

The Avifauna of the Miocene Fossil-Lagerstätte Sandelzhausen (Bavaria, Southern Germany)

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ABSTRACT

The early Middle Miocene (MN5) fossil site of Sandelzhausen (Upper Freshwater Molasse, Bavaria, Southern Germany) is well-known for its vertebrate fauna, especially its mammals. This study presents the complete avifauna, which is the rarest represented vertebrate class in Sandelzhausen despite approximately 600 remains. 14 different taxa of 6 orders can be confirmed with the passeriforms most frequently represented. Additionally Galliformes (Phasianidae: *Mio-*

phasianus altus, *Palaeortyx intermedia*, Phasianidae gen. et sp. indet.), Anseriformes (Anatidae: *Mionetta blanchardi*, *Mionetta natator*; Anseriformes gen. et sp. indet.), Accipitriformes (gen. et sp. indet. A, B, C), Strigiformes (gen. et sp. indet. A, B) and Gruiformes (Gruidae: *Palaeogrus mainburgensis*, Gruiformes indet.) are identified. *Palaeogrus mainburgensis* is a unique species found only in Sandelzhausen.

KURZFASSUNG

Die früh-mittelmiozäne (MN5) Fossilfundstelle Sandelzhausen (Obere Süßwassermolasse, Bayern, Süddeutschland) ist bekannt für ihre reiche Wirbeltierfauna und besonders ihre Säugetiere. Diese Arbeit stellt die gesamte Vogelfauna vor, die mit immerhin 600 Stücken die quantitativ am wenigsten gut repräsentierte Wirbeltiergruppe in Sandelzhausen ist. 14 verschiedene Taxa, verteilt auf 6 Ordnungen, konnten nachgewiesen werden, wobei die Passeriformes mit Abstand zahlen-

mäßig dominieren. Belegt sind weiterhin die Galliformes (Phasianidae: *Miophasianus altus*, *Palaeortyx intermedia*, Phasianidae gen. et sp. indet.), Anseriformes (Anatidae: *Mionetta blanchardi*, *Mionetta natator*; Anseriformes gen. et sp. indet.), Accipitriformes (gen. et sp. indet. A, B, C), Strigiformes (gen. et sp. indet. A, B) und Gruiformes (Gruidae: *Palaeogrus mainburgensis*, Gruiformes indet.). *Palaeogrus mainburgensis* ist bisher nur aus Sandelzhausen bekannt.

1. INTRODUCTION

The site of Sandelzhausen is located near the town of Mainburg in Bavaria (Southern Germany), about 70 km north of Munich in the center of the North Alpine Foreland Basin (fig. 1). The latter is bounded by the river Danube in the north and the Alps in the south and is filled with Tertiary sediments. Its

uppermost part that crops out superficially is the Miocene limnofluviatile Upper Freshwater Molasse. Teams from the Institute for Palaeontology and the Bavarian State Collection Munich conducted systematic excavations in Sandelzhausen from 1969 to 1975 and from 1994 to 2001 under the supervision

of V. FAHLBUSCH (Munich). To date, these excavations have yielded approximately 30,000 identifiable specimens, representing about 170 palaeozoological species (pers. comm. V. FAHLBUSCH), most of them vertebrates. The richness of this continental vertebrate fauna and the extraordinary systematic diversity make Sandelzhausen an exceptional site. The fauna is dominated by vertebrates, although only represented by isolated disarticulated remains. Molluscs are represented by freshwater and terrestrial gastropods as well as rare freshwater bivalves (GALT 1972). Freshwater ostracods (WITT 1998), algal gyrogonites, and fruits of terrestrial angiosperms (*Celtis*, *Gleditsia*) are also rare components. Within the vertebrates, mammals are the most common fossils, followed by fishes, amphibians, and reptiles. Birds are the rarest vertebrates found, with around 600 remains. The presence of birds in the deposits of Sandelzhausen has been known since the beginning of the diggings (FAHLBUSCH & GALT 1970: 393), but they have never been determined or described. This study deals with the entire bird material and presents the complete avifauna of Sandelzhausen.

1.1 GEOLOGY

The fossiliferous limnofluviatile deposits in Sandelzhausen reach a maximum of 3 meters in thickness. In general, the marly sediments show a decrease of quartz pebbles in frequency and size from the bottom to the top. In the lower half of the section there is a brown-colored "coaly" lignite layer of 2,5 - 5 cm (fig. 7). Some horizons show a concentration of carbonate concretions. The fossils are concentrated in and around the humous "coaly" layer, while large-sized fossils are more often found in the deposits below the "coaly" layer. The deposits arguably cover a time span ranging from some hundred to thousands of years (SCHMID 2001).



Fig. 1: Geographic position of the site Sandelzhausen with schematic illustration of the extension of the Upper Freshwater Molasse without Quaternary cover.

Investigations by HESSIG (1997) on mammal biostratigraphy of the Upper Freshwater Molasse in Bavaria showed the faunal position of Sandelzhausen in the early Middle Miocene (MN 5 = European Mammal Neogene Unit MN5, Badenian) with an absolute age of around 16 Ma. Several studies on the geology and on different faunal groups of Sandelzhausen have already been published (cited in FAHLBUSCH & LIEBREICH 1996 and ZILGLIER 2000).

1.2 METHODS

Most of the bird remains, as well as thousands of invertebrate and vertebrate microfossils, were obtained by screen-washing in the field. The osteological terminology principally follows BAUMHÜTER et al. (1993) and occasionally BALLMANN (1969a, b); measurements were taken after VON DEN DRIFSCHE (1976).

Abbreviations

Osteology – CMC: carpometacarpus, TT: tibiotarsus, TMT: tarsometatarsus, dist.: distal, prox.: proximal, sin.: sinister, dext.: dexter, cran.: cranial, caud.: caudal.

Measurements – GL: greatest length, L: length, Bp: width proximal, Bd: width distal, BTd: width Trochlea distal, Dp: diagonal proximal, Dd: diagonal distal, KC: smallest width of corpus, Hp: height proximal, Hd: height distal, HpA: diagonal height proximal with apophysis flexoris inclusive, Td: depth distal, Tp: depth proximal.

The material is housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSP). Only a few specimens are held at the Staatliches Museum für Naturkunde in Stuttgart (SMNS).

Collections – BMNH: British Museum of Natural History, London; BSP: Bayerische Staatssammlung für Paläontologie und Geologie, München; SAPM: Staatssammlung für Anthropologie und Paläoanatomie, München; FSL: Faculté des Sciences de la Terre, Université Claude Bernard Lyon 1, Villeurbanne; ISEAK: Instytut Systematyki i Ewolucji Zwierząt, Krakow (Institute of Systematics and Evolution, Polish Academy of Sciences); LAC: Laboratoire d'Anatomie comparée, Muséum National d'Histoire Naturelle, Paris; LPVM: Laboratoire de Paléontologie des Vertébrés, Université Montpellier; MAFI: Magyar Állami Földtani Intézet, Budapest (Hungarian Geological Survey); MH: Muséum d'Histoire Naturelle (Musée Guimet), Lyon; MNHN: Muséum National d'Histoire Naturelle, Paris; NMB: Naturhistorisches Museum Basel; RGM: Rijksmuseum van Geologie en Mineralogie, Leiden (= Nationaal Natuurhistorisch Museum Leiden); SMNS: Staatliches Museum für Naturkunde, Stuttgart; UPM: Department des Sciences de la Terre, Marseille.

Country: A: Austria, D: Germany, F: France, I: Italy, H: Hungary, CZ: Czech Republic, E: Spain, MOL: Moldavia, PL: Poland, R: Romania, SL: Slovakia (see tab. 6)

2. SYSTEMATIC PALAEONTOLOGY

Order Anseriformes WAGLER, 1831

Family Anatidae VIGORS, 1825

Subfamily Dendrocheninae LIVEZELY & MARTIN, 1988

Genus *Mionetta* LIVEZELY & MARTIN, 1988

Mionetta blanchardi (MILNE-EDWARDS, 1863)

(pl. 1, figs. 1, 2, 3)

Synonymy:

- 1863 *Anas blanchardi* – MILNE-EDWARDS: 60.
v 1983 *Dendrochen blanchardi* (MILNE-EDWARDS, 1863) – CHENEVAL: 88-91, pl. 1, fig. 1 (with synonymy).

Locus typicus: St.-Gérand-le-Puy (Allier, France).

Stratum typicum: Lower Miocene, Aquitanien, MN2a.

Lectotype: TT (MNHN Av 8231) assigned by CHENEVAL (1983: 88, 91).

Original diagnosis: MILNE-EDWARDS (1863: 160).

Extended diagnosis: CHENEVAL (1983: 90): «tibiotarse d'une taille intermédiaire entre celle des espèces actuelles *Dendrocygna javanica* (dendrocygne de Java) et *D. viduata* (dendrocygne veuf); surface articulaire interne bien creusée, à bord postérieur très développé; crête enémiennne externe importante, crête fibulaire longue; gouttière tendineuse large, à bord interne très fin et à bord externe creusé d'une gouttière du peroneus profundus profonde; condyle interne très fin (longueur = 77,7 mm, largeur de l'épiphysse distale = 9,1 mm).»

Stratigraphical and geographical distribution: France: St.-Gérand-le-Puy (Lower Miocene, MN2a, MILNE-EDWARDS 1863, CHENEVAL 1983); Germany: Ravolzhausen (Lower Miocene, MN1-2, Rheinhessen, MARTINI 1974), Weisenau (Lower Miocene, MN1, LAMBRECHT 1933); Czech Republic: Skiritz (Lower Miocene, MN3-4, LAMBRECHT 1933); Romania: Credin, a (Upper Miocene, KESSLER 1992), Malușteni (Lower Pliocene, MN15, KESSLER, 1992).

Remarks: FRAAS (1870) described *M. blanchardi* in Steinheim (Middle Miocene, MN7), but VON AMMON (1918) changed this determination to *Anas risgoviensis*.

Created as *Anas blanchardi* by MILNE-EDWARDS in 1863, CHENEVAL (1983) moved *blanchardi* to *Dendrochen* - Subfamily Dendrocheninae REICHENBACH, 1850 - a genus created by MILLER (1944) for a humerus from the Lower Miocene of South Dakota, USA. Based on osteological and phylogenetically significant characters of the Anseriformes, LIVEZELY & MARTIN (1988) placed *blanchardi* in their new genus *Mionetta*.

Previous osteological descriptions were provided by MILNE-EDWARDS (1863), HOWARD (1964), CHENEVAL (1983), LIVEZELY & MARTIN (1988).

Material and measurements (mm):

BSP 1959 II

Humerus dext., prox. half	8271	KC: 5.2, Bp: 17.5
Humerus sin., dist. end	8274	KC: 5.4, Bd: (11)
CMC sin., prox. end	8380	Bp: 9.1
CMC dext., prox. end	8292	Bp: 9.1
CMC sin., dist. half	8301	Dd: 5.8
Radius sin., prox. half	8288	Dp: 4.3

Description:

Humerus: one proximal half (BSP 1959 II 8271) and one distal end (BSP 1959 II 8274) of a humerus are preserved. The crista bicipitalis is broken off on BSP 1959 II 8271. The fossa pneumotricipitalis is shallow and closed (non pneumatic) and the opening of the fossa pneumotricipitalis is nearly horizontal, also in ventral view. The fossa pneumotricipitalis is enclosed by a prominent edge, also at its cranial side. In ventral view the crus ventrale fossae is rectilinear, nearly horizontal, somewhat ascending caudally; the tuberculum ventrale is barely protruding distally. On the caudal side the caput humeri is limited distally by a distinct margin; in its ventral half the caput is somewhat undermined distally. The tuberculum dorsale is roundish and prominent. The margo caudalis flattens in proximal direction proximally before reaching the caput humeri and the tuberculum dorsale. The sulcus transversus extends and deepens ventrally. On the distal humerus, BSP 1959 II 8274, the epicondylus ventralis and the processus flexorius are broken off. The impression in the fossa musculi brachialis is shallow, but distinct and broadens proximodorsally. The fossa olecrani bears a longish horizontal furrow. The sulcus humerotricipitalis is shallow and short.

Carpometacarpus: Proximal end (BSP 1959 II 8380) with a trochlea carpalis is somewhat extended proximodistally. The processus pisiformis is protruding cranially. Processus extensorius is slender and long with a processus alularis protruding dorsally. The distal half (BSP 1959 II 8301) consists only of the os metacarpale major; the os metacarpale minor is missing. The cross-section of os metacarpale major is rounded triangular. The longitudinal tendon furrow along the sulcus interosseus narrows dorsally. The shallow sulcus tendineus starts at the middle level of the symphysis metacarpalis distalis and slightly broadens as it extends proximocranially.

Radius: The proximal half (BSP 1959 II 8288) with a roundish cotyla humeralis. The tuber bicipitalis radialis is blunt and close to the cotyla. The cross-section of the corpus is roundish.

Comparison and discussion: Within the four species of anseriforms in Sandelzhausen *Mionetta blanchardi* is represented with the most specimens (at least four individuals). The most diagnostic fossil is the proximal humerus, specimen BSP 1959 II 8271. It is characterized specifically by a shallow and closed (non pneumatic) fossa pneumotricipitalis; herewith it differs from the genus *Anas* and the Anserinae in general. Following WOOLFENDEN (1961) and LIVEZELY & MARTIN (1988: 198, 207) the genus *Anas* and the Anserinae are characterized by an open pneumatic fossa pneumotricipitalis. Although the

genus *Aythya* is also marked by a closed fossa pneumotricipitalis (CHENEVAL 1987: 150), the fossa is deeper in comparison. Moreover the humerus of the Miocene species *Aythya chauvireae* is a little smaller (CHENEVAL 2000, tab. 1). Although clearly corresponding morphometrically with *M. blanchardi* from St.-Gérand-le-Puy, the present proximal humerus differs by one feature: the enclosure of the fossa pneumotricipitalis has a prominent edge all around; the craniodistal margin clearly separates the fossa from the shaft. The distal humerus (BSP 1959 II 8274) is morphometrically in accordance with *M. blanchardi*, but is also very similar to that of *Anas velox*. Comparisons show no distinct features between the distal humerus end of *M. blanchardi* from St.-Gérand-le-Puy and *A. velox* from Sansan.

Because of the closed fossa pneumotricipitalis and the relatively longer wing bones (in proportion to the leg bones) MILNI-EDWARDS (1863: 160) and LIVETZUY & MARTIN (1988: 196) concluded that *Mionetta blanchardi* was moderately specialized for diving rather than for flying.

Mionetta natator (MILNI-EDWARDS, 1867)

(pl. I, figs. 4, 5)

Synonymy:

- v 1867 *Anas natator*, nov. sp. – MILNI-EDWARDS, vol. I: 148, pl. 25, fig. 14-22.
- v 1983 *Dendrochen blanchardi* (MILNI-EDWARDS, 1867-71) – CHENEVAL: 93-94, pl. I, fig. 3 (with synonymy).

Locus typicus: St.-Gérand-le-Puy (Allier, France).

Stratum typicum: Lower Miocene, Aquitanien, MN2a.

Lectotype: Ulna (MNHN Av 6428) figured by MILNI-EDWARDS (1867-71: pl. 25, fig. 21-22), assigned by CHENEVAL (1983: 93).

Original diagnosis: MILNI-EDWARDS (1867-71: 148ff).

Extended diagnosis: CHENEVAL (1983: 93): «Cubitus d'une taille très inférieure à celle de *Dendrochen blanchardi*; saillie du ligament articulaire antérieur peu marquée; impression du brachialis anticus peu profonde, mais allongée le long de la diaphyse; tubérosité carpienne bien courbée vers le côté interne; dépression radiale inférieure étroite et profonde (longueur = 50,8 mm, largeur de l'épiphyse proximale = 6,6 mm, largeur de l'épiphyse distale = 5,3 mm).»

Stratigraphical and geographical distribution: France: St.-Gérand-le-Puy (Lower Miocene, MN2a, MILNI-EDWARDS 1863, CHENEVAL 1983); Germany: Weisenau (Lower Miocene, MN1, LAMBRECHT 1933), Kastel Bruch (Upper Oligocene, LAMBRECHT 1933); Czech Republic: Skiritz (Lower Miocene, MN3-4, LAMBRECHT 1933, MLIKOVSKÝ 2000a); Moldavia: Kishinev (Upper Miocene, MN9, KESSLER 1992).

Material and measurements (mm):

	BSP 1959 II
Coracoid sin., prox. end	8269 KC: 3.1
Coracoid sin., prox. end	8982 KC: 3.4
Humerus sin., prox. end	8272 Bp: 11.3
Ulna sin., dist. end	8284 Dd: 5.7
TT sin., dist. end	8312 Bd: 4.9, Td: 5.0

Description:

Coracoid: Both remains are only proximal fragments with the processus procoracoideus broken off. The processus acrocoracoideus is damaged on BSP 1959 II 8982. Both specimens

Plate 1

All figures double size.

Mionetta blanchardi (MILNI-EDWARDS, 1863)

Fig. 1: Humerus dexl. proximal end; a: caudal, b: cranial, c: medial (BSP 1959 II 8271).

Fig. 2: Humerus sin., distal end; cranial (BSP 1959 II 8274).

Fig. 3: Carpometacarpus sin., proximal end; a: dorsal, b: ventral (BSP 1959 II 8380).

Mionetta natator (MILNI-EDWARDS, 1867)

Fig. 4: Humerus sin., proximal end; a: caudal, b: cranial (BSP 1959 II 272).

Fig. 5: Coracoid sin., proximal half; dorsal (BSP 1959 II 8982).

Anseriformes gen. et sp. indet.

Fig. 6: Ulna sin., proximal end; cranial (BSP 1959 II 8281).

Fig. 7: Phalanx dig. II 1 dext.; a: dorsal, b: ventral (BSP 1959 II 8379).

Stringiformes gen. et sp. indet. B

Fig. 8: Phalanx III 2; a: dorsal, b: lateral, c: plantar (BSP 1959 II 8336).

Fig. 9: Phalanx III terminahts, claw; medial (BSP 1959 II 8330).

Strigiformes gen. et sp. indet. A

Fig. 10: Phalanx III terminalis, claw; medial (SMNS 54005).

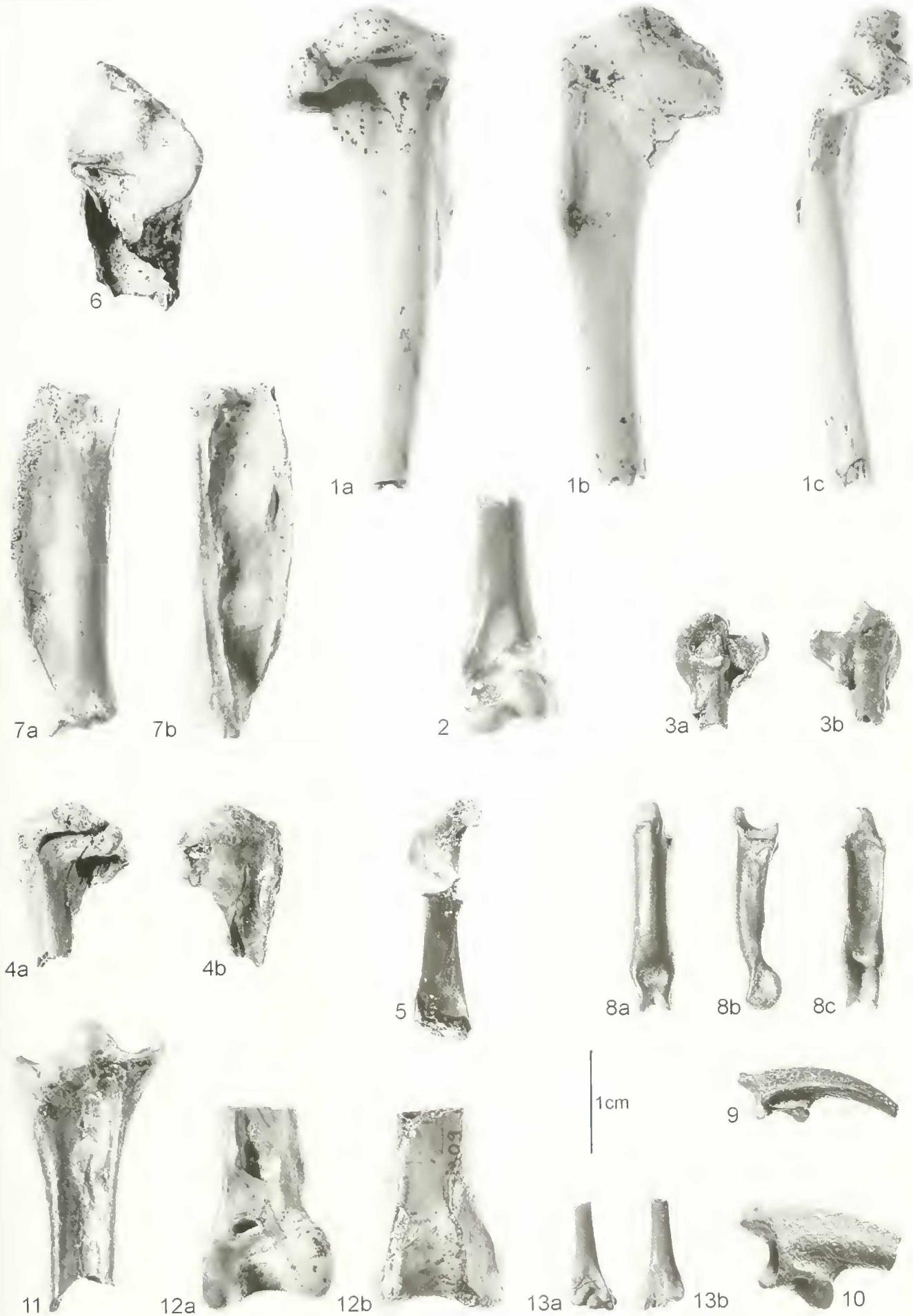
Palaeognathus mamburgensis (GOHLICH, in press)

Fig. 11: Tarsometatarsus dext., proximal end; dorsal (BSP 1959 II 8319, paratype).

Fig. 12: Tibiotarsus sin., distal end; a: cranial, b: caudal (BSP 1959 II 8309, holotype).

Gruiformes indet.

Fig. 13: Humerus dext., distal end; a: cranial, b: caudal (BSP 1959 II 8279).



are characterized by a rounded off triangular-shaped and deep cotyla scapularis, and by a shallow concave facies articularis humeralis with a laterally protruding margin. The impressio ligamenti acrocoracohumeralis is distinct and longish oval. The distal edge of the processus acrocoracoideus (tuberculum brachiale) medially shows a little incision between the facies articulares clavicularis. Whereas BSP 1959 H 8982 lies within the metrical variability of *M. natator* from St.-Gérand-le-Puy, BSP 1959 H 8269 is a bit smaller (own direct comparison).

Ulna: The preserved distal end represents a tiny ulna with a short but pointed tuber carpale. A sulcus intercondylaris is present distoventrally, but is absent distally. No incisura tendinosa can be observed.

Tibiotarsus: Only the distal fourth is preserved. The pons supratendineus is damaged. Both condylus medialis and lateralis are slender and therefore the incisura intercondylaris is wide. Along the preserved corpus, the sulcus extensorius is bounded medially by a crest. The sulcus musculus fibularis, epicondylus medialis and lateralis and tuberculum retinaculi musculi fibularis are very weak.

Humerus: Only the proximal end is preserved. The interior of the fossa pneumotricipitalis is badly preserved, but seems to be shallow. The opening of the fossa pneumotricipitalis is nearly horizontal in ventral view. The caput humeri is slightly damaged, caudally it is bordered distally by a distinct margin and it is somewhat hollowed out distally in its ventral half. The tuberculum ventrale is barely protruding distally. The tuberculum dorsale is longish, but weak. The sulcus transversus extends and deepens ventrally.

Comparison and discussion: All described elements are distinctly smaller than *Mionetta blanchardi*, *M. consobrina*, *Anas sansanensis* and *Aythya chauvirei*. The small sized *Anas velox* from Sansan metrically corresponds in some bones (e. g. ulna dist.), or is only little larger (e. g. tibiotarsus dist.), but the apparent shallow fossa pneumotricipitalis of the humerus contradicts an allocation of these small sized anatids from Sandelzhausen to *Anas* (see WOOLFENDEN 1961, LIVEZI & MARTIN 1988: 198, 207). The proximal humerus and the distal tibiotarsus from Sandelzhausen are a little smaller than those of *M. natator* from St.-Gérand-le-Puy (humerus prox. Bp: 13.6–15.0 mm, n=3; tibiotarsus dist. Bd: 5.7–7.4 mm, n=4, CHENFVAI 1983, tab. 1), but the latter represent only a very few specimens. The distal tibiotarsus from Skiritz (Czech Republic) is also a little smaller than those from St.-Gérand-le-Puy (Bd: 5.5 mm, LAMBRECHT 1933: 358).

Mionetta natator and *Mionetta blanchardi* were formerly known from Early and Late Miocene deposits (tab. 6), thereby the specimens from Sandelzhausen are the first evidence in the Middle Miocene.

Anseriformes gen. et sp. indet. (pl. 2, figs. 6, 7)

Material and measurements (mm):

BSP 1959 II

Ulna sin., prox. end	8280	Bp: 12.6
Ulna sin., prox. end	8281	Bp: 14.1, Dp: 18.2
Phalanx prox. digitii majoris dext.	8379	L: 33.7, GL: 34.6, Bp: 8.7

Description and discussion: The specimens belong to an anseriform taxon of distinctly larger size than the two species described above.

Ulna: Only represented by two proximal ends. The olecranon projects ventrally and surpasses the roundish cotyla ventralis ventrally. The cotyla dorsalis is protruding dorsally and cranially turns down distally in form of a lip. Dorsally beneath the processus cotylaris dorsalis lies a dent with the impressio scapulotricipitalis. The tuberculum ligamenti collateralis beneath the olecranon bears a distinct longish facies, that deepens at its proximal half. The impressio brachialis (only preserved on BSP 1959 II 8280) is longitudinal and narrow.

By the means of their size, these proximal ulnas probably belong to the Anserinae. Specimen BSP 1959 II 8280 is somewhat smaller than BSP 1959 II 8281. However, comparisons with the measurements of some extant Anserinae (BACHER 1967) show that the dimensions (width prox. of ulna) of both specimen are within the metrical variability.

For most of the Neogene anserine species the ulnas are not known. The proximal end of the ulna of *Anser oenningensis* (Middle Miocene, Oeningen, Germany, VON MEYER 1865) and of *Anserorbranta tarabukini* (Upper Miocene, Kishinev, Romania, KUROCHKIN & GANEA 1972) are somewhat larger; that of *Cygnus cygniformis* (Middle Miocene, Steinheim, Germany) is distinctly larger.

Phalanx proximalis digitii majoris (Ph. dig. II 1): The complete preserved bone is long and slender. The pila cranialis is cranially flattened; dorsally a weak sulcus runs along the whole pila. The caudal wing is about the same width along the distal $\frac{2}{3}$ and distally surpasses the pila a little bit. The wing shows a longish and shallow concavity on the ventral side and dorsally there are two concavities with the proximal one more shallow than the distal one. Between them, there is a longitudinal protuberance close to the caudal end of the wing. The proximal end is triangular with a two-pointed dorsal end. The ventral and caudal margin of the proximal end are weakly concave.

Because of missing comparative fossil material, all these specimens are not determinable.

Order Accipitriformes VIILLOT, 1816

Three taxa of accipitriforms can be distinguished by their size, although they are not taxonomically determinable. For morphometrical comparisons the following extant and fossil (European Neogene) species have been considered:

Extant: *Pandion haliaetus*, *Pernis apivorus*, *Milvus milvus*, *Milvus migrans*, *Accipiter gentilis*, *Accipiter nisus*, *Buteo buteo*, *Buteo lagopus*, *Hieraetus fasciatus*, *Aquila chrysaetos*, *Aquila heliaca*, *Heliacetus albicilla*, *Heliacetus leucocephalus*, *Aegypius monachus*, *Gyps fulvus*, *Circus cyaneus*, *Circus aeruginosus*, *Falco peregrinus*, *Falco subbuteo* (these studied extant species are housed in the SAPM).

Fossil: *Buteo pusillus*, *Aquila pannatooides*, *A. delphinensis*, *Aquilavus depredator*, *A. corroyi*, *A. priscus*, *Hieraetus edwardsi* (including Syn. *Aquila minutus*), *Haliacetus piscator*, *Milvus deperditus*, *Promilho incertus*, *Palaeobuteo gervaisii*, *Garganoactus freudenthali*, *G. murivorus*, *Falco medius*,

Pelargopappus magnus [these fossil species are studied either by means of their original description or personally by the author (for the localities: St.-Gérard-le-Puy, Sansan, La Grive), see tab. 1].

Family Accipitridae VIEU LOT, 1816

Accipitridae gen. et sp. indet. A
(figs. 2, 3)

Material and measurements (mm):

BSP 1959 II

TMT sin. distal halt	8320	KC: 4.5, Bd: 10.8, Td: 7.0
TMT dext. distal end	8997	Bd: 13.9, Td: 8.5
TT sin. distal end	8308	Bd: 10.4, Td: (7)
Phalanx IV? terminalis (claw)	8329	Bp: 3.1, Hp: 3.8, HpA: 5.2
Phalanx I/II terminalis (claw)	8996	Bp: 5.8, Hp: 6.5, HpA: 10.1

Description:

Tarsometatarsus: One distal half of a tarsometatarsus sin. and one distal end of a tarsometatarsus dext. are preserved. The tarsometatarsus BSP 1959 II 8997 is somewhat larger than

BSP 1959 II 8320. The latter is relatively delicate. The trochleae metatarsi II and III are the same length while trochlea metatarsi IV is a little shorter. In dorsal view the trochlea metatarsi III is very slightly oblique from distally lateral to proximally medial. Maximal width of the trochlea metatarsi III is 3.2 mm (BSP 1959 II 8320) and 4.1 mm (BSP 1959 II 8997). The fossa metatarsi I is slender and 8 mm in length (BSP 1959 II 8320). Distally it extends to the level of the proximal end of the foramen vasculare distale.

Tibiotarsus: The distal end of the tibiotarsus is damaged caudally. The trochlea cartilaginis tibialis caudally stretches far proximally. The condyli are relatively short. The canalis extensorius passes obliquely from distally medial to proximally lateral. The oblique distal aperture of the canalis extensorius reaches up to the medial edge of the diaphysis. The proximal aperture of the canalis extensorius is located approximately midwidth of the diaphysis; it tapers off distally and extends to the level of the proximal end of the distal aperture.

Phalanx IV? terminalis (claw): The small claw is nearly complete, only the outermost tip is broken off. The apophysis

Species	Locality	age	Collection	GL	Dp	KC	Bd	Td
TT								
Accipitridae indet. A	Sandelzhausen D	MN5	BSP	-	-	-	10.4	(7)
Garganoaetus freudenthalii	San Giovannino* (Gargano), I	MN13	RGM	(210)	-	14	26	-
Hieraatus edwardsi (formerly <i>Aquila minuta</i>)	Sansan*, F	MN6	MNHN	-	-	-	9.0	7.1
Hieraatus edwardsi	Sansan*, F	MN6	MNHN	-	15.5	-	-	-
Aquilavus predator	St.-Gérard-le-Puy*, F	MN2a	MNHN	-	-	8.6	-	-
Aquilavus priscus	St.-Gérard-le-Puy*, F	MN2a	MNHN	-	-	9.2	16.9	(13)
Pelargopappus magnus	Phosphorites of Quercy*, F	Eocene/ Oligocene	MNHN	-	-	-	15.3	18.0
Pelargopappus schlosseri	Phosphorites of Quercy*, F	Eocene/ Oligocene	ML, LPVM MNHN	-	-	10.0-10.5 [3]	15.2-17.0 [3]	17.2-18.5 [2]
TMT								
Accipitridae indet. A	Sandelzhausen, D	MN5	BSP	-	-	4.5	10.8	7.0
			BSP	-	-	-	13.9	8.5
Garganoaetus freudenthalii	San Giovannino* (Gargano), I	MN13	RGM	132	23-26	-	-	25-27
Garganoaetus murivorus	Chiro 10C* (Gargano), I	MN13/14	RGM	-	-	-	-	18
Aquila delphinensis	La Grive*, F	MN7+8	ML	-	19.7 (10.7)	<11.2	-	-
Aquila pennatoides	La Grive*, F	MN7+8	ML	-	13.3	<6.6	-	-
Hieraetus edwardsi	Sansan*, F	MN6	MNHN	-	-	4.5	12.3	(7)
Palaeohirax gervaisii	St.-Gérard-le-Puy*, F	MN2	MNHN	88.7	16.9	14	8.6-9.7 [2]	18.1
Promilio (<i>Milvus</i>) incertus	Chavroches, St.-Gérard-le-Puy*, F	MN2	ML	56.9	9.5	6.4	4.4	10-11 (5)
<i>Milvus</i> perdeperitus	St.-Gérard-le-Puy*, F	MN2	MNHN	46.1	8.8 (5.7)	4.2	(10)	-
Aquilavus predator	St.-Gérard-le-Puy*, F	MN2	MNHN	102.9	16.1	13.3	8.2-9.8	20.6
Aquilavus priscus	St.-Gérard-le-Puy*, F	MN2	MNHN	(100)	-	-	(10)	(22)
Aquilavus corroyi	Phosphorites of Quercy*, F	Eocene /Oligocene	UPM	62.5	11.4	-	6.1	12.6
Aquila? hypogea	Phosphorites of Quercy, F	Eocene /Oligocene	? ML	-	-	-	4.8	10
Pelargopappus magnus	Phosphorites of Quercy*, F	Eocene /Oligocene	MNHN	214.1	21.8	20.0	8.3	20.0-20.4
	St.-Gerand-le-Puy, F	MN2a	MNHN	(215)	21.8	18.6	8.3	[2] 20.4
Pelargopappus schlosseri	Phosphorites of Quercy*, F	Eocene /Oligocene	ML, LPVM MNHN	-	-	-	7.4	16.0-18.2
							[2]	[5] 10.2-12.0
								[6]

Tab. 1: Comparison of measurements of Tertiary accipitrid tibiotarsi and tarsometatarsi. Own measurements, except those from Sansan (CHENEVAL 2000: tab. 2), from the Phosphorites of Quercy (MOURER-CHAUVIR & CHENEVAL 1983: tab. 1), from Gargano (BALLMANN 1973, 1976) and for *Aquilavus priscus* measured from MILNE-EDWARDS (1867-71: pl. 184, fig. 1-4). Type locality marked by *; estimated measurements in (); number of specimen in [].

extensoris is long. The proximal articular facet is relatively symmetrical and pyriform. The apophysis flexoris is also long and ends plantarely to a pointed edge.

Phalanx I/II terminalis (claw): The claw is complete. It is long and slender and distinctly larger than the Ph. IV terminalis described above.

Comparison and discussion: Based on their dimensions, these elements might belong to the same species. They represent the smallest of the three recorded taxa of accipitrids in Sandelzhausen. The two recorded tarsometatarsi differ in size. But studies on extant accipitrids show that the size of the tarsometatarsi can vary up to 25% (concerning the distal width) e. g. in *Accipiter gracilis*, which is known to have the largest dimorphism in size (SCHMIDT-BURGER 1982: 116). So the difference in size of the two described tarsometatarsi, amounting to 22%, can be assumed to be within the variation of one species. Beyond that, the two tarsometatarsi are morphologically identical. The tibiotarsus and tarsometatarsus differ from the family Falconidae by the lack of an additional second distal opening of the canalis extensorius on the tibiotarsus and by the more plantar position of the trochlea metatarsi IV and the more medial orientation of the processus of the trochlea metatarsi II on the tarsometatarsus (in distal view). Compared with extant taxa of Accipitridae and by means of morphology, the tarsometatarsus and the tibiotarsus seem to be closest to the buzzard *Buteo buteo*.

The Tertiary European species like *Aquilaetus predator*, *A. priscus*, *Aquila delphinensis*, *A. pomatioides*, *Palaeohierax gervaisii*, *Garganoaetus freudenthalii*, *G. murivorus*, and *Pelargopappus magnus* are distinctly larger (see tab. 1). The distal tarsometatarsi of both *Aquila pannatoides* and *A. delphinensis* from La Grive (MN7+8, France) are not known. However, *A. delphinensis* has a much broader shaft than can be assumed for the present specimens. *Aquilaetus predator* and *A. priscus* (both from St.-Gérand-le-Puy, MN2, France) differ by a larger distal tarsometatarsus. *Aquilaetus corroyi* (from the Paleogene of Quercy, France) is similar in size, but is distinguished by a shortened trochlea IV (in dorsal view) and a lacking plantar protuberance on trochlea II (in medial view).

Promicho incertus (formerly in *Milvus*) from the Lower Miocene of St-Gerand-le-Puy (France) is metrically similar to the distal end of the tarsometatarsus from Sandelzhausen, but in distal view the medial processus of the trochlea metatarsalis II is shorter and the plantar processus of the trochlea metatarsalis IV is not present in *P. incertus*.

In the distal half of the tarsometatarsus of *Milvus perditus* from the Lower Miocene of St-Gerand-le-Puy (France) the fossa metatarsi I is somewhat elongated proximally, thereby longer. Additionally, in contrast to the Sandelzhausen specimen, the processus of the trochlea metatarsalis II in dorsal view surpasses the trochlea distally and in distal view it arises from the trochlea metatarsalis II by a well-marked angle.

Hieraetus edwardsi (Sansan, MN6, France) is similar in size, but differs in morphology: the trochlea metatarsalis III of

Hieraetus edwardsi is oriented more obliquely in dorsal view. *Palaeohierax gervaisii* (St-Gérand-le-Puy, MN2, France) is distinctly larger. *Milvus perditus* (St-Gérand-le-Puy, MN2, France) is only known by the holotype, a tarsometatarsus without trochlea II. In comparison the trochlea III is distinctly smaller. *Promicho incertus* (Chavroches, France) is similar in size, but differs by the lack of the plantarely protruding protuberance on the trochlea IV. *Pelargopappus magnus* and *P. schlosseri* (Phosphorites of Quercy, France, Eocene to Oligocene) as well as *Garganoaetus freudenthalii* and *G. murivorus* (Gargano, Italy) are distinctly larger.

Unfortunately there are some Neogene accipitrid taxa where both the tarsometatarsus and tibiotarsus are not known - like the fossil buzzard *Buteo pusillus* (carpometacarpus from La Grive, MN 7+8, BALLMANN 1969a) or the fossil eagle *Haliaetus pector* (carpometacarpus and phalanges from Sansan, MNI - EDWARDS 1867-71, CHENEVAL 2000). After BALLMANN (1973: 10f), the tarsometatarsus of buzzards and eagles can only be distinguished by characters of the proximal end, but which is not yet represented in Sandelzhausen. So with the present osteological knowledge of fossil accipitrids, a definitive systematic determination of these bones is not possible.

The claws are referred to this taxon on account of their size; they are too small to belong to the both larger taxa of accipitrids from Sandelzhausen. Metrically the phalanges are very similar to the claws of digit IV and I/II of extant *Buteo buteo*.

Accipitrids gen. et sp. indet. B (fig. 5)

Material and measurements (mm):

BSP 1959 II

Phalanx I I dext. 8376 L: 23.5, Bp: 9.5, IIp: 5.1, KC: 5.0, BTd: 5.7
Phalanx I I dext. 8377 L: 23.3, Bp: 9.7, IIp: 5.5, KC: 5.3, BTd: 6.0

Description:

Phalanx I I: Both specimens are complete. The proximal end is dorsoplantarely flattened and shows a medial indentation. The plantar side of the shaft is weakly concave. The distal trochlea is flattened proximally.

Comparison and discussion: These phalanges represent the middle-sized of the three recorded accipitrid taxa. As mentioned before, taxon A is comparable in size with extant *Buteo buteo* and taxon C is in the size range of the Golden Eagle (*Aquila chrysaetos*), which will be shown below. Compared with these species and considering the sexual dimorphism, the phalanges I I are definitively too big to belong to the accipitrid taxon A and too small to belong to the accipitrid taxon C.

There are only a few taxonomically determined fossil phalanx I I. Three specimens are known from Sansan and determined all to belong to *Hieraetus edwardsi* (CHENEVAL 2000: 341, tab. 2). According to own studies the variation in size of these phalanges seems to be too large to refer them all to the same species. The phalanx I I from Sandelzhausen correspond to the two smaller specimens from Sansan.

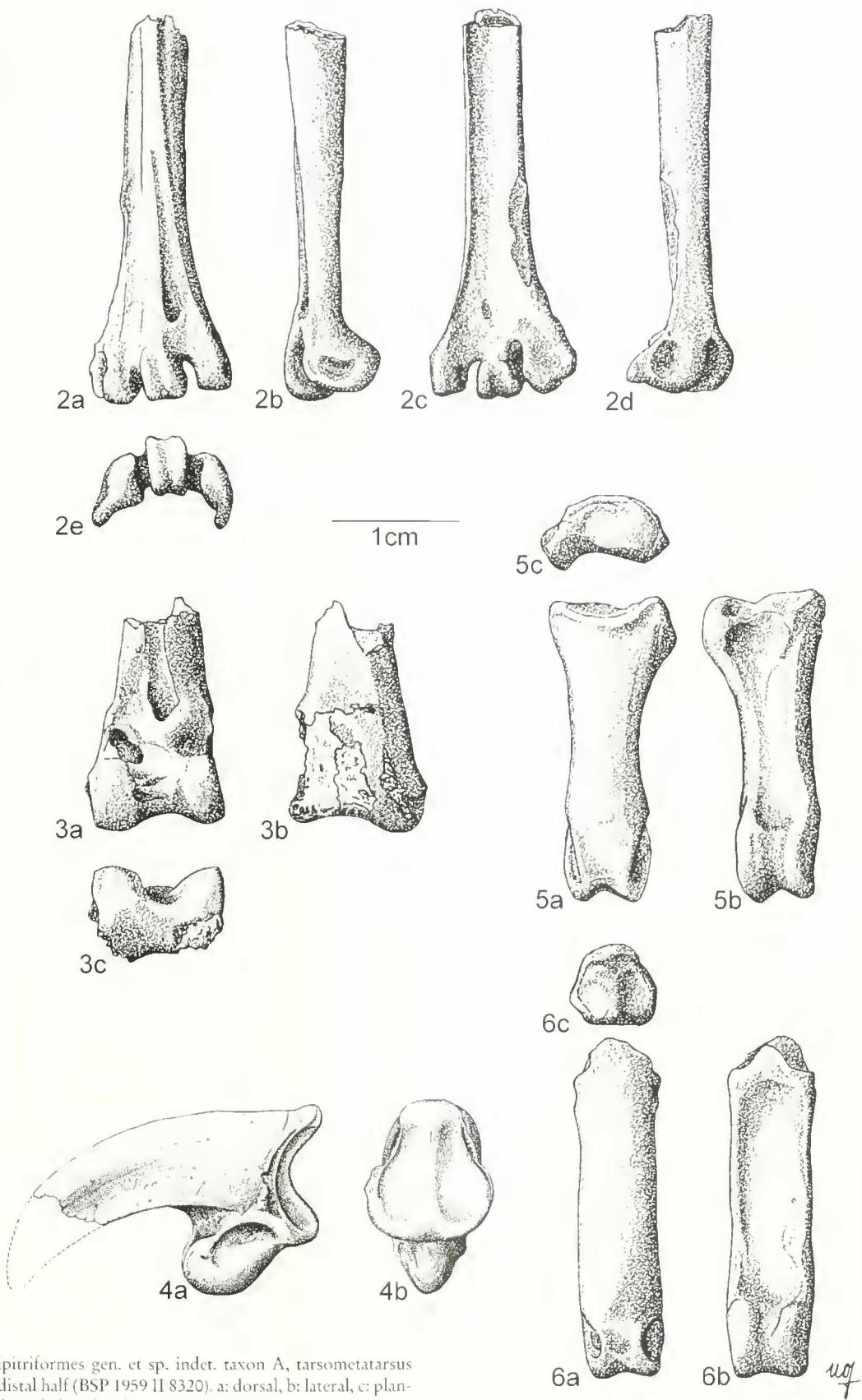


Fig. 2: Accipitridae gen. et sp. indet. taxon A, tarsometatarsus sin. distal half (BSP 1959 II 8320). a: dorsal, b: lateral, c: planter, d: medial, e: distal.

Fig. 3: Accipitridae gen. et sp. indet. taxon A, tibiotarsus sin. distal end (BSP 1959 II 8308). a: cranial, b: caudal, c: distal.

Fig. 4: Accipitridae gen. et sp. indet. taxon C, phalanx I/II terminalis (claw) (BSP 1959 II 8327). a: lateral/medial, b: proximal.

Fig. 5: Accipitridae gen. et sp. indet. taxon B, phalanx I I dext. (BSP 1959 II 8377). a: dorsal, b: plantar, c: proximal.

Fig. 6: Accipitridae gen. et sp. indet. taxon C, Phalanx III 3 (BSP 1959 II 8378). a: dorsal, b: plantar, c: proximal.

Accipitriformes gen. et sp. indet. C
(figs. 4, 6)

Material and measurements (mm):

BSP 1959 II

Phalanx I/II terminalis (claw)	8326	Bp: 8.6, Hp: 9.8, HpA: 15.3
Phalanx I/II terminalis (claw)	8327	Bp: 9.1, Hp: 10.5, HpA: 15.1
Phalanx III 3	8378	GL: 26.0, Bp: 6.6, Hp: 6.2, BTd: 6.4

Description:

Phalanx I/II terminalis (claw): The two claws with broken off tips belong to the digit I or II. Both specimen show a long apophysis extensoris and apophysis flexoris. Both the apophysis extensoris and flexoris of BSP 1959 II 8327 are a little longer than those of BSP 1959 II 8326, especially in dorsal and plantar view. The proximal two-parted articular facet is pyriform and symmetrical.

Phalanx III 3: In lateral view the phalanx is bent proximally convex. The proximal two-parted articular facet is relatively symmetrical. The plantar side of the corpus is concave. The distal trochlea is dorsoplantarely flattened.

Comparison and discussion: These phalangeal remains represent the large sized accipitrid taxon. In lateral view the claws show a characteristic apophysis extensoris as well as a long protruding slender apophysis flexoris. Both features are known from buzzards, eagles and hawks. Vultures, however, generally do not show a clear apophysis extensoris (BALLMANN 1973: 12). The claws are distinctly larger than those of *Hieraetus edwardsi* from the Middle Miocene of Sansan (France, see MILNE-EDWARDS 1867-71, CHENEVAL 2000). However, they are morphometrically similar to those from St-Gérand-le-Puy (France, Lower Miocene, see MILNE-EDWARDS 1867-71: pl. 183, figs. 17-21), which are not taxonomically determined.

In comparison with extant accipitriforms the phalanx III 3 is very close in size and morphology to that of the Golden Eagle (*Aquila chrysaetos*). Compared with the few known suitable fossils, the phalanges III 3 of *Hieracetus edwardsi* from Sansan are smaller (see CHENEVAL 2000: tab. 2), and a single undetermined specimen from St-Gérand-le-Puy (MILNE-ED-

WARDS 1867-71: pl. 183, fig. 26-29) is larger and somewhat more slender. Very close in size and morphology are the fossils of *Haliaetus piscator* from Sansan (CHENEVAL 2000: 337ff). But the scanty material allows no allocation.

Order Galliformes TEMMINCK, 1820

Family Phasianidae VIGORS, 1825

The galliforms are represented by 3 taxa of Phasianidae in the avifauna of Sandelzhausen. Within the galliforms partridges are in general represented more abundantly in the European Miocene than pheasants (CHENEVAL 2000: 343), as is the case in Sandelzhausen. Most of the galliform remains of Sandelzhausen belong to *Palaeortyx intermedia* followed in quantity by *Miophasianus altus*; only two fragments represent a tiny Phasianidae indet.. *Palaeortyx intermedia* has been known from older deposits and can now be confirmed in MN 5 (tab. 6).

Genus *Miophasianus* LAMBERT, 1933

Miophasianus altus (MILNE-EDWARDS, 1869)

(pl. 2, figs. 1-4)

Synonymy:

- ✓ v 1869 *Phasianus altus*, nov. sp. – MILNE-EDWARDS, vol. 2: 239-241, pl. 131, fig. 27-36.
- v 2000 *Miophasianus altus* (MILNE-EDWARDS, 1869-71) – CHENEVAL: 351-352, figs. 9-11 (with synonymy).

Lectotype: tarsometatarsus dext., prox. end (MNHN Sa 1221), lectotype fixation by CHENEVAL (2000: 351f), figured in MILNE-EDWARDS (1869-71: pl. 131, fig. 27-29).

Locus typicus: Sansan (Gers, France).

Stratum typicum: Middle Miocene, Astarac, MN 6.

Original diagnosis: MILNE-EDWARDS (1869-1971: 239ff): «L'une d'elles [Gallinacés de Sansan] paraît très-voisine des Faisans, et à raison de ses dimensions, je l'ai désignée sous le nom de *Phasianus altus*.»

«La portion supérieure du métatarsale de ce Faisan présente en effet les caractères propres aux oiseaux dont le genre

Plate 2

Figures 1-4 in natural size, figures 5-10 in double size.

Miophasianus altus (MILNE-EDWARDS, 1869)

Fig. 1: Femur sin.; a: cranial, b: caudal, c: proximal, d: distal (BSP 1959 II 8382).

Fig. 2: Tarsometatarsus dext.; a: dorsal, b: plantar, c: distal (BSP 1959 II 2207).

Fig. 3: Ulna dext. distal end; a: dorsal, b: ventral (BSP 1959 II 8980).

Fig. 4: Tibiotarsus sin.; a: cranial, b: lateral, c: caudal, d: proximal, e: distal (BSP 1959 II 8381).

Palaeortyx intermedia BALLMANN, 1969

Fig. 5: Tarsometatarsus sin., distal end; a: dorsal, b: plantar (SMNS 54006/1).

Fig. 6: Humerus sin., distal end; a: cranial, b: caudal (BSP 1959 II 8273).

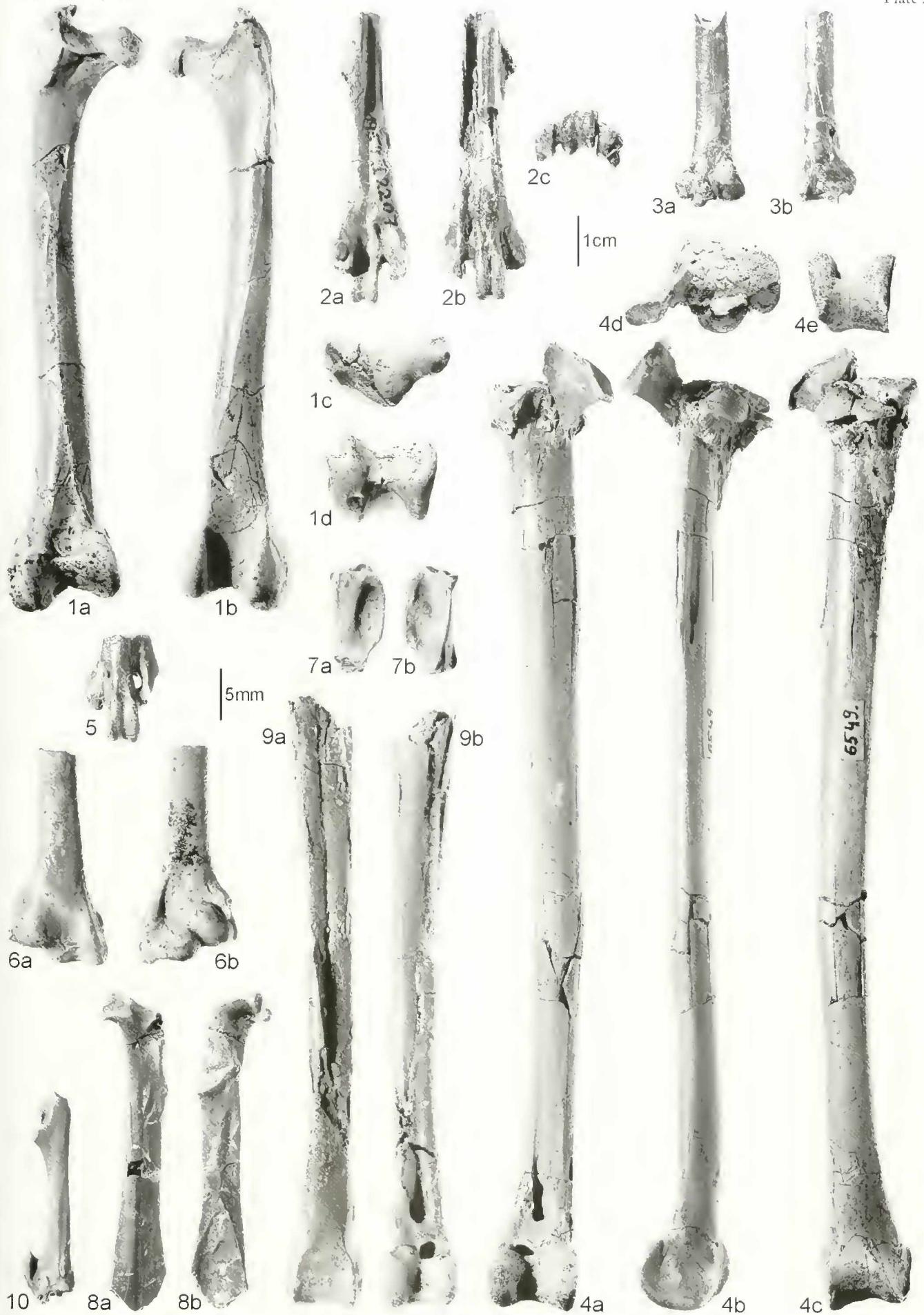
Fig. 7: Phalanx dig. II 1 dext.; a: dorsal, b: ventral (BSP 1959 II 8331).

Fig. 8: Coracoid sin.; dorsal (BSP 1959 II 8270).

Fig. 9: Tibiotarsus dext., distal end; a: cranial, b: caudal (BSP 1959 II 8307).

Phasianidae indet.

Fig. 10: Carpometacarpus dext., distal 2/3; dorsal (BSP 1959 II 8291).



Phasianus se compose, et elle ressemble plus à celle du Faisan commune qu'à toute autre espèce. L'impreinte d'insertion du muscle tibial antérieur est située un peu plus bas que d'ordinaire; elle est unique et assez saillante. La dépression qui la surmonte est évasée, et, au fond, on aperçoit l'ouverture des deux pertuis supérieurs qui sont placés à la même hauteur. La coulisse de l'extenseur des doigts est assez large et limitée de chaque côté par une petite crête bien marquée. Les facettes articulaires tibiales, situées à peu près au même niveau, sont grandes, arrondies et séparées par une tubérosité intercondylienne peu saillante. Le talon est bien développé; la gouttière tubulaire est largement ouvert, et sa surface postérieure présente trois coulisses dont l'externe très-courte est séparée de l'interne par une crête forte et arrondie. [...] ...et os [métatars]...aurait dépassé en longueur celui du plus grand Phasianide actuel, le *Crossoptilon auritum*... .[.]»

«La tête articulaire inférieure [du tibia] est presque aussi grosse que celle de Paon; mais le corps de l'os est notablement plus grêle. [...] La coulisse de l'extenseur commun des doigts est évasée, mais sa levre interne est peu saillante. Le pont osseux sustendineux est moins large que chez le Tetras et disposé comme dans le genre *Phasianus*. La coulisse du court pectorier est située sur le bord externe et limitée de chaque côté par une petite crête bien accusée. Le condyle externe est peu élargi et la gorge intercondylienne antérieure est plus évasée et moins profonde que chez les Paons. La gorge rotulienne est lisse et ses bords sont très-saillants latéralement. [...] À raison de sa taille, on ne peut pas davantage le [*Phasianus altus*] confondre avec les espèces provenant de Pikermi et décrites par M. GAUDRY sous le nom de *Phasianus archiaci* et de *Gallus aesculapii*.»

Stratigraphical and geographical distribution:
 France: La Grive (Middle Miocene, MN7+8, BAILMANN 1969b), Sansan (Middle Miocene, MN6, CHENEVAL 2000), Vieux Collonges (Lower Miocene, MN4; BAILMANN 1972; *Miophasianus* sp., might belong to *M. altus* after CHENEVAL 2000: 352). Germany: Attenfeld (Middle Miocene, MN6?; SCHLOSSER 1916), Dechbetten near Regensburg (Middle Miocene, MN5, VON AMMON 1918; *M. augustus*), Oehningen (Middle Miocene, MN7, LYDFKIR 1891), Steinheim (Middle Miocene, MN7, HETZMANN & HESSE 1995). Poland: Przeworno II (Middle Miocene, MN6-7, BOCHENSKI 1987). Slovakia: Devinska Nova Ves (= Neudorf an der March, Middle Miocene, MN 6, VEC 1986). Spain: Corcoles (Middle Miocene, MN 5, ALFREZ et al. 1982; *Miophasianus* sp., may belong to *M. altus* after CHENEVAL 2000: 352), Valles Penedes (Upper Miocene, VILLAITA & CRUSAJONT PAIRO 1950).

Material and measurements (mm):

	BSP 1959 II
Scapula sin., cran. end	8383c Dc: 16.1, B: 6.5
Humerus dext., fragm.	8383d Bp:((18)), Bd: ((17.5)) strongly deformed
Ulna dext., dist. third	8980 KC: 6.6, Dd: 13.7, Bd (Trochlea): 11.8
Femur sin.	8382 GI: 116, L: 109, Bp: 24.0, Tp: 14.3, KC: 9.5, Bd: 21.7, Td: 17.5
TT sin.	8381 GL: (188), La: 178, Dp: ((32)) KC: 8.8, Bd: 17.5, Td: 16.3
TT dext., dist. end, fragm.	8314 Td: (16.3)
TT sin., dist. end	8383a Bd: 13.4, Td: 12.7
TT dext., dist. end	8383b Bd: 12.9, Td: (12.6)
TMT dext., male, dist. half	2207 Bd: 17.8
TMT dext., female, dist. half	8995 -

Species	Locality	Age	Collection	GL	Bp	Tp	KC	Bd	Td
Scapula									
<i>Miophasianus altus</i>	Steinheim, D	MN7	SMNS	-	-	-	(15 2-15 4) [2]	-	-
Humerus									
<i>Miophasianus altus</i>	La Grive, F	MN7+8	ML, FSL, BMNH	103 2	24 3-26 1 [4]	-	9 9	20 7-21 1 [2]	-
	Steinheim, D	MN7	SMNS	100 5	(25 9)-27 0 [2]	-	9 6-10 0 [2]	19 7-21 0 [2]	-
<i>Palaeoperdix medius</i>	La Grive, F	MN7+8	ML	-	17 7	-	6 4	-	-
	Przeworno II, Pl	MN6-7	ISEAK	-	(15.5)-16 4	-	-	-	-
Femur									
<i>Miophasianus altus</i>	Steinheim, D	MN7	SMNS	101	21	-	-	19	-
	Dechbetten, D	MN5	?	100	20	-	-	20	-
TT									
<i>Miophasianus altus</i>	Sansan*, F	MN6	MNHN	-	-	-	7 8	>16	15.1
	La Grive, F	MN7+8	FSL	-	-	-	8 3	13 3-15 8 [2]	12 2-15 8 [3]
	Can Mas, E	MN3	?	-	-	-	-	16	-
	Steinheim, D	MN7	SMNS	-	-	-	-	15-16 [3]	15-16 [3]
<i>Palaeoperdix medius</i>	La Grive, F	MN7+8	FSL	-	-	-	-	(10)	(10 1)-10 3 [2]
	Przeworno II, Pl	MN6-7	ISEAK					10.7	(10 5)
TMT									
<i>Miophasianus altus</i>	Sansan*, F	MN6	MNHN*	-	15 3	13 7	-	-	-
	La Grive, F	MN7+8	ML, FSL, BMNH	-	15 1-18 5 [7]	15 4-16 5 [3]	7 5 [2]	16 4-18 0 [3]	-
<i>Palaeoperdix medius</i>	Sansan*, F	MN6	MNHN*	-	-	-	-	12 0	-
	La Grive, F	MN7+8	ML, FSL	-	(10 5)-12 0 [4]	11 2-12 0 [2]	5 2-(5 4) [2]	-	11.3

Tab. 2: Comparison of measurements (mm) of *Miophasianus altus* and *Palaeoperdix medius*. Own measurements, except those from Przeworno II (from BOCHENSKI 1987, tab. 2). Dechbetten (from VON AMMON 1918, formerly *Phasianus augustus*), and Can Mas (SANCHEZ-MARCO 1999). Type locality marked by *; estimated measurements in (); number of specimen in [].

All the remains with the Coll. No. BSP 1959 II 8383 apparently belong to the same individual since all of these bones were found within close proximity of one another. The same is applicable for the well-preserved femur and tibiotarsus (BSP 1959 II 8381-8382).

Description:

Scapula: The cranial extremity and a part of the affiliated crushed corpus are preserved. Although the acromion is slightly damaged, it can be recognized to be long, longer than in extant *Phasianus colchicus*.

Humerus: Proximal half and distal third of one humerus are badly crushed craniocaudally; proximal extremity additionally deformed dorsoventrally. The epicondylus ventralis is broken off. The condyli ventralis and dorsalis are galliform-shaped.

Ulna: The cross-section of the corpus is triangular. The incisura tuberculi carpalis is narrow and deep. The condylus ventralis ulnae is pointed and protruding distally. The sulcus intercondylaris is deepest in the cranial half.

Femur: Complete and well preserved; only the proximal ridge of the trochanter femoris is slightly damaged. The caput femoris shows two foveae ligamenti capitatis, with the cranial one a little larger than the caudal one. The trochanter femoris is cranially non pneumatic like in pheasants; instead there are just two slight dents. Laterocaudally the trochanter major ends in a projecting ridge. In lateral view well-marked impressiones obturatoriae (proximocaudally), an impressio musculi iliotrochanterici posterior (proximocranially) and below this, an impressio musculi iliotrochanterici anterior and the impressiones musculi iliofemoralis and ischiofemoralis (see BALLMANN 1969b) can be observed. The sharp-edged crista trochanteris flows into the linea intermuscularis cranialis, which extends distally to the medial condyle. The linea intermuscularis caudalis starts medially below the femoral caput and takes its course over the middle of the cranial corpus distally to the medial condyle. The corpus is slightly bent mediocaudally. The distal end of the femur is marked in cranial view by a broad sulcus patellaris and in medial view by a prominent proximo-craniial projection of the condylus medialis and by a large impression of the ligamentum collaterale mediale. Conspicuous in caudal view of the distal extremity is a large and distinct impressio ansae musculi iliofibularis. The supracondylar fossa poplitea is characteristically divided by two horizontal lineae.

Tibiotarsus: represented by the most specimens; three distal ends [BSP 1959 II 8383 a+b, BSP 1959 II 8314 (only a lateral half of the distal extremity, largest tibiotarsus specimen)] and one complete tibiotarsus (BSP 1959 II 8381), which is described here. The tibiotarsus is straight and slender. The surface of the proximal extremitas is damaged; the crista patellaris, crista enemialis cranialis and facies articulares lateralis and medialis are only partly preserved. Width of the facies articulares lateralis and medialis is about 20 mm. The crista fibularis is about 35 mm long. The cross section of the corpus is transverse-oval; two weak parallel ridges (linea interna and externa musculi peronei) along the lateral corpus side start from below the crista fibularis. Along the distal shaft lineas bound the sulcus peronei brevi; the lateral ridge (linea externa) flows into the longish tuberculum retinaculi m. fibularis. The apophysis externa

ligamenti obliqui is strong but blunt. The apophysis interna ligamenti obliqui is pointed. The sulcus extensorius tapers upwards in the lower third. The pons supratendineus is cranially weakly concave. The condylus medialis is somewhat more slender and proximally shorter than the condylus lateralis. The incisura intercondylaris cranially bears two transverse impressiones ligamenti intercondylaris, whereby the distal one is deeper (especially medially) than the proximal one. Caudally the trochlea cartilaginis tibialis is sharp-crested on both sides.

Tarsometatarsus: only two distal halves are preserved. BSP 1959 II 2207 (male): The corpus is craniocaudally compressed. A spur is present, but partly broken off. The plantar processus of the trochlea metatarsi IV is broken off. The trochlea metatarsi IV is somewhat shorter distally than the trochlea metatarsi II. The incisura intertrochlearis lateralis is wide. BSP 1959 II 8995 (female): The corpus is smashed, the trochlea II is broken off. There is a crista plantaris medialis along the medioplantar side of the shaft strong, but without a spur. This tarsometatarsus is a little smaller and more gracile than the male tarsometatarsus (BSP 1959 II 2207).

Comparison and discussion: *Miophasianus altus* is the largest species of phasianids from the European Miocene. Following VEC (1986), BOCHENSKI (1987) and CHENEVAL (2000) the species *Miophasianus desnoyeri* (MILNE-EDWARDS 1869-71), only known by a carpometacarpus from Touraine, France, and *Phasianus augustus* (VON AMMON 1918), represented only by a femur from Dechbetten near Regensburg, Germany, can be synonymized with *M. altus*. The validity of the taxon *Miophasianus maximus* (LYDEKKER 1893), only documented by a coracoid from La Grive, France, is not yet verified.

The smaller species *Miophasianus medius* was moved to *Palacoperdix* by CHENEVAL (2000); it is recorded in France (La Grive: BALLMANN 1969a, Sansan: CHENEVAL 2000), SW-Poland (Przeworno II: BOCHENSKI 1987) and Germany (Steinheim: HEIZMANN & HESSE 1995). Therefore, the genus *Miophasianus* contains only one species.

BALLMANN (1969a) and CHENEVAL (2000: 343) emphasize the approximation of *M. altus* to peacocks within the Phasianinae.

The scapula is morphometrically close to the only known scapulae of *M. altus* from Steinheim (SMNS 50881, 57963), where the acromion also is broken off.

The femora of *M. altus* have, as yet, been rarely found; the femur from Sandelzhausen is the largest known.

The complete tibiotarsus (BSP 1959 II 8382) is the largest known of *M. altus*. An additional distal tibiotarsus fragment can be assumed to be the same size. The other tibiotarsal remains are smaller (BSP 1959 II 8383a+b), but anyway larger than those of *P. medius* (tab. 2). Remains of similar small-sized *M. altus* are also found in La Grive. As previously recognized (e. g. HEIZMANN & HESSE 1995, *M. altus* from Steinheim), *Miophasianus* and the galliforms in general (e. g. ERBERSDOBLER 1968) show a sexual dimorphism with respect to size; males are distinctly larger than females. For the distal width of the tibiotarsus in extant *Phasianus colchicus* the maximum range within both males and females can be calculated (by the

measurements from ERBERSDOBLER 1968: 45, Bd max.: 11.8 mm, Bd min.: 8.8 mm) to be 34%; the variation of the same measurements of the fossil tibiotarsi studied here, is 35% (Bd max.: 17.5 mm, Bd min.: 12.9 mm). Therefore, the size range of the fossils is close to the maximum variation in extant *Phasianus colchicus*.

The two tarsometatarsi, one with the rest of a spur and one without any spur, represents each a male and a female individual, whereby the female specimen is smaller.

The species *Miophasianus altus* is represented in Sandelzhausen by at least 5 individuals.

Genus *Palaeortyx* MILNI-EDWARDS, 1869

Palaeortyx intermedia BALLMANN, 1969

(pl. 1, figs. 5-9)

Synonymy:

v 1969b *Palaeortyx? intermedia* n. sp. - BALLMANN: 33-34, pl. 1, figs. 1, 2.

v 1992 *Palaeortyx intermedia* BALLMANN 1966 - MOURER-CHAVIRE: 87, figs. 5h, i, 10a, b, n, 11a, d, e (with synonymy).

Diagnosis: see BALLMANN (1969b: 33). „Kleiner Hühnervogel, in der Größe zwischen *Palaeortyx gallica* und *Palaeortyx phasianoides*. [...]“ - For the osteological characters of the different bones see the descriptions in BALLMANN 1969b: 31, 33.

Lectotype: Coracoid (BSP 1937 H 18103), figured in BALLMANN (1969b: pl. 1, fig. 1-2).

Locus typicus: Wintershof-West, Southern Germany.

Stratum typicum: Lower Miocene, MN3.

Stratigraphical and geographical distribution: France: Phosphorites of Quercy (Eocene to Oligocene, MOURER-CHAUVIRE 1992), St.-Gérand-le-Puy (Lower Miocene, MN2; MILNI-EDWARDS 1867-71; MIKOVSKÝ 2000b does not approve *P. intermedia* in St.-Gérand-le-Puy, but put it into synonymy with *P. phasianoides*), Vieux-Collonges (Lower Miocene?, MN4?, BALLMANN 1972). Germany: Wintershof-West (Lower Miocene, MN3; BALLMANN 1969b) and Sandelzhausen (early Middle Miocene, MN5). Austria: Grund (early Middle Miocene, MN5, cf. *P. intermedia*, GOHRIK in press b).

Material and measurements (mm):

BSP 1959 II

Coracoid sin., prox. 2/3	8270	KC: 3.7
Humerus sin., dist. half	8273	KC: 3.9, Bd: 10.1
Humerus sin., dist. end	8275	Bd: 10.3
Humerus sin., dist. end	8981	Bd: 10.3
Humerus dext., dist. end	8384	Bd: 10.0
Ulna sin., dist. half	8283	KC: 3.7, Dd: 6.6
Phalanx proximalis digitii majoris dext.	8331	GL: 10.4
Phalanx proximalis digitii majoris sin.	8333	GL: 10.0
Phalanx proximalis digitii majoris sin.	8334	GL: 10.8
Phalanx proximalis digitii majoris dext.	8335	GL: 10.4
TT dext., dist. half	8307	Bd: 7.5, Td: 7.1
TT dext., dist. half	8311	KC: 3.7, Bd: 7.0, Td: (7.2)
TT sin., dist. half	8310	KC: 3.4, Bd: 7.0, Td: 6.9
TT dext., dist. end	8306	Bd: 7.1, Td: 7.1
TT sin., dist. end	8315	Bd: 7.0, Td: 7.1
TT sin., dist. end	8316	Bd: 6.5, Td: (6.4)
TT dext., dist. end	8317	Bd: 6.8
MI dext., dist. fragment	8322	trochlea metatarsi III: B: 3.0, T: 4.1
TT sin., corpus	8325	KC: 3.6

Material and measurements (mm) (continued):

SMNS

TMT sin., dist. fragment 54006/1 trochlea metatarsi III: B: 3.2, T: 4.5

Description:

Coracoid: The caudal end including facies is broken off. The processus procoracoideus is short and blunt. Foramen pneumaticum is absent. The impressio ligamentum acrocoracohumeralis is distinct and concave. The facies articularis scapularis is oriented obliquely to the longitudinal axis, its caudal half is a little concave. In medial view, the caudal end of the tuberculum brachiale is straight.

Humerus: Only distal ends are represented. The insertion of the musculus entepicondylo-radialis sublimis is located on the cranial crest of the epicondylus ventralis. The processus flexorius is lengthened ventrally in the distal direction, even surpassing the condylus ventralis; the processus flexorius is slender caudally and in ventral view its distal end is rather pointed in comparison. The condylus ventralis is strongly swollen distally, with distinct incisures to the condylus dorsalis and to the epicondylus ventralis. The fossa musculi brachialis lies very close to the ventral margin of the bone. Medially it is bordered by a sharp crest which flows into the tuberculum supracondylare ventrale. This is especially prominent in specimen BSP 1959 H 8273. On the cranial side above the processus supracondylaris dorsalis there is a roundish facet for the musculus extensor metacarpi radialis. Caudally a weak fossa olecrani is present; this is most distinct in specimen BSP 1959 H 8346.

Ulna: One distal half of an ulna is available. The condylus dorsalis ulnaris is distinct larger than the condylus ventralis ulnaris. The latter is distally sharp and protruding distally. The incisura tendinosa is indistinct.

Phalanx II 1 dig.: Four complete phalanges proximales digitii majoris are preserved. The small phalanges are short. The pila cranialis phalangis is flattened cranially and broadens distally. The fossa ventralis is longish-oval and deep. In ventral view the pila and fossa are about the same width in the middle of the bone. The fossa dorsalis is shallow and separated craniodistally to caudoproximally by a very weak bulge. In dorsal view the pila is thin and sharp-crested. The proximal facies articularis metacarpalis shows two parallel oblique crests, surpassed by the caudal end of the facies. The distal facies articularis phalangealis is an inverted heart shape.

Tibiotarsus: Represented only by distal halves or ends. The corpus and distal end is slender. The condylus medialis is thinner than the condylus lateralis. The incisura intercondylaris bears two vertical ligamental grooves. Cranially above the condylus lateralis, laterally of the pons supratendineus and at the level of the distal opening of the canalis extensorius there is a stout tubercle. The canalis extensorius runs a little oblique from distally medial to proximally lateral. The sulcus extensorius is midwidth of the corpus. Craniolaterally at the level of the proximal opening of the canalis extensorius, the sulcus peronei brevi begins. Specimen BSP 1959 H 8307 differs from the others by a more roundish shape of the distal opening of the canalis extensorius and by somewhat closer ligamental grooves in the incisura intercondylaris. These morphological deviation are apparently due to variability.

Tarsometatarsus: Only three fragments are preserved; one corpus with neither proximal nor distal ends (BSP 1959 II 8325), one fragmentary distal end with only the trochlea metatarsi II and III (SMNS 54006/1), and one fragmentary distal end with only the trochlea metatarsi III (BSP 1959 II 8322). In addition to the foramen vasculare distale, the specimen SMNS 54006/1 shows another tiny foramen at the same level, but above the incisure between the trochleae metatarsi III and IV. In distal view the plantar process of the trochlea metatarsi IV is oriented plantolaterally.

Comparison and discussion: For comparisons the following Neogene European galliform taxa were considered: *Palaeortyx phasianoides*, *P. gallica*, *P. prisca* (new combination and including *P. sansaniensis*, after CHENEVAL 2000), *P. brevipes*, *P. grivensis*, and *P. depereti* [which might be synonymous with *P. grivensis* after BALLMANN (1969a: 181, 1973: 25)], *Palaeocryptonyx grivensis*, *P. donnezani*, *P. hungaricus*, *P. edwardsi*, *Palaeoperdix longipes*, *P. sansaniensis*, *Plioperdix joleaudi*, *P. ponticus*, *P. capeki*, *P. subfrancolinus*, *Alectoris bavarica*, *Taoperdix miocaena*, *Coturnix miocaena*.

The present specimens of *Palaeortyx intermedia* differ from *P. phasianoides* by their smaller and from *P. gallica*, *P. brevipes*, *P. grivensis*, and *P. depereti* by their larger size (tab. 3, 4, 5). As typical for the humerus of *Palaeortyx* (BALLMANN 1969b: 31),

the processus flexorius is slender and caudally crest-like and the condylus ventralis is distally swollen. One of the more distinctive characters between *Palaeortyx* and *Palaeocryptonyx*, namely the more shallow fossa pneumotricipitalis in the latter, can not be considered due to lack of proximal humerus remains in the Sandelzhausen material. However, with respect to their larger size, they differ from all species of *Palaeocryptonyx* from La Grive, (France, MN 7+8; BALLMANN 1969a) and Perpignan (France, MN 15, DEPERET 1890). Following BALLMANN (1969b: 31), the straight caudal end of the tuberculum brachiale of the coracoid (in medial view) is typical for *Palaeortyx*. The coracoid corresponds well morphometrically with the type coracoid of *P. intermedia* from Wintershof-West, Germany. Although the tarsometatarsi are only preserved very fragmentary, these remains correspond well in direct comparison with those of *P. intermedia* from St.-Gérand-le-Puy. Until now no phalanx II 1 dig. of *P. intermedia* has been described. However, due to their galliform shape and their size, these remains are referred to *P. intermedia*.

In general, *Palaeoperdix longipes*, represented only by a few specimens from Sansan (France, MN6; CHENEVAL 2000), differs by its larger dimensions. Additionally the distal humeri of *P. longipes* are distinguished by a distinctly ventrodistally shorter entepicondyle. Measurements of the available fragmentary ulna and tibiotarsus correspond to those of *Palaeoperdix prisca*.

Species humerus	Locality	Age	Collection	GL	Bp	KC	Bd
<i>Palaeortyx phasianoides</i>	Wintershof-West, D	MN3	BSP	53 5-59 0 [3]	14 5-15 9 [3]	4 5-5 6 [3]	11 1-12 1 [3]
<i>Palaeortyx phasianoides</i> <i>grivensis</i> (incl. <i>Palaeortyx</i> <i>edwardsi</i> , see BALLMANN 1969b)	La Grive*, F	MN7+8	FSL, ML, BMNH	55 7-56 7 [4]	13 0-15 [7]	4 3-5 2 [4]	9 4-11 4 [7]
<i>Palaeortyx grivensis</i> (incl. <i>Palaeortyx depereti</i> , see BALLMANN 1969b 181, 1973: 25)	La Grive*, F	MN7+8	ML, FSL	32 9-37 0 [7]	8 0-9 3 [10]	2 7-3 3 [10]	6 1-7 5 [10]
	Gargano, I	MN13-14	RGM	30-33 [20]	-	-	-
<i>Palaeortyx brevipes</i>	St.-Gérand-le-Puy*, F	MN2	MNHN	35 6-35.7 [2]	8 2-9 3 [2]	2 6-3 0 [2]	7 0-7 2 [2]
	Phosphorites of Quercy		NMB	33 7	8.4	3 0	6.6
<i>Palaeortyx gallica</i>	St.-Gérand-le-Puy*, F	MN2	MNHN	42 4-43 2 [3]	10 7-11 2 [4]	3 5-4 9 [5]	8 0-8 6 [4]
<i>Palaeortyx? gallica</i>	Vieux-Collonges, F	MN4	FSL	(36)	-	-	-
<i>Palaeortyx intermedia</i>	Wintershof-West*, D	MN3	BSP	47.5-50 6 [8]	12 8-14 1 [4]	4 1-4 9 [7]	9 8-10 7 [6]
<i>Palaeortyx prisca</i>	Sansan*, F	MN6	MNHN	(43 3)	12 0-12 3 [2]	-	-
<i>Alectoris bavarica</i>	Wintershof-West*, D	MN3	BSP	-	-	5 2	-
<i>Taoperdix miocaena</i>	Wintershof-West*, D	MN3	BSP	-	-	4 5-4 9 [3]	10 9-11 0 [2]
<i>Palaeoperdix longipes</i>	Sansan*, F	MN6	MNHN	-	-	-	12.0-12.5 [2]
<i>Palaeocryptonyx grivensis</i>	La Grive*, F	MN7+8	ML	37 1	9.6	3.5	(7.0)
<i>Palaeocryptonyx donnezani</i>	Perpignan*, F	MN15	FSL	38 2	10 1	3.3	7.2
<i>Palaeocryptonyx edwardsi</i> (incl. <i>Palaeortyx miocaena</i> , <i>Palaeocryptonyx gailliardi</i> , see BALLMANN 1969a)	La Grive*, F	MN7+8	FSL, ML	44 3-47.3 [6]	11 4-12 4 [9]	4 2-4 7 [4]	8 7-9.9 [4]
<i>Palaeocryptonyx? miocaena</i>	Polgárdi, H	MN13	MAFI	37-38 [5]	8.8-9 7 [4]	3.3-3 9 [5]	6 8-7.6 [4]
<i>Plioperdix joleaudi</i>	La Grive*, F	MN7+8	ML	28 8	7 5	2.5	5.6

Tab. 3: Comparison of measurements of humeri of Tertiary European Phasianidae and Gallinuloididae. Own measurements, except those from Polgárdi (JANOSSY 1991) and Gargano (BALLMANN 1973). Type locality marked by *; estimated measurements in (); number of specimen in [].

In difference to *Taoperdix miocaena* from Wintershof-West (BALLMANN 1969b) the following characters are observed in the Sandelzhausen *P. intermedia*. The distal humeri are somewhat smaller, the insertion of the *musculus entepicondyllo-radialis sublimis* is on the cranial crest of the entepicondyle instead of the ventral side of the epicondylus ventralis;

the processus flexorius (in caudal view) is more lengthened ventrodistally and the distal end (in ventral view) is somewhat more pointed, instead of blunt and rounded. The distal tarsometatarsus lacks this characteristic little dent dorsally above the trochlea metatarsi III, which is present in the only known tarsometatarsus of *T. miocaena* (BSP 1937 II 18112).

Species	Locality	Age	Collection	GL	L	Dp	KC	Bd	Td
TT									
<i>Palaeortyx phasianoides</i>	Wintershof-West, D	MN3	BSP	-	-	13 8-14 3 [2]	3 7-3 8 [3]	8 0	7 9
<i>Palaeortyx phasianoides grivensis</i>	La Grive*, F	MN7+8	FSL	69 7-70 [3]	67 4-68 2 [3]	12 0-12.5 [3]	3 7-4 0 [7]	7 0-7 8 [4]	7 7-8 1 [4]
<i>Palaeortyx grivensis</i>	Gargano, I	MN13-14	RGM	41 5-42 [3]	-	-	-	-	-
<i>Palaeortyx brevipes</i>	St -Gérand-le-Puy*, F	MN2	MNHN	50 1	48 5	7 1 [2]	2 2 [2]	4 2-4 7 [2]	4 1-4 5 [2]
<i>Palaeortyx gallica</i>	St -Gérand-le-Puy*, F	MN2	MNHN	58 6	56 5	9 1 [4]	2 6-2 9 [3]	5 3-6 0 [3]	5 2-6 0 [3]
<i>Palaeortyx? intermedia</i>	Wintershof-West*, D	MN3	BSP	-	-	-	3 3 [6]	6 2-7 1 [6]	6 1-7 2 [6]
<i>Palaeortyx edwardsi</i>	La Grive*, F	MN7+8	ML	-	-	12 6	-	-	-
<i>Palaeortyx prisca</i>	Sansan*, F	MN6	MNHN	-	-	-	2 9 [2]	5 5-6 7 [2]	5 6-6 6 [2]
<i>Palaeocryptonyx donnezani</i>	Perpignan*, F	MN15	FSL	-	-	10 8	-	5 4	-
<i>Palaeocryptonyx edwardsi</i>	La Grive*, F	MN7+8	FSL	-	-	(9 5) [2]	3 1-3 3 [2]	(6 0) [2]	(6 0)

Tab. 4: Comparison of measurements of tibiotarsi of Tertiary European Phasianidae and Gallinuloididae. Own measurements except those from Gargano (BALLMANN 1973). Type locality marked by *; estimated measurements in (); number of specimen in [].

Species	Locality	Age	Collection	GL	Bp	Tp	KC	Bd
TMT								
<i>Palaeortyx phasianoides</i>	Wintershof-West, D	MN3	BSP	(39 5)-39 7 [2]	7 7-8 3 [4]	7 8-8 9 [3]	3 6-3 7 [4]	(8 9)
<i>Palaeortyx phasianoides</i> (incl. <i>Palaeortyx miocaena</i> , see BALLMANN 1969a 179)	La Grive*, F	MN7+8	ML	43 8	8 6	8 5	3 6	8 9
<i>Palaeortyx phasianoides grivensis</i> (incl. some <i>Palaeortyx edwardsi</i> , see BALLMANN 1969a 178)	La Grive*, F	MN7+8	FSL, BMNH	40 6-41 6 [2]	7 8-9 1 [7]	6 8-7 2 [4]	3 6-4 7 [7]	8 5-8 9 [2]
<i>Palaeortyx grivensis</i> (formerly <i>P. depereti</i> , BALLMANN 1973 25)	La Grive*, F	MN7+8	ML	31 6	5 4	(5 3)	2 6	6 0
<i>Palaeortyx grivensis</i>	Gargano, I	MN13-14	RGM	21 5-24 [8]	-	-	-	-
<i>Palaeortyx brevipes</i>	St -Gérand-le-Puy*, F	MN2	MNHN	27 2	4 9	(4 1)	2 4	5 5
	Phosphorites of Quercy, F	Eocene	NMB	27 5	5 3	4 8	2 8	-
<i>Palaeortyx gallica</i>	St -Gérand-le-Puy*, F	MN2	MNHN	34 4	5 8	5 4	2 7	5 0
<i>Palaeortyx? intermedia</i>	Wintershof-West*, D	MN3	BSP	-	-	-	3 2	-
<i>Palaeortyx intermedia</i>	Vieux-Collonges, F	MN4	FSL	-	-	-	-	-
<i>Palaeortyx prisca</i>	Sansan*, F	MN6	MNHN	-	7 1	6 4	-	-
<i>Alectoris bavarica</i>	Wintershof-West*, D	MN3	BSP	43 4	9 0	-	4 0	9 7
<i>Taoperdix miocaena</i>	Wintershof-West*, D	MN3	BSP	-	-	-	-	8 2
<i>Palaeoperdix longipes</i>	Sansan*, F	MN6	MNHN	-	8 6-9 7 [3]	8 4-9 0 [2]	4 0	-
<i>Palaeortyx edwardsi</i>	La Grive*, F	MN7+8	ML	46 0	10 7	-	4 7	10 8
<i>Palaeocryptonyx donnezani</i>	Perpignan*, F	MN15	FSL	-	(7 1)	-	3 4	-
<i>Palaeocryptonyx edwardsi</i>	La Grive*, F	MN7+8	FSL	37 0	(6 8) [2]	(6 6)	3 4-3 5 [2]	7 7
<i>Palaeocryptonyx hungaricus</i>	Polgárdi, H	MN13	MAFI	27 4-29 6 [4]	4 5-5 5 [4]	-	2 2-2 6 [4]	5 2-6 2 [4]

Tab. 5: Comparison of measurements of tarsometatarsi of Tertiary European Phasianidae and Gallinuloididae. Own measurements except those from Polgárdi (JANÓSSY 1991) and Gargano (BALLMANN 1973). Type locality marked by *; estimated measurements in (); number of specimen in [].

The species of *Palaeocryptonyx* from La Grive (BAUMLANN 1969a) and Perpignan (France; DEPERET 1890) are all of smaller dimensions. *Alectoris bavarica* is only represented from Wintershol-West (Germany; BAUMLANN 1969b) and only by a damaged distal two thirds of both a humerus and a tarsometatarsus. In comparison, the humerus of *A. bavarica* is larger. *Plioperdix joleaudi*, *P. capeki*, and *P. ponticus* are distinguished by their smaller size (see MLÍKOVSKÝ 1995, tab. I). Only *P. subfrancolinus* coincides in the distal width of the humerus, but this taxon is known only from Plio-Pleistocene deposits (MLÍKOVSKÝ 1995: 116). *Miogallus longaevus*, represented only by a coracoid fragment from Regensburg (VON AMMON 1918, fig. 8), is distinctly larger. *?Coturnix muocaena* is known only by a fragmentary carpometacarpus (VILALTA 1963) and therefore can not be considered.

Phasianidae gen. sp. indet.
(pl. 2, fig. 10)

Material and measurements (mm):

BSP 1959 II

CMC dext., dist	8291	Dd: 4.3
TMT sin., dist fragm.	8321	trochlea metatarsi III: B: 2.3, T: 3.0

Description and discussion:

Tarsometatarsus: only the distal end with the trochleae metatarsi II and III is preserved.

Carpometacarpus: The distal third of the carpometacarpus, but only the metacarpale majus with the processus intermetacarpalis are present.

In side by side comparison, both remains are smaller than those of *Palaeoryx intermedia*. Because both specimens are very fragmentary, they are hardly comparable morphometrically. The distal width of the carpometacarpus is smaller than that of *Palaeoryx prisca* from Sansan (CHENEVAL 2000: tab. 3).

Order Strigiformes WAGLER, 1830

The strigiforms are represented only by phalangeal remains, mainly claws. More precise determination is not possible. Because of their size, two taxa of owls can be confirmed.

However, an allocation to the families Strigidae or Tytonidae is not possible on the basis of these phalangeal bones. Both families are known from the Middle Miocene; Strigidae are known since the Early Miocene (St-Gérand-le-Puy, MN2, France); Tytonidae are recorded since the Upper Eocene (Phosphorites of Quercy, France; MOURER-CHAUVIRE 1987). For morphometrical comparisons, the following extant owls were considered: *Strix aluco*, *Strix nebulosa*, *Strix uralensis*, *Nyctea scandiaca*, *Asio otus*, *Asio flammeus*, *Bubo bodo*, *Otus scops*, *Ketupa zeylonensis*, *Tyto alba* (these studied extant species are housed in the SAPM).

Strigiformes gen. et sp. indet. A
(pl. 1, fig. 10)

Material and measurements (mm):

SMNS

Phalanx III terminalis sin. (claw) 54005/1 Bp:(7.5), Hp:8.5, HpA:12.2

Description: Phalanx III terminalis (claw): The tip of the claw is broken off. Along the medial side of the claw there is a weak ridge, typical only for the claw of the third digit. The apophysis extensoris is long but stout. The apophysis flexoris is short and broad in plantar view. The proximal two-parted articular facet is rounded and seems to have been symmetrical, but the lateral margin is slightly damaged.

Comparison and discussion: The terminal phalanges (claws) of the digit III are characterized by a weak ridge along their lateral side. Because there are two claws of digit III known from Sandelzhausen that differ distinctly in size, at least two taxa of owls can be distinguished. The claws of owls can be differentiated from those of accipitriforms by their rounded (not flattened) plantar facies of the claws and by their curve.

The size of this claw indicates a huge owl. Compared with extant strigiforms this claw is of the same size as the Horned Owl, *Bubo bubo*, the largest of the extant European owls. Claws of fossil owls are barely known and published and much less taxonomically determined.

Strigiformes gen. et sp. indet. B
(pl. 1, figs. 8-9)

Material and measurements (mm):

BSP 1959 II

Phalanx III 2	8336	Gl.: 20.0, Bp: 4.7, Hp: 5.0
Phalanx III terminalis sin. (claw)	8330	GL: (16.5), Bp: 5.5, Hp: 4.8, DHp: 7.8
Phalanx I? terminalis (claw)	8328	Gl.: (13.5), Bp: 3.6, Hp: 5.3, DHp: 8.0
Phalanx II? terminalis (claw)	8195	Gl.: (13.0), Bp: 3.9, Hp: 5.0, DHp: 6.9

Description:

Phalanx III 2: The complete phalanx is slender with an extraordinary long apophysis extensoris. The proximal two-parted articular facies is symmetrical. At its plantar margin there is a protruding, somewhat oblique peak in the middle. In lateral view the corpus is slightly bent proximally. There is a round dent proximal to the distal trochlea, the latter is dorsally flattened. The plantar side of the diaphysis is concave, especially in its proximal half and proximally the distal trochlea.

Phalanx III terminalis (claw): The outermost tip of the claw is broken off. Along the medial side of the claw there is a distinct ridge. The apophysis extensoris is long but stout. The apophysis flexoris is short and broad in plantar view. The proximal two-parted articular facet is symmetrical. This claw is distinctly smaller than that of the above mentioned strigiform species (A) from Sandelzhausen.

Phalanx I? terminalis (claw): The outermost tip of the slender claw is broken off. The apophysis extensoris is long. The apophysis flexoris is long and slender in plantar view. The proximal two-parted articular facet is symmetrical and medio-laterally flattened.

Phalanx II? terminalis: The outermost tip of the claw is broken off. The apophysis extensoris is long but stout and the apophysis flexoris is short and broad in plantar view. The proximal two-parted articular facet is symmetrical and medio-laterally flattened.

Comparison and discussion: These remains (claws and phalanx III 2) fit together with respect to their size. Comparisons with extant taxa show that phalanx III 2 of *Tyto alba*, *Atbene noctua*, *Aegolius funereus*, *Glaucidium passerinum*, and *Otus scops* are distinctly smaller, those of *Asio otus* and *Asio flammeus* are smaller, and that of *Strix aluco* are little smaller. The phalanx III 2 of *Bubo bubo* and *Ketupa zeylonensis* are distinctly larger and of *Nyctea scandiaca* are somewhat larger; they all are more stout. This owl of Sandelzhausen corresponds in size to *Strix uralensis* and *Strix nebulosa* - therefore it was quite large. The latter also is the closest in morphology of the compared extant species. Metrical comparisons with known phalanx III 2 of fossil taxa show that *Tyto gigantea* is much larger, *Tyto robusta* is somewhat larger, and *Tyto sanctialbani* and *Strix? perplexata* are somewhat smaller.

For most of the fossil taxa the phalanx III 2 is not known. Using the measurements of the limbs of extant *S. uralensis* and *S. nebulosa* for comparisons with fossil taxa, it can be concluded that *Strix collonensis* (coracoid), *Otus wintershofensis* (CMC), *Strix brevis* (TMT), *Tyto campiterae* (femur, CMC, TMT), *Tyto sanctialbani* (TMT, CMC), *Prosybris antiqua* (TMT), *Necrobyas arvernensis* (TMT, TT, humerus), *Necrobyas edwardsi* (femur) are smaller; *Bubo longicaevus* (TT), and *Bubo poirrieri* (TMT) may have been of similar size.

Compared with the Sandelzhausen claw III the apophysis flexoris of *S. nebulosa* is much slender in plantar view and shorter in lateral view. Concerning these features, the claw of Sandelzhausen corresponds much better to that of *S. uralensis*. The apophysis flexoris of *N. scandiaca* is larger, whereas it is smaller in *B. bubo*, *A. otus*, and *S. aluco*.

Order Gruiformes BONAPARTE, 1854

Superfamily Gruoidea VIGORS, 1825

Family Gruidae VIGORS, 1825

Genus *Palaeogrus* PORTIS, 1885

Palaeogrus manburgensis GOHLICH [in press a]

(pl. I, figs. 11-12)

Synonymy:

in press a *Palaeogrus manburgensis* n. sp. - GOHLICH: figs. 2-4.

Diagnosis: From GOHLICH (in press a): «Smallest species of the genus *Palaeogrus*. Tibiotarsus with caudal trochlea cartilaginis tibialis distinctly surpassing cranial condyles in proximal direction (in lateral and medial view), reaching further proximally than in *P. excelsa* and *P. princeps*. Condylus lateralis distally rounded to slightly flattened (not notched); condylus lateralis thicker than condylus medialis, but of same length craniocaudally. Tubercle on pons supratendineus moderately developed and separated from tuberositas retinaculi extensorius by groove, and thereby not connected as in *Palaeogrus bordwellensis*. Pons supratendineus proximodistally high, higher than in *Palaeogrus princeps*. Tuberositas retinaculi extensorius vertical, crestlike, and separated from sulcus musculi fibularis by vertical sulcus-like groove (in *P. bordwellensis* not clearly separated, but merged). No grooves distally

on trochlea tibialis along inner margin of the condyles. Sulcus extensorius very broad, broader than in *Palaeogrus bordwellensis*.»

«Tarsometatarsus with eminentia intercotylaris well developed and somewhat pointed (although still rounded), more pointed than in *Palaeogrus excelsa*. Sulcus ligamentosus shallow. Hypotarsus moderately long proximodistally, somewhat longer than in *Palaeogrus excelsa*.»

Holotype: Tibiotarsus sin., dist. end. (BSP 1959 II 8309).

Paratypes: Tarsometatarsus dext., prox. end (BSP 1959 II 8319), radius sin., dist. end (BSP 1959 II 8998).

Locus typicus: Sandelzhausen, about 2 km southeast of the city of Mainburg (Lower Bavaria, Southern Germany), topographic map 7336 Mainburg, r: 44 85 580, h: 53 87 700.

Stratum typicum: Early Middle Miocene, Badenian, MN5.

Material and measurements (mm):

	BSP 1959 II
TT sin., dist. end	8309
TMT dext., prox. end	8319
Radius dext., dist. half	8998
tentatively referred specimen:	
Coracoid dext., prox. end	8385
	width of cotyla scapularis: 4.3 length of facies artic. humeralis: 9.3

Palaeogrus manburgensis is a new species of a crane, known only from the site of Sandelzhausen. It is the smallest species within *Palaeogrus*. *Palaeogrus manburgensis* is the only known gruid taxon from Sandelzhausen. For description, comparisons, and systematic discussion see GOHLICH (in press a).

Gruiformes indet.

(pl. I, figs. 13)

Material and measurements (mm):

	BSP
Humerus dext., dist. end	1959 II 8279

KC: 1.9, Bd: 4.8, Td: 2.2

Description and discussion: Only the distal half of the humerus is preserved. Remarkable are the ventrodistally elongated epicondylus ventralis and processus flexorius, which surpasses both the condylus ventralis and dorsalis in the distal direction. The condylus ventralis is characterized by its very round shape, in contrast to the land birds such as Coraciiformes, Pici, and Passerines, in which this condyle is flattened. A small tuberculum supracondylare ventrale is situated far distally at the level of the condylus dorsalis. Only a little more proximally, at the level of the proximal end of the condylus dorsalis, a weak processus epicondylaris dorsalis - just a tuberculum - is present on the dorsal border of the distal bone. The fossa musculi brachialis is deep and narrow. It is situated proximally to the processus epicondylaris dorsalis along the sharp-crested dorsal border of the distal end of the humerus. Also outstanding is the small but deep fossa olecrani.

Remarks: Despite extensive comparisons with extant taxa, the combination of morphological characters allowed no certain allocation to any family as yet. But it seems to be probable by its morphology to refer this specimen to any gruiform family, probably the Rallidae.

Order Passeriformes LINNE, 1758

Passeriformes indet.

The passeriforms are the quantitatively dominant fossil bird group in Sandelzhausen with about 500 remains, all of them fragmentary.

Although the Passeriformes are the most important group of extant birds with more than 5000 species assigned to about 60 families, studies on fossil passeriforms are rare, as well as the knowledge of osteological distinctive features within this order is very poor. BOCHF-SKI (1997) listed only 10 species in 4 families for the European Tertiary. Considering the distinctive features for the Passeres, the Eurylaimi, and Tyranni on the

distal humerus and proximal ulna reported by BALLMANN (1969b: 47f), only the Passeres are evident in Sandelzhausen. It is long known that the osteology within the Passeres is very uniform. The proximal humerus and the distal tarsometatarsus are supposed to show some taxonomically useful characters (BALLMANN 1969b: 49, JANOSSY 1983). However, the studied material consists of approximately two thirds of undeterminable little claws, and about one third of bone fragments; not one single bone is complete. Herein only one proximal end of a humerus was found, but very fragmentary; there are several distal tarsometatarsi fragments, but mostly with at least one trochlea broken off. Therefore, these conditions allow no taxonomical determinations.

3. PALAEOECOLOGY

The fossil avifauna can contribute to the palaeoecological and/or paleoenvironmental interpretations of deposits, especially when considering the ecological adaptions and the ecological behavior of the most closely related modern species. The distribution of bird remains within the fossiliferous deposits in Sandelzhausen (fig. 7), meaning the presence and the quantity of different groups or species in different layers, provides only limited evidence. All in all, the fossils of the different bird taxa are too rare to be statistically informative and their distribution within the section possibly does not

depend only on different ecological conditions and environments, but also on other facts: There may be enrichments of bones due to birds of prey and carnivores; the presence of many small passeriforms may be due to owl pellets. On the other hand, most of the small bird remains come from screen washings, and therefore the different layers have been sampled in different quantitative intensity. Most material for the screen washing comes from layer B, followed by layer C and D, whereas layer A is much too coarse-grained to have been screen washed.

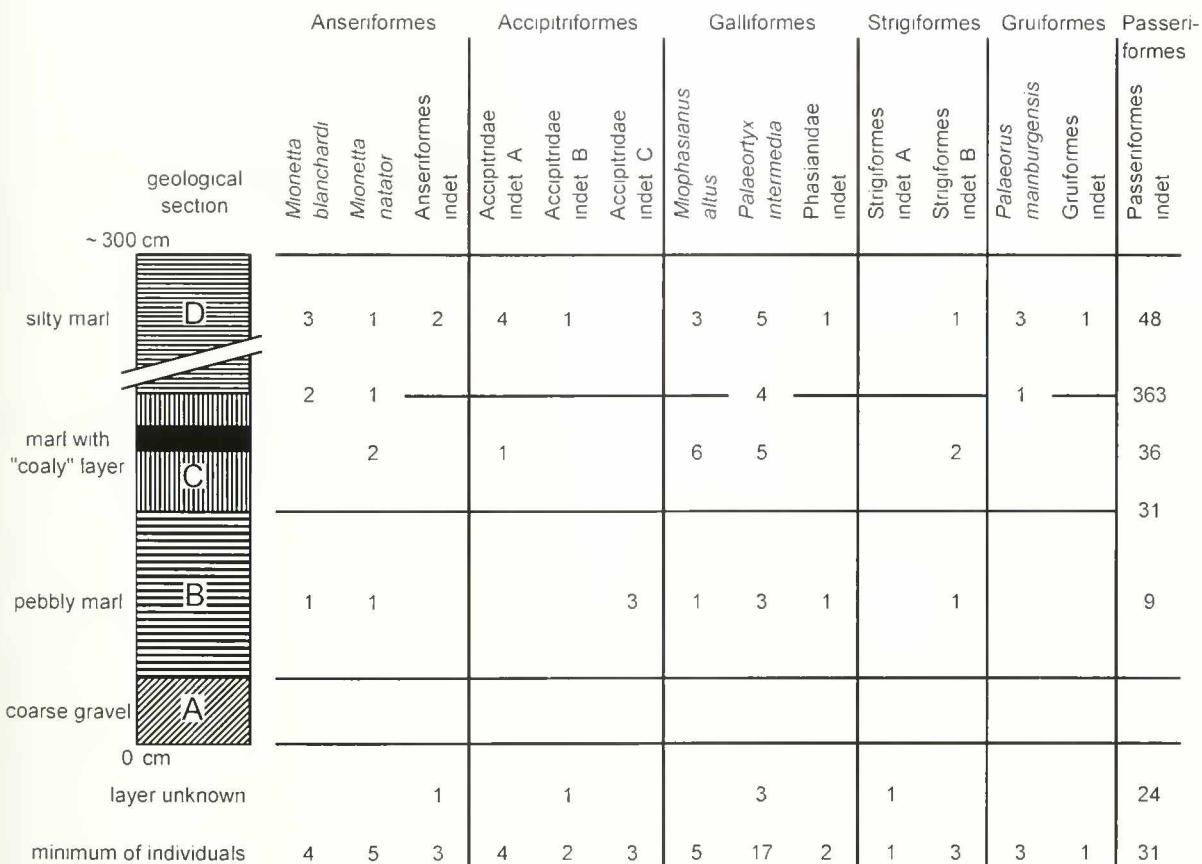


Fig. 7: Quantitative distribution of the fossil bird remains within the section of Sandelzhausen.

In general, an increase of bird fossils can be observed from the bottom to the top of the deposit (fig. 7), as is observed for all other vertebrate remains (pers. comm. V. FAHIBUSCH). Most of the bird species are found in all of the three marly layers (B, C and D). Only the undeterminable large sized accipitrid taxon C seems to be restricted to the bottom layer, whereas the smaller accipitrid taxa A and B and the both representatives of the gruiformes are only found in the deposits above. But the specimens are too rare to allow definitive ecological interpretations.

However, representatives of three different environments can be seen. The anseriforms *Mionetta blanchardi* and *Mionetta natator* are aquatic species. *Miophasianus altus* and the crane *Palaeogrus mainburgensis* are adapted to a terrestrial mode of life. Although extant galliforms are predominantly terrestrial, CHENFVAI (2000: 380) takes into account that *Palaeortyx* might

have lived arboricole. Most of todays passeriforms and several of the extant strigiforms and accipitrids are arboricole forms, even if occasionally terrestrial. Extant owls and Accipitridae are geographically and climatically widespread and therefore allow no conclusions about special faunal regions.

Comparisons with the ecological adaptions and the ecological behavior of the most closely related modern species allow some indication on the paleoecology and paleoclimatology.

Besides the aquatic anatids and the finfoot, the terrestrial crane also indicates nearby aquatic habitats. Extant cranes prefer open landscapes in swamps, bogs, or close to lakes and ponds; only a few species live in steppes (MAKATSCH 1970: 111, 114). Following CHENFVAI (2000: 379), *Miophasianus altus* is close to peacocks (*Pavo*), which predominantly live today in open forested landscapes.

4. CONCLUSIONS

The avifauna of Sandelzhausen comprises 6 orders of birds with at least 14 different taxa. Quantitatively dominating are the Passeriformes, but their fragmentary and poor preservation prevents their determination. Following in terms of quantity are the Phasianidae (Galliformes), represented by *Miophasianus altus*, *Palaeortyx intermedia*, and a small sized undeterminable taxon. Some of the remains of *Miophasianus altus* found in

Sandelzhausen are the largest ever known. *Miophasianus altus* and *Palaeortyx intermedia* were known from older and younger European deposits before, and now can be confirmed in MN 5 (Early Middle Miocene).

The Anseriformes are represented by the anatids *Mionetta blanchardi*, *Mionetta natator* and one larger sized, but undeter-

localities	age	<i>Mionetta blanchardi</i>	<i>Mionetta natator</i>	<i>Palaeortyx intermedia</i>	<i>Miophasianus altus</i>	<i>Palaeogrus mainburgensis</i>
Malusteni (R)	MN 15	●				
Credinta (R)	U-Miocene	●				
Kishinev (MOL)	MN 9		●			
Hostales de Piérola (E)	MN 7+8				●	
La Grive (F)	MN 7+8			●	●	
Steinheim (D)	MN 7				●	
Oeningen (D)	MN 7				●	
Przeworno II (PL)	MN 6-7				●	
Attenfeld (D)	MN 6				●	
Sansan (F)	MN 6				●	
Devinska Nova Ves (SL)	MN 6				●	
Corcoles (E)	MN 5				●	
Grund (A)	MN 5			●		
Sandelzhausen (D)	MN 5	●	●	●	●	●
Dechbetten (D)	MN 5				●	
Dolnice (CZ)	MN 4			●		
Vieux Collonges (F)	MN 4			●	●	
Skiritz (CZ)	MN 3-4	●	●			
Can Mas (E)	MN 3					
Wintershof-West (D)	MN 3				●	
St -Gérand-le-Puy (F)	MN 2	●	●	●		
Ravolzhausen (D)	MN 1-2		●			
Weisenau (D)	MN 1	●	●			

Tab. 6: Stratigraphical distribution of the species represented in Sandelzhausen. (A: Austria, CZ: Czech Republic, D: Germany, E: Spain, F: France, MOI: Moldavia, PL: Poland, R: Romania, SL: Slovakia)

minable anserine taxon. For *Mionetta blanchardi* and *M. nata-*
tor, it is the youngest record in Western and Central Europe.
KESSLER (1992) described these two species from the Upper
Miocene of Romania and Moldavia and additionally *Mionetta*
blanchardi from the Pliocene (MN15) of Malușteni, Romania.

Three species of Accipitriformes and two species of Strigiformes can be distinguished by their different size. However, they are represented almost only by phalangeal remains and therefore are not taxonomically determinable.

Within the Gruiformes one representative each of the Gruidae (cranes) and a Gruiformes indet. - probably a Rallidae -

can be found. The crane *Palaeogrus munburgensis* is only known from Sandelzhausen. It is the smallest species of the genus *Palaeogrus*.

The avifauna represents aquatic species as well as terrestrial and arboricole taxa. Based on several investigations of the fauna, flora, and sedimentology of the deposits in Sandelzhausen, it has been suggested that this locality was a meadow environment with temporary ponds embedded in a braided river system in a warm temperate to subtropical climate (SCHMID 2001). The presented avifauna reflects well the different habitats in such a reconstructed environment.

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ERRATA
ZITTELIANA 22

We kindly ask to apologize the following printing errors:

- | | | |
|------------------------|-----------------|------------------|
| p. 171: | for 'Credin,a' | read 'Credinča' |
| p. 172, 182, 185, 190: | for 'MLÍKOVSK,' | read 'MLIKOVSKY' |
| p. 180, 189: | for 'BOCHENSKI' | read 'BOCHENSKI' |
| p. 187: | for 'BOCHE-SKI' | read 'BOCHENSKI' |
| p. 180, 181: | for 'ŠVEC' | read 'ŠVEC' |

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