacarpus	Locality	Age	GL	Wp	Ws	Wd
Humerus		Age	GL	Wp	Ws	Wd
Palaeocryptonyx edwardsi	Gratkorn	MN(7+)8	~46–47	~12.5	~5	-
P. edwardsi	La Grive-Saint-Alban[c]	MN7+8	44.3–47.3 ($n=12$)	11.6–12.5 ($n=12$)	4.2–4.7 ($n=12$)	8.7–9.6 ($n=10$)
Carpometacarpus				Dp		
P. edwardsi	Gratkorn	MN(7+)8		7.3		
P. edwardsi	La Grive-Saint-Alban[c]	MN7+8		~6.7–8.0 ($n=13$)		

[a] Measurements are given in millimetres and definitions of measurement abbreviations are given in the Material and methods section

[b] Measurements of comparative material by UBG in the collections of FSL and ML

[c] Type locality

All four bones (humerus, cmc, furcula, sternum) are assumed to belong to a single fossil phasianid taxon due to their dimensions, which are most similar to small-sized specimens of extant *P. perdix*.

The systematic determination is based on one morphological character of the humerus and the dimensions of humerus and cmc, which correspond best with those of *P. edwardsi* from the type locality from La Grive-Saint-Alban (MN7+8, France) and differ from those of the species of *Palaeortyx*. However, no furcula or sternum has been described to date of *Palaeocryptonyx*. The assignment of the latter two bones from Gratkorn, which are undoubtedly galliform, to this species is based only on their dimensions. Due to this fact and the damaged and/or fragmentary preservation of the humerus and carpometacarpus, respectively, all of these specimens are determined here as cf. *Palaeocryptonyx edwardsi*.

cf. *Palaecryptonyx sp*. (Fig. 3h)

Stratigraphical and geographical distribution of the genus: Late Early Miocene to Pleistocene in Europe (Göhlich and Mourer-Chauviré 2005, Göhlich and Pavia 2008, Sanchez Marco 2009, Pavia et al. 2012).

Material: Proximal end of right humerus, damaged (UMJGP 210965).

Remarks: The humerus fragment represents a small-sized galliform taxon, smaller than the species *Palaeocryptonyx edwardsi* described above. Compared to extant partridges and quails, it is smaller than *A. rufa*, *A. graeca* and *P. perdix*, but larger than the quail *Coturnix coturnix*. Compared to the Neogene galliforms from Europe, the material is metrically similar to the small-sized taxa of *Palaeocryptonyx* (*P. depereti*, *P. donnezani*, *P. hungaricus*) as well as of *Palaeortyx* (*P. gallica*).

Description and comparison

Humerus (Fig. 3h): Only a crushed proximal third of a right humerus is preserved. The presence of a double fossa pneumotricipitalis (fossa pneumotricipitalis ventralis and dorsalis) and the shape of the caput humeri and incisura capitis identify the humerus as galliform. As mentioned above, the main differences in the humerus morphology between *Palaeocryptonyx* and *Palaeortyx* are a shallower dorsal and a non-pneumatized ventral pneumotricipital fossa in *Palaeocryptonyx*. The dorsal pneumotricipital fossa in the Gratkorn specimen seems shallower than that in in *Palaeortyx*, but this might be forged by its crushed preservation; the ventral pneumotricipital fossa is partly filled with unremovable sediment which prevents evaluation of the presence of pneumatization. Another difference between *Palaeortyx* and *Palaeocryptonyx* (Zelenkov 2009) is a shallow and proximally indistinctly outlined sulcus ligamenti transversus for the latter genus, which is the case in the Gratkorn humerus. The distal border of the ventral pneumotricipital fossa—even if crushed—seems to be formed by a bony crest, often observed in *Palaeocryptonyx* (Göhlich and Pavia 2008).

Also the metrical comparisons are ambiguous. The humerus is only faintly larger (prox. width) than *P. depereti* and *P. hungaricus* and just overlaps with *P. donnezani* (all from their type localities), but it is also close in size to *Palaeortyx gallica* (Table 3). However, based on the morphological resemblance a reference to *Palaeocryptonyx* seems more likely.

To date, *P. donnezani* is recorded only from the Early Pliocene (MN15) to the Pleistocene (Sanchez Marco 2009), and *P. hungaricus* from the latest Miocene (MN13), whereas *P. depereti* is known from the Middle Miocene (MN7+8). Metrical comparisons would suggest a determination of the humerus as *P. donnezani*, but due to the disagreement with the stratigraphical record of this species and the fragmentary preservation of the bone the specimen is only determined with reservation on genus level.

Galliformes indet. (Fig. 3i)

Material: Distal end of right tibiotarsus (UMJGP 210963); fragmentary furcula (UMJGP 210964).

Description and comparison

Tibiotarsus (Fig. 3i): The distal third of a right tibiotarsus is preserved. The circular lateral condyle (in lateral view) and the general shape of the condyles, of the sulcus extensorius and of the pons supratendineus identify the specimen as belonging to a galliform. Morphologically, the tibiotarsi of *Palaeocryptonyx* and *Palaeortyx* cannot be distinguished (Göhlich and Mourer-Chauviré 2005), and they are only known for a few species of *Palaeocryptonyx* (see Table 4); no tt are known of *P. depereti* and *P. hungaricus* for comparison. The distal tt from Gratkorn is too small to belong to *P. edwardsi*, especially concerning the distal depth of the tt (Table 4). Unlike the above-described humerus fragment (UMJGP 210965) from Gratkorn referred to cf. *Palaeocryptonyx* sp., the tt is slightly larger than in *P. donnezani* but falls in the size range of *P. gallica* (defined as in Göhlich and Mourer-Chauviré 2005) (Table 4). However, the specimen allows no unambiguous systematic determination.

Furcula: A sternal portion of a furcula with its apophysis furculae is preserved; its projecting hypocleidium is broken off. The furcula can be identified as galliform due to its v-shape and the concavity of the caudal surface of the extremitates setrnales clavicularum. This furcula fragment is similar in size to the above-described furcula (UMJGP 204072) referred to cf. *P. edwardsi*, but differs from it by a distinct median ridge caudally on the apophysis furculae. The fragment allows no more precise determination.

Coliiformes Murie, 1872

Table 3 Measurements[a] of the proximal humerus of a small-sized species of cf. *Palaeocryptonyx* from Gratkorn (Austria) and of comparative material of different species of *Palaeocryptonyx* and of the similar-sized *Palaeortyx gallica* from their type localities in France (La Grive-Saint-Alban, Perpignan, and Saint-Gérand-le-Puy) and in Hungary (Polgàrdi)[b]

Humerus	Locality	Age	Wp
cf. Palaeocryptonyx	Gratkorn	MN(7+)8	~9.8
P. depereti	La Grive-Saint-Alban[c]	MN7+8	9.1–9.6 (n=3)
P. edwardsi	La Grive-Saint-Alban[c]	MN7+8	11.6–12.5 (n=12)
P. hungaricus	Polgàrdi[c]	MN13	8.8-9.7 (n=4)
P. donnezani	Perpignan[c]	MN15	9.7–10.1 (n=2)
P. gallica	Saint-Gérand-le-Puy[c]	MN2	10.0–11.2 (n=10)

[a] Measurements are given in millimetres and definitions of measurement abbreviations are given in the Material and methods section

[b] Measurements of comparative material by UBG in the collections of FSL and ML, measurements of *P. hungaricus* from Jánossy (1991)

[c] Type locality

Coliidae Swainson, 1837
Necrornis Milne-Edwards, 1871
Necrornis cf. *palustris* Milne-Edwards, 1871 (Fig. 4a–c)

Type locality: Sansan (Gers, France), Middle Miocene, Astaracian, MN6.
Stratigraphical and geographical distribution: Late Oligocene/Early Miocene of Germany (Mainz Basin) (Mayr 2010) and Middle Miocene of France [Sansan (MN6) and La Grive-Saint-Alban (MN7+8)]
Material: distal end of left tarsometatarsus (UMJGP 210968), two claws (ungual phalanges) of uncertain toe affiliation (Fig. 4d) (UMJGP 204144, UMJGP 210967).
Remarks: Todays' mousebirds (coliiforms) are restricted to Africa south of the Sahara and comprise six mostly frugivorous extant species within two genera. They are the sparse relicts of a once much more diversified bird group; the Paleogene fossil record was quite extensive in Europe and North America (Mayr 2009; Zelenkov and Dyke 2008; Mayr 2011; Mayr 2013). During the Early and Middle Miocene the number of coliid taxa decreased to three species (Zelenkov and Dyke 2008; Mayr 2010): *Necrornis palustris* Milne-Edwards, 1871, *Limnatornis archiaci* Milne-Edwards, 1871, and *L. paludicula* (Milne-Edwards, 1871) (including "*Picus*" *consobrinus* Milne-Edwards, 1871; see Brodkorb 1971). All of these species are described and documented from French localities (Milne-Edwards 1869; Ballmann 1969a; Cheneval 2000), and only *N. palustris* is additionally known from German deposits (Mayr 2010). Furthermore, Mlíkovský (2002) mentions an undescribed *Urocolius* sp. from the Late Miocene (MN10) from Austria (Kohfidisch). From the earliest Pliocene on, the fossil record of Coliidae is restricted to Africa (Rich and Haarhoff 1985; Zelenkov and Dyke 2008).

Description and comparison

Tarsometatarsus (Fig. 4a–c): The preserved distal end of the tmt can be identified as Coliidae due to the shape of the distal trochleae, especially the lateral wing-like flange of trochlea IV and the moderate medial wing-like flange of trochlea II. The general shape and arrangement of the distal trochlea II to IV resemble that of the extant *Colius*; however, in the Gratkorn specimen the medial flange of trochlea II is more distinct and more projecting plantarly; in the dorsal/plantar view trochlea II and IV are longer than in extant *Colius* whereby trochlea II reaches distally the level of trochlea III. In the Gratkorn specimen, the fossa metatarsi I is marked but not concave and situated medially but extending slightly on the plantar

Table 4 Measurements[a] of the distal tibiotarsus of a small-sized galliform species from Gratkorn and of comparative material of species of *Palaeocryptonyx* and of the similar-sized *Palaeortyx gallica* from their type localities in France[b]

Tibiotarsus	Locality	Age	Ws	Wd	Dd
Galliformes indet.	Gratkorn	MN(7+)8	2.8	5.8	5.7
Palaeocryptonyx edwardsi	La Grive-Saint-Alban[c]	MN7+8	3.0–3.4 (n=17)	5.9–6.5 (n=17)	6.0–6.5 (n=15)
P. donnezani	Perpignan[c]	MN15	2.6–2.7 (n=2)	5.3–5.5 (n=3)	5.4–5.5 (n=2)
P. gallica	Saint-Gérand-le-Puy[c]	MN2	2.6–3.1 (n=5)	5.3–6.0 (n=4)	5.2–6.0 (n=4)

[a] Measurements are given in millimetres and definitions of measurement abbreviations are given in the Material and methods section

[b] Measurements of comparative material by UBG in the collections of FSL, ML and MNHN and Göhlich and Mourer-Chauviré (2005) and Pavia et al. (2012)

[c] Type locality

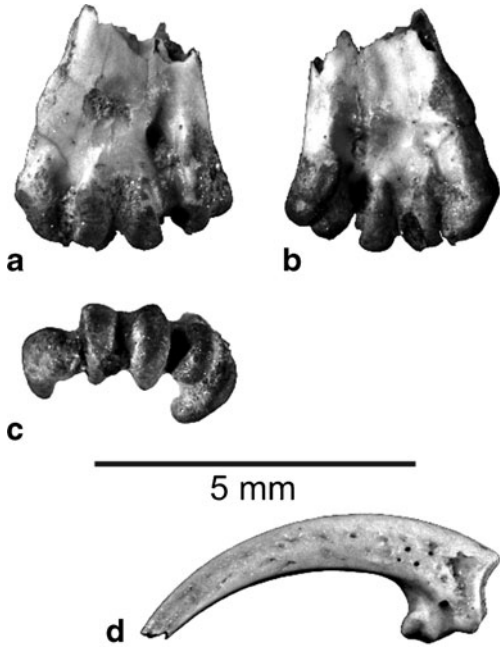

Fig. 4 *Necrornis* cf. *palustris* (**a**–**d**) from the late Middle Miocene of Gratkorn (Austria). Distal end of left tarsometatarsus (UMJGP 210968), dorsal view (**a**), plantar view (**b**), distal view (**c**), ungual phalanx (UMJGP 204144), lateral/medial view (**d**)

side. The foramen vasculare distale is relatively large and placed in a sulcus which is distally leading in the incisura intertrochlearis lateralis.

Tarsometatarsi of Miocene taxa are only known of *N. palustris* and of an *Urocolius* sp. With respect to the latter, which is mentioned by Mlíkovský (2002) from Kohfidisch (MN10, Austria), the Gratkorn tmt is slightly smaller (Table 5) and the trochlea metatarsi III differs in being shorter distally (only minimally surpassing trochlea II) and has slightly less prominent trochlea crests; furthermore trochlea II is slightly less abducted medially in the Gratkorn mousebird. *Necrornis palustris* is recorded from the late Oligocene/Early Miocene of the Mainz Basin (Germany) and the Middle Miocene of Sansan and La Grive-Saint-Alban, whereas the other two coliid species (*L. archiaci*, *L. paludicula*) are only known to date from the early Early Miocene (St-Gérand-le-Puy, France). The present distal tmt from Gratkorn morphologically and metrically corresponds well with those of *N. palustris* from the type locality Sansan (see Milne-Edwards 1869, pl. 178, figs 6–10; Cheneval 2000, fig. 24). The only slight deviance of the Gratkorn tmt in comparison with *N. palustris* from Sansan is that the medial trochlea of the second digit seems to be faintly longer distally. Therefore, the Gratkorn specimen is determined as *N*. cf. *palustris*.

Table 5 Measurements[a] of the distal tarsometatarsus of *N*. cf. *palustris* from Gratkorn (Austria) and of available comparative material[b]

Ncrornis. cf. *palustris* and comparable material	Locality	Age	Wd
N. palustris	Gratkorn (Austria)	MN(7+)8	3.4
N. palustris	Sansan (France)[c]	MN6	3.4–3.5 (*n* = 2)
Urocolius sp.	Kohfidisch (Austria)	MN10	3.8

[a] Measurements are given in millimetres and definitions of measurement abbreviations are given in the Material and methods section

[b] . Measurements of comparative material by UBG in the collections of MNHN and NHMW

[c] Type locality

Claws (ungual phalanges) (Fig. 4d): Unlike passerine claws, the two preserved ungual phalanges are proportionally very long and show no neurovascular sulcus along the medial and lateral side of the corpus. The plantar surface of the claws is flattened. No pedal claws of *Necrornis* or any other Miocene European coliidae are known so far. However, the claws of the extant mousebird genera *Colius* and *Urocolius* are very similar to the Gratkorn claws in overall shape and are also characterised by the absence of the neurovascular sulcus (Mayr 2013, Appendix 2). Therefore, the two claws are referred to the identified coliid taxon.

Aves indet. (Fig. 4d)

Material: Coracoid fragment, missing proximal and distal end (UMJGP 210966), preserved in situ in a sediment chunk with its dorsal surface exposed; distal end of a cmc (UMJGP 210969), half of a distal trochlea of a tt (UMJGP 210.970)

The listed bone fragments are all from small-sized birds. No systematic determination is possible due to their extremely fragmentary preservation or because the elements show no characteristic features.

Conclusion

The avifauna from Gratkorn is documented only by sparse fossils. At least three taxa of galliforms and a mousebird could be identified. *Miogallus altus* is the largest phasianid in the Miocene of Europe and is closest related to peafowl (*Pavo cristatus*) (Ballmann 1969a); the middle sized quail (cf. *Palaeocryptonyx edwardsi*) and a small-sized one (cf. *Palaeocryptonyx* sp.) are determined under reserve as the bones are fragmentary hampering definite systematic affiliation. Another small-sized galliform bone fragment seems not to belong to the small-sized cf. *Palaeocryptonyx* sp., but might represent a fourth taxon. All these galliform taxa have been known before from other Middle Miocene localities in Europe. Noteworthy is the presence of mousebirds, which have only very rarely been proven in the Miocene of Europe and which are restricted today to the African continent south to the Sahara. The fossils were identified here as *Necrornis* cf. *palustris* and are the first evidence of this species in Austria. A number of

other bird fossils were too fragmentary to be determined systematically. All identifiable taxa are typical terrestrial birds; there is no evidence of any aquatic bird taxon in the fossil record of Gratkorn. Today's mousebirds inhabit a broad range of afrotropical habitats from dry habitats (semideserts, savannas and scrubland) to woodlands (and anthropogenic landscapes, such as parks, etc.) only avoiding dense forests (De Juana 2001). Water birds have been discussed by Gross et al. (2011) as possible passive dispersers for allochthonous charophyte gyrogonites found in Gratkorn, but there is no evidence of aquatic birds by fossils as yet. Prieto et al. (2010) and Gross et al. (2011) explained the extreme local concentration of small vertebrate fossils found in Gratkorn as the result of pellet accumulations at feeding/resting places of birds of prey, especially owls. Even if we agree with this interpretation, no raptor remains could be found so far in the Gratkorn avifauna.

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