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THE PRESENT STATE OF KNOWLEDGE OF THE TERTIARY BIRDS OF CENTRAL EUROPE

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ABSTRACT. Tertiary birds are recorded from 132 localities of Central Europe that range in age from the Late Paleocene to the latest Pliocene. The Early and Middle Miocene localities have furnished particularly significant numbers of fossil birds. Most of the birds collected have not yet been described, and many of those described are often in need of revision. At least 88 species and subspecies of Tertiary birds (excepting *nomina nuda*, but including two alleged bird species) are based on fossil material originating from Central Europe. Approximately 54 percent of these taxa were not listed in Brodkorb's (1963, 1964, 1967, 1971, 1978) *Catalogue of Fossil Birds*.

New taxonomic conclusions are as follows: (1) *Cygnus csakvarensis* belongs in the genus *Olor*; (2) *Anas isarensis* is an indeterminate member of the tribe Aythyini; (3) *Anas atava* belongs in the genus *Cygnus*; (4) *Anas eppelsheimensis* is Anseridae incertae sedis; (5) *Athene noctua veta* is synonymous with the modern *Aegolius funereus*; (6) *Ardea lignitum* is synonymous with the modern *Bubo bubo*; and (7) *Eleutherornis helveticus*, *Anas risgoviensis*, *Anas meyerii*, *Gallus longaeus*, *Totanus praecursor*, *Scolopax baranensis*, *Gallinago veterior*, and *Turdoides borealis* should be considered *Aves incertae sedis* until their types are restudied.

ZUSAMMENFASSUNG. Die tertiären Vögel wurden bisher in 122 Lokalitäten Mitteleuropas gefunden, die über den Zeitraum vom späten Paläozän bis zum jüngsten Pliozän verbreitet sind. Davon haben insbesondere früh- und mittelmiozäne Fundstellen bedeutende Mengen von Vogelknochen geliefert. Leider sind die meisten der gesammelten Vögel noch nicht beschrieben worden und diejenigen, deren Beschreibungen bereits publiziert worden sind, brauchen in vielen Fällen eine Revision. Wenigstens 88 Arten und Unterarten von tertiären Vögeln (ausschliesslich von *Nomina nuda*, aber einschliesslich von 2 Arten angeblicher Vögel) wurden auf dem aus Mitteleuropa stammenden Material begründet. Ungefähr 54 Prozentig davon wurde im Brodkorb's (1963, 1964, 1967, 1971, 1978) *Catalogue of Fossil Birds* nicht registriert.

Folgende taxonomische Schlussfolgerungen sind neu: (1) *Cygnus csakvarensis* gehört der Gattung *Olor* an; (2) *Anas isarensis* ist ein nicht näher unbestimmbares Vertreter des Tribus Aythyini; (3) *Anas atava* gehört der Gattung *Cygnus* an; (4) *Anas eppelsheimensis* ist ein Anseridae incertae sedis; (5) *Athene noctua veta* ist mit dem rezenten *Aegolius funereus* synonym; (6) *Ardea lignitum* ist mit dem rezenten *Bubo bubo* synonym; und (7) *Eleutherornis helveticus*, *Anas risgoviensis*, *Anas meyerii*, *Gallus longaeus*, *Totanus praecursor*, *Scolopax baranensis*, *Gallinago veterior*, und *Turdoides borealis* sind, solange ihre Typen nicht revidiert werden, als *Aves incertae sedis* zu betrachten.

Key words: Aves, Tertiary, Central Europe.

INTRODUCTION

The fossil record of birds is often considered too incomplete to be useful in phylogenetic, stratigraphic, or faunal studies. A recent review by Olson (1985) showed that much information is contained in the avian fossil record, but highlighted the necessity to reevaluate the results of those workers who based their taxonomic determinations and/or descriptions of fossil birds on inadequate materials, or whose work was subject to other potential kinds of errors.

Reviews of previous studies of fossil birds may be pursued either by taxon or by region. Whereas the former approach allows more insight into the evolution of the taxon under study, the latter makes it possible to recover local publications on the topic and to be more up-to-date with local geographic and stratigraphic data. The present paper aims to contribute to the latter kind of work by summarizing our present knowledge of the Tertiary birds of Central Europe, which is defined for the purposes of this paper as an area including Germany, Poland, Czechoslovakia, Hungary, Austria, Liechtenstein, and Switzerland (Fig. 1). The area covers approximately 1,015,632 km².

HISTORY OF TERTIARY AVIAN RESEARCH IN CENTRAL EUROPE

Bird remains from Tertiary deposits of Central Europe were first mentioned by Swiss naturalist Johann Jacob Scheuchzer (1670–1733), who described an “ante-diluvian” (=Middle Miocene) feather from Öhningen, Germany (Scheuchzer, 1708). Regular research was started much later, around the middle of the nineteenth century, by German paleontologist Hermann von Meyer (1801–1869). Meyer (1844) also formally named the first Tertiary bird species of Central Europe, *Protornis glarniensis* from the Lower Oligocene of Matt, Switzerland. During the remainder of the nineteenth and early twentieth centuries, no workers were regularly studying Tertiary birds of Central Europe. Those that were, were only marginally interested in fossil birds, such as Oskar Fraas (1824–1897), Gustav Carl Laube (1839–1923), and Ludwig von Ammon (1850–1922), all of whom produced paleornithological works of generally low quality.

The classical period of Central European paleornithology culminated with the Hungarian paleornithologist Kálmán Lam-

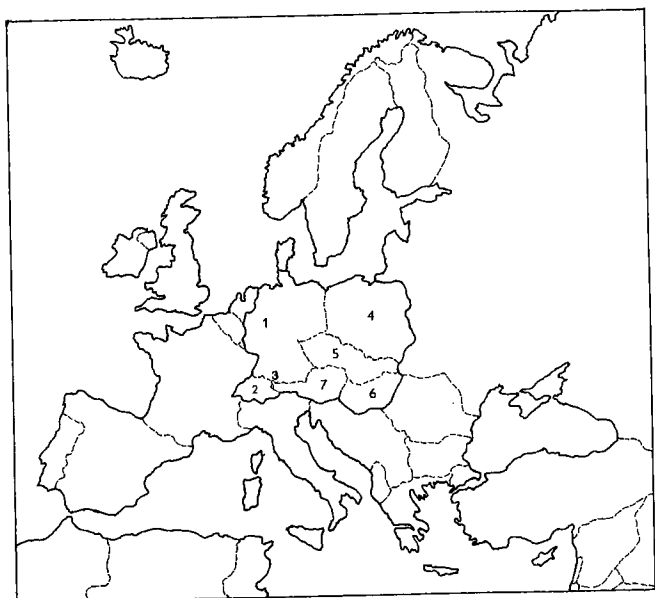


Figure 1. Map of Europe, indicating the area of Central Europe covered in the present paper. 1, Germany; 2, Switzerland; 3, Liechtenstein; 4, Poland; 5, Czechoslovakia; 6, Hungary; 7, Austria.

brecht (1889–1936), who described fossil birds from such Tertiary localities of Central Europe as Geisel Valley, Ipolytarnóc, and Aumeister or Eppelsheim (see later) and presented the first comprehensive review of these birds (Lambrecht, 1933). Following his death, a hiatus appeared in Central European paleornithology that lasted until the late 1960s. Thereafter, research revived slowly and is at present carried out by Peter Ballmann, Dieter Stefan Peters, Angelika Hesse, and Karl-heinz Fischer in Germany, Zygmunt Bocheński in Poland, and Dénes Jánossy in Hungary. Several other workers of Central Europe intensively study Quaternary birds but have yet to contribute significantly to the study of the Tertiary birds of the region.

METHODS

I list all avian species and subspecies based on materials recovered from the Tertiary of Central Europe of which I am aware. The sequence of families follows, as far as possible, Wetmore (1960) for the sake of clarity, although considerable disagreement currently exists among avian systematists about this last standard offshoot of the classical Fürbringer–Gadow–Wetmore clade of avian classifications (Wolters, 1975–1982; Craft, 1981; Mlíkovský, 1985; Olson, 1985). To facilitate the reader's orientation, I list all of the species in the systematic position that they occupied in the last catalogue of fossil birds (Brodkorb, 1963, 1964, 1967, 1971, 1978), if they were included in it, with only a few exceptions. I also follow this order because the taxonomic fate of many taxa is still unclear. For every species or subspecies, data on their original description, holotypes, and their location (if known) and on their age and locality from which they were described are given. Where appropriate, remarks are added. Figures in parentheses after each locality name refer to their numbers in the following section. [Localities with a letter added to their identifying number were added at press time; they are not included in the figures.—Ed.] Anatomical

nomenclature follows Baumel et al. (1979) throughout the present paper.

Four species frequently listed among the Tertiary birds of Central Europe are not included here: (1) *Plotus pannonicus* Lambrecht 1916 was described from Tataros, a locality that was formerly in Hungary, but now lies in Rumania and is thus outside the region of concern; (2, 3) *Pliogallus crassipes* Gaillard 1939 and *Pliogallus kormosi* Gaillard 1939, formerly thought to be Pliocene phasianids of Hungary, were found to be based upon remains of Recent domestic hen (Jánossy, 1976a, 1976b); and (4) *Odontopteryx longirostris* Spulski 1910 was based upon a skull of unknown origin. Although it could have come from the Tertiary of Hamburg, northern Germany, as sometimes believed, this remains unproven (Olson, 1985:198) and the state of preservation of bones of the Tertiary birds of northern Germany and Denmark (Hoch, 1973, 1975) makes this improbable.

In addition, *Ornitholithes ralli* Anonymous is an etiquette name given for what was thought to represent a bird from the Middle Miocene of Öhningen, Germany (Karg, 1805:26), but which turned out to be a forgery (Pfannenstiel, 1958:854, fig. 1).

For stratigraphic divisioning of the Central European Tertiary, I follow Russell et al. (1982) for the Paleogene and Steininger et al. (1987) for the Neogene. Mammal Neogene units (*sensu* Steininger et al., 1987) are abbreviated as MN. It is recognized that the age of some localities is known only approximately and that disagreement still prevails among European stratigraphers as to the limits of many stratigraphic units. Consequently, the allocation of individual localities to specific stratigraphic units may be subject to future change.

Abbreviations used throughout are as follows.

BMNH:	Natural History Museum, London, United Kingdom; formerly British Museum (Natural History)
BSP:	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
CHI:	Conservation Hall, Ipolytarnóc, Hungary
DP FNSP:	Department of Paleontology, Faculty of Natural Sciences, Charles University, Praha, Czechoslovakia
GIB:	Geological Institute, Budapest, Hungary
GIH:	Geologisches Institut, Hamburg, Germany
GM:	Geiseltalmuseum, Halle (Saale), Germany
GPIW:	Geologisch-Paläontologisches Institut der Universität, Würzburg, Germany
IZK:	Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Kraków, Poland
KD:	Mrs. Kessler, private collection, Darmstadt, Germany
MB:	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
MR:	Naturkundemuseum Ostbayern, Regensburg, Germany
MZ:	Paläontologisches Museum der Universität, Zürich, Switzerland
NFS:	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt (Main), Germany
NHMB:	Naturhistorisches Museum, Basel, Switzerland
NMB:	National Museum, Budapest, Hungary
NMP:	National Museum, Praha, Czechoslovakia
NMW:	Naturhistorisches Museum, Wien, Austria
RMT:	Regional Museum, Teplice, Czechoslovakia
SMNS:	Staatliches Museum für Naturkunde, Stuttgart, Germany

UM: Dr. U. Maschwitz, private collection, München,
Germany
ZGIB: Zentrales Geologisches Institut, Berlin, Germany

SYSTEMATICS

Class Aves Linnaeus 1758

Subclass Ornithurae

Haeckel 1866

Infraclass Ratitae Merrem 1813

Order Struthioniformes

(Latham 1790)

Family Palaeotididae

Houde and Haubold 1987

Palaeotis weigelti

Lambrecht 1928

Palaeotis weigelti Lambrecht, 1928:20, text-fig. 6; pl. 1, figs. 1–4.

HOLOTYPE. Distal end of left tarsometatarsus with associated phalanx 1 digiti II; GM Ce I/4415 and Ce I/4418 (Haubold and Krumbiegel, 1984).

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (S).

REMARKS. When I studied the Geisel Valley bird fossils in 1983, I found that what was exhibited in the museum as the type of *Palaeotis weigelti* was, in fact, another specimen. The specimen on exhibit was a crushed partial skeleton, GM 4362, first mentioned in the literature probably by Weigelt (1942:30). The time of, and the reasons for, this substitution were unknown (H. Haubold, pers. comm., 1983).

Palaeotis weigelti was a flightless paleognathous bird (Houde and Haubold, 1987; Peters, 1988).

Palaeogrus geiseltalensis

Lambrecht 1935

Palaeogrus geiseltalensis Lambrecht, 1935:361, pl. 1, fig. 1.

Ornitocnemus geiseltalensis: Brodkorb, 1967:148 (new combination).

HOLOTYPE. Associated right tibiotarsus, right tarsometatarsus, and two basal phalanges digitorum pedis; GM 5882. The phalanges were not described or figured by Lambrecht (1935).

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (S).

REMARKS. This species is synonymous with *Palaeotis weigelti* Lambrecht (1928) from the same horizon and locality (Houde and Haubold, 1987).

Family Struthionidae Vigors 1825

Struthio pannonicus Kretzoi 1954

Struthio (*Pachystruthio*) *pannonicus* Kretzoi, 1954:232, pls. 1, 2.

HOLOTYPE. Left pedal phalanx 1 digiti III; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Kisláng (114).

REMARKS. Kretzoi (1955) described additional material of this species. Mikhailov (1988) and Mikhailov and Kurochkin (1988) restudied associated eggshells and subsequently synonymized *Struthio pannonicus* with *Struthiolithus* (= *Struthio*) *chersonensis* Brandt 1873.

Infraclass Carinatae Merrem 1813

Order Gaviiformes

Wetmore and Miller 1926

Family Gaviidae Allen 1897

Gavia egeriana Švec 1982

Gavia egeriana Švec, 1982:251, text-fig. 8a, pl. I, fig. 1a, b.

HOLOTYPE. Distal end of left humerus; DP FNSP 4816.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. Additional finds from the same horizon and locality have been reported by Švec (1985).

Order Podicipediformes

Fürbringer 1888

Family Podicipedidae

Bonaparte 1831

Miobaptus walteri Švec 1982

Miobaptus walteri Švec, 1982:246, text-fig. 1a, b, pl. I, fig. 2.

HOLOTYPE. Proximal end of right humerus; DP FNSP 4810.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. *Miobaptus walteri* is closely related to grebes of the modern genus *Tachybaptus* Reichenbach 1852 (Švec, 1982, 1984). As comparisons were made with only one species of the latter, *Tachybaptus ruficollis* (Pallas 1764), it is possible that the slight differences noted between *Tachybaptus* and *Miobaptus* are only a result of intrageneric variability.

Order Procellariiformes

Fürbringer 1888

Family Diomedeoidea

Fischer 1985

Diomedeoides minimus

Fischer 1985

Diomedeoides minimus Fischer, 1985:114, figs. 1–6, 12, 13, 15, 16.

HOLOTYPE. Right humerus; MB Av. 764.

HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Order Pelecaniformes Sharpe 1891

Family Pelecanidae Vigors 1825

Pelecanus intermedius Fraas 1870

Pelecanus intermedius Fraas, 1870:281, pl. 13, figs. 3, 4.

Miopelecanus intermedius: Cheneval, 1984:77 (new combination).

HOLOTYPE. Skull with associated partial mandible; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Hahnenberg, Nördlinger Ries (82).

REMARKS. Cheneval (1984) transferred this species to the genus *Miopelecanus*, which he established for *Pelecanus gracilis* Milne-Edwards 1867 from the Lower Miocene (MN 2) of France. He indicated that the two species might be synonymous.

Pelecanus fraasi Lydekker 1891

Pelecanus fraasi Lydekker, 1891:44, fig. 10a.

HOLOTYPE. Skull; BMNH 47862.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Lierheim, Nördlinger Ries (82).

REMARKS. This appears to be a valid species of *Pelecanus* Linnaeus 1758 (Cheneval, 1984).

Family Phalacrocoracidae Bonaparte 1853

Phalacrocorax praecarbo Ammon 1918

Phalacrocorax praecarbo Ammon, 1918:28, fig. 3.

HOLOTYPE. Humeral end of left coracoid; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Brodkorb (1980) synonymized *Phalacrocorax praecarbo* with *Ardea* (= *Phalacrocorax*) *brunhuberi* Ammon 1918 from the same horizon and locality. See *Ardea brunhuberi* for further discussion.

Carbo risgoviensis Fraas 1908

Carbo risgoviensis O. Fraas in Engel, 1908:567 (*nomen nudum*).

Order Ardeiformes (Wagler 1830)

Family Plataleidae Bonaparte 1838

Rhynchaetes messelensis Wittich 1899

Rhynchaetes messelensis Wittich, 1899:103, pl. 2, figs. 1–17.

HOLOTYPE. Partial skeleton in a slab; location unknown. Peters (1983:4, fig. 2) selected a nearly complete skeleton in a slab, NFS ME 1045, as a neotype of this species because the holotype appears to have been lost.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

REMARKS. Wittich (1899) thought that *Rhynchaetes messelensis* was intermediate in morphology and taxonomic position between waders and rails, remarking that a similar position is occupied by the modern genus *Rostratula* Vieillot 1816. This was sufficient for Lambrecht (1933) to include *Rhynchaetes* in the Rostratulidae. Peters (1983) showed that the species actually belongs in the Plataleidae, where *Rhynchaetes messelensis* apparently represents a valid species. The status of *Rhynchaetes* within the Plataleidae has not been evaluated.

Plumumida lutetialis Hoch 1980

Plumumida lutetialis Hoch, 1980:40, figs. 2–6.

HOLOTYPE. Incomplete skeleton in a slab; GIH S.G.P.I. 2183.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

REMARKS. *Plumumida lutetialis* is a synonym of *Rhynchaetes messelensis* Wittich 1899, described from the same horizon and locality (Peters, 1983).

Family Ardeidae Vigors 1825

Ardeacites molassicus Haushalter 1855

Ardeacites molassicus Haushalter, 1855:11, pl. 2, fig. 1.

HOLOTYPE. Right humerus; location unknown.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Harbatshofen (55).

REMARKS. Brodkorb (1980:91) relegated this species to *Aves incertae sedis*, stating that it is not a heron but that he was "... unable to get it in an order, much less a family."

Botaurites avitus Ammon 1918

Botaurites avitus Ammon, 1918:31, figs. 5, 6.

HOLOTYPE. Cervical vertebra; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Olson (1985:67) determined that the holotype of this species is "almost certainly from a cormorant" of the size of *Ardea* (= *Phalacrocorax*) *brunhuberi* Ammon 1918 from the same horizon and locality, and he suggested that *Botaurites avitus* is best synonymized with that species.

Ardea similis Fraas 1870

Ardea similis Fraas, 1870:284, pl. 7, fig. 14a–c.

Botaurites similis: Lambrecht, 1933:315 (new combination).

HOLOTYPE. Distal end of right tibiotarsus; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933:315) thought he saw similarities between the holotype of *Ardea similis* and the same element of the modern ardeid genus *Botaurus* Stephens 1819. He transferred *Ardea similis* to the extinct, supposedly also bittern-like genus *Botaurites* Ammon 1918. Brodkorb (1963:282) followed him, but Olson (1985:166), restudying the figure of the holotype, concluded that "this specimen is from a large phasianid, possibly *Miophasianus altus* [Milne-Edwards (1869)]" described from the Middle Miocene of France.

Ardea brunhuberi Ammon 1918

Ardea brunhuberi Ammon, 1918:30, fig. 4.

HOLOTYPE. Proximal end of left carpometacarpus; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Brodkorb (1980) determined that this is actually

a species of cormorant that may be valid, or which may be synonymous with *Graculus* (= *Phalacrocorax*) *intermedius* Milne-Edwards 1867, described from the Middle Miocene (MN 6) of France. I prefer the latter because the slight difference in age between *Phalacrocorax intermedius* and *P. brunhuberi* does not itself substantiate specific separation of the two taxa and the slight difference in size between the two species (Brodtkorb, 1980) may easily be attributed to intraspecific variability.

Ardea lignitum Giebel 1860

Ardea lignitum Giebel, 1860:152, pl. 1, fig. 2.

Bubo lignitum: Brodtkorb, 1980:90 (new combination).

HOLOTYPE. Distal end of left femur; location unknown.

HORIZON AND LOCALITY. Middle Pliocene (MN 15-16) of Rippersroda 1 (106).

REMARKS. Brodtkorb (1980) showed that this is actually an owl of the modern genus *Bubo* Duméril 1806, similar in size and morphology to the modern European Eagle-Owl, *Bubo bubo* (Linnaeus 1758). Because he thought that the specimen came from the Sarmatian (Middle Miocene), he considered *Bubo lignitum* a valid species. Because it is, in fact, much younger, I synonymize it here with the modern *B. bubo*.

Ardea effosa Meyer 1883

Ardea effosa Meyer in Lepsius, 1883:146 (*nomen nudum*).

Ardea effosa Meyer in Lepsius, 1892:623 (*nomen nudum*).

Ardea latipes Meyer 1883

Ardea latipes Meyer in Lepsius, 1883:146 (*nomen nudum*).

Ardea latipes Meyer in Lepsius, 1892:623 (*nomen nudum*).

Family Palaelodidae Stejneger 1885

Palaelodus steinheimensis Fraas 1870

Palaelodus steinheimensis Fraas, 1870:285, pl. 7, fig. 13.

HOLOTYPE. Distal end of left tibiotarsus; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. This is a large anseriform, according to Olson and Feduccia's (1980) reexamination of its description and the figure in Fraas (1870).

Family Phoenicopteridae Bonaparte 1831

Juncitarsus merkei Peters 1987

Juncitarsus merkei Peters, 1987b:141, figs. 1, 3-8.

HOLOTYPE. Skeleton on slab; KD, uncatalogued.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Order Anseriformes Linnaeus 1758

Family Anseridae Vigors 1825

Cygnavus senckenbergi Lambrecht 1931

Cygnavus senckenbergi Lambrecht, 1931:3, pl. 1, figs. 3, 4; pl. 2, figs. 9-12.

SYNTYPES. Left femur with abraded ends, distal end of left tibiotarsus and pedal phalanx; NFS, uncatalogued.

HORIZON AND LOCALITY. Lower Miocene (MN 2) of Wiesbaden (50).

REMARKS. This species is based on three rather undiagnostic elements, and it was probably their size alone that led Lambrecht (1931, 1933) and others (Brodtkorb, 1964; Howard, 1964) to consider it a swan. However, the syntype femur differs from the same element of Anserinae in having the border of condylus lateralis less extended cranially. Although the species appears to be correctly assigned to the Anseriformes, there is little information as to its taxonomic position within that order, and until restudied it should be relegated to Anseriformes *incertae sedis*.

Cygnus csakvarensis Lambrecht 1933

Cygnus csakvarensis Lambrecht, 1931:4 (*nomen nudum*).

Cygnus csakvarensis Lambrecht, 1933:283, fig. 128g, h.

Cygnanser csakvarensis: Kretzoi, 1957:240 (new combination).

Cygnanser csakvarensis: Brodtkorb, 1964:210 (spelling emended).

Olor csakvarensis Mlíkovský, this paper (new combination).

LECTOTYPE. Proximal end of left carpometacarpus; GIB, uncatalogued; selected by Kretzoi (1957:240).

PARALECTOTYPES. Distal end of right carpometacarpus, phalanx 1 digiti majoris; GIB, uncatalogued. All syntypes are figured in Kretzoi (1957:figs. 37-43).

HORIZON AND LOCALITY. Upper Miocene (MN 10) of Csákvár (96).

REMARKS. Based on a study of two referred elements, an anterior portion of a sternum and fragmentary dentale, from the same horizon and locality, Kretzoi (1957) concluded that *Cygnus csakvarensis* was intermediate in morphology between *Cygnus* Bechstein 1802 and *Anser* Brisson 1760 and created a new genus, *Cygnanser*, for it. This action seems unsubstantiated because the lectotype carpometacarpus agrees well with the same element of swans. Moreover, it differs from the same element of *Cygnus* (*sensu stricto*) and agrees with that of *Olor* Wagler 1832 in having the following: (1) fovea carpalis caudalis shallow, and (2) facies dorsalis ossis metacarpalis allularis less deepened. With no evidence to the contrary, I consider *Olor csakvarensis* (Lambrecht) new combination a valid species.

Cygnus bilinicus Laube 1909

Cygnus bilinicus Laube, 1909:161, pl. I.

HOLOTYPE. Proximal end of ulna, proximal end of radius and carpometacarpus, lacking processus extensorius, in a slab; all apparently from a single individual. The bones are too flattened to reveal from which side of the body they originated. RMT, uncatalogued.

HORIZON AND LOCALITY. Lower Miocene (?MN 3) of Břešťany (59).

REMARKS. Lambrecht (1933) and others (Howard, 1964; Brodkorb, 1978) thought that *Cygnus bilineatus* is actually a raptor, but a restudy of the holotype showed that it is an indeterminate stork, family Ciconiidae (Mlíkovský and Švec, 1989).

Anas cygniformis Fraas 1870

Anas cygniformis Fraas, 1870:276, pl. 13, fig. 2a, b.
Anser cygniformis: Lambrecht, 1933:369 (new combination).

LECTOTYPE. Left coracoid, figured in Fraas (1870:pl. 13, fig. 2a, b); selected here. SMNS, uncatalogued.

PARALECTOTYPES. Two tarsometarsi and 3 pedal phalanges; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933) transferred *Anas cygniformis* to the modern genus *Anser* Brisson 1760 on the basis of more developed lineae intermusculares on the impressio muscoli sternocoracoidei. This character is not valid according to my observations, but other aspects of the lectotype coracoid support Lambrecht's (1933) judgment. The angle between the axis of the corpus coracoidei and the sternal facet, a blunt angulus medialis, and the presence of foramina pneumatica under the facies articularis clavicularis coracoidei are sufficient to refer *Anas cygniformis* to the Anserinae. Within that subfamily, the lectotype coracoid differs from the same element of the Cygnini and agrees with that of the Anserini in having the following: (1) canalis triosseus between the processus procoracoideus and the lateral border of the processus acrocoracoideus deep, and (2) foramina pneumatica under the facies articularis clavicularis coracoidei larger and limited to the lateral side of the sulcus muscoli supracoracoidei. The latter character, and the fact that facies articularis clavicularis coracoidei appears less clearly bordered by the canalis triosseus, is sufficient to allocate *Anas cygniformis* to the genus *Anser*.

The specific status of *Anser cygniformis* is much less certain because *Anas* (= *Anser*) *oeningensis* Meyer 1865 (see below), described from a similarly aged (MN 7), nearby deposit is about the same size. Direct comparison is presently impossible, so I hesitate to synonymize the former with the latter, but the possibility that *Anser cygniformis* is not a valid species should be kept in mind in future studies.

Anas oeningensis Meyer 1865

Anas oeningensis Meyer, 1865:126, pl. 30, fig. 2.
Anser oeningensis: Milne-Edwards, 1867:127 (new combination).

HOLOTYPE. Incomplete skeleton in a slab, including a sternum, partial scapulae, sternal end of coracoid, humeri, ulnae, radii, distal end of carpometacarpus, phalanx 1 digiti majoris, and rib fragments; BMNH 42804.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Öhningen (86).

REMARKS. Milne-Edwards (1867:127–28) transferred this species to the modern genus *Anser*. The shape of the spina externa sterni and the position of the dorsal linea intermuscularis sterni, which are quite visible in Meyer's (1865) illustration of the holotype, clearly support this decision. *Anser oeningensis* appears to be a valid species of goose.

Anas basaltica Bayer 1882

Anas (?) *basaltica* Bayer, 1882:20, fig. 8/1.
Anas (?) *basaltica* Bayer, 1883:62, fig. 1 (here labeled "n. sp.").

HOLOTYPE. Imprints of right coracoid lacking facies articularis sternalis, proximal end of right humerus, cranial end of right scapula, and a rib fragment, probably all from a single individual; NMP ČM 1519. See Mlíkovský and Švec (1989) for additional information.

HORIZON AND LOCALITY. Middle Oligocene of Varnsdorf (22).

REMARKS. This is an indeterminate heron of the tribe Ardeini (Mlíkovský and Švec, 1989).

Anas skalicensis Bayer 1882

Anas (?) *skalicensis* Bayer, 1882:21, fig. 8/2.
Anas (?) *skalicensis* Bayer, 1883:64, fig. 2 (here labeled "n. sp.").

HOLOTYPE. Scraps of long bones; NMP ČM 1520.

HORIZON AND LOCALITY. Middle Oligocene of Skalica (23).

REMARKS. The holotype of this species is indeterminate, even at the ordinal level (Mlíkovský and Švec, 1989).

Anas isarensis Lambrecht 1933

Anas isarensis Lambrecht, 1933:361, fig. 123a.

HOLOTYPE. Cranial end of right scapula; BSP 1926 v 12b.

HORIZON AND LOCALITY. Middle/Upper Miocene (MN 8–9) of Aumeister (91).

REMARKS. As seen in the original illustration, the holotype scapula differs from the same element of Anatini and agrees with that of Aythyini in having the following: (1) acromion more slender, (2) acromion more perpendicular to the axis of scapula, (3) whole extremitas cranialis more slender, and (4) longitudinal furrow on the facies costalis between tuberculum coracoideum and acromion deeper. Within Aythyini, however, the scapula is indeterminate (Woolfenden, 1961), so *Anas isarensis* will remain as Aythyini *incertae sedis*.

Anas risgoviensis Ammon 1918

Anas risgoviensis Ammon, 1918:41, unfigured.

SYNTYPES. Left and right coracoids; BMNH 48165 and 48165a.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Lierheim, Nördlinger Ries (82).

REMARKS. This is nearly a *nomen nudum*. Until the syntypes of *Anas risgoviensis* are restudied, it should be considered *Aves incertae sedis* (see also Cheneval, 1987:147).

Anas eppelsheimensis Lambrecht 1933

Anas eppelsheimensis Lambrecht, 1933:362, fig. 124.

HOLOTYPE. Right coracoid, lacking extremitas sternalis and processus acrocoracoideus; ZGIB, uncatalogued.

HORIZON AND LOCALITY. Upper Miocene (MN 9) of Eppelsheim (94).

REMARKS. Based on a study of the figure of the holotype in Lambrecht (1933), I consider this fossil indeterminate at even the tribal level within the Anseridae and thus relegate *Anas eppelsheimensis* to Anseridae *incertae sedis*.

Anas meyerii Milne-Edwards 1867

Anas meyerii Milne-Edwards, 1867:129, unfigured.
Aythya meyerii: Brodkorb, 1964:228 (new combination).

HOLOTYPE. Crushed tarsometatarsus with associated phalanges in a slab; BMNH 42805.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Öhningen (86).

REMARKS. Both Meyer (1865), who described and figured the specimen, and Milne-Edwards (1867), who named the species, mentioned the badly crushed state of the holotype. It is quite possible that the figure in Meyer (1865) is a reconstruction. Brodkorb (1964) transferred the species to the modern genus *Aythya* Boie 1822, probably inspired by Milne-Edwards' (1867) remark that the specimen exhibits some similarities to the same element of Fuligules (=Aythyini). This is a doubtful action and I recommend considering *Anas meyerii* as *Aves incertae sedis* until the holotype is restudied. There is a high probability that the species will be found to be based upon indeterminate remains.

Anas albae Jánossy 1979

Anas albae Jánossy, 1979:16, unfigured.

HOLOTYPE. Left carpometacarpus, NMB Vt.84.

HORIZON AND LOCALITY. Upper Miocene (MN 13) of Polgárdi (100).

REMARKS. The holotype of *Anas albae* was originally determined by V. Čapek (in Lambrecht, 1912a, 1912b) as "*Mergus* sp." Jánossy (1979) placed the species in the modern genus *Anas* Linnaeus 1758.

Anas atava Fraas 1870

Anas atava Fraas, 1870:275, pl. 13, fig. 1a-c.

Anser atavus: Lambrecht, 1933:369 (new combination).

Cygnus atavus: Mlíkovský, this paper (new combination).

HOLOTYPE. Proximal end of right femur; SMNS, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87).

REMARKS. Lambrecht (1933) transferred *Anas atava* to the modern genus *Anser*, but, as judged from the illustrations in Fraas (1870), the holotype femur differs from the same element of Anserini and agrees with that of Cygnini in having the following: (1) processus trochantericus inclined in norma caudalis, and (2) collum femoris more reduced. The latter character, and the transverse ridge on the facies articularis antitrochanterica, is sufficient to distinguish the specimen from the same element of *Olor* and to refer it to *Cygnus* (*sensu stricto*). Here, *Cygnus atavus* (Fraas) new combination is probably a valid species.

Anas submajor Jánossy 1979

Anas submajor Jánossy, 1979:11, fig. 4/2.

HOLOTYPE. Left ulna; NMB Vt.83.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány Mountains. Exact locality was not given by Jánossy (1979), but it was probably Villány 3 (115).

REMARKS. This species belongs to the modern genus *Tadorna* Oken 1817, where it is inseparable from, and synonymous with, the extant *Tadorna tadorna* (Linnaeus 1758) (Mlíkovský, 1982).

Order Falconiformes Sharpe 1874

Family Vulturidae Illiger 1811

Eocathartes robustus
Lambrecht 1935

Eocathartes robustus Lambrecht, 1935:362, pl. 18, fig. 2.

HOLOTYPE. Partial skeleton in a slab, including pelvis, left and right femur, right tibiotarsus, right tarsometatarsus, and associated basal phalanges of toes II-IV; GM 6883.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. According to Houde (in Olson, 1985:191), this is almost certainly not a vulturid, but its true affinities are still unclear.

Order Galliformes Linnaeus 1758

Family Gallinuloididae
Lucas 1900

Taoperdix miocaena
Ballmann 1969

Taoperdix miocaena Ballmann, 1969:29, pl. II, fig. 14a, b.

HOLOTYPE. Proximal end of left carpometacarpus; BSP 18111.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Family Tetraonidae Vigors 1825

Tetrao macropus Jánossy 1976

Tetrao macropus Jánossy, 1976a:17, pl. I, fig. 6.

HOLOTYPE. Distal end of left tibiotarsus; GIB V.10348.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

Tetrao conjugens Jánossy 1974

Tetrao conjugens Jánossy, 1974b:537, pl. 23, fig. 9.

HOLOTYPE. Proximal end of left carpometacarpus; IZK, uncatalogued.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Węże 1 (101).

Lagopus lagopus atavus
Jánossy 1974

Lagopus lagopus atavus Jánossy, 1974b:534, pl. 24, figs. 4-8.
Lagopus atavus: Jánossy, 1976a:33 (new rank).

SYNTYPES. Thirty-three bone fragments, listed in Jánossy (1974b:534); IZK, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 1 (107).

REMARKS. Jánossy (1976a) elevated this subspecies to the species rank, but since the Willow Grouse, *Lagopus lagopus* (Linnaeus 1758), was rather variable in the late Cenozoic (Bocheński, 1974, 1985; Potapova, 1986), its taxonomic validity should be reevaluated.

Family Phasianidae Vigors 1825

Palaeortyx intermedia
Ballmann 1969

Palaeortyx (?) intermedia Ballmann, 1969:33, pl. 1, figs. 1, 2.

HOLOTYPE. Left coracoid; BSP 18103.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Phasianus augustus Ammon 1918

Phasianus augustus Ammon, 1918:45, figs. 9, 10.

Miophasianus augustus: Lambrecht, 1933:440 (new combination).

HOLOTYPE. Left femur; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. This species was transferred to *Miophasianus* by Lambrecht (1933). It was subsequently synonymized with *Phasianus* (= *Miophasianus*) *altus* Milne-Edwards 1871, described from the Middle Miocene (MN 6) of France (Švec, 1986; Bocheński, 1987).

Gallus longaevus Ammon 1918

Gallus longaevus Ammon, 1918:41, fig. 8.

Miogallus longaevus: Lambrecht, 1933:442 (new combination).

HOLOTYPE. Humeral end of left coracoid; MR, uncatalogued.

HORIZON AND LOCALITY. Middle Miocene (MN 7–8) of Dechbetten (90).

REMARKS. Ammon (1918) was unable to determine the affinities of this species within the Phasianidae and decided to place it "... in the best known genus *Gallus*, which in the present case is to be understood in its broadest sense, so to say as a group name" [my translation]. Lambrecht (1933), without seeing the holotype, established the genus *Miogallus* for *G. longaevus* because of its great age. *Gallus longaevus* is obviously *Aves incertae sedis* until its holotype is restudied.

Gallus beremendensis
Jánossy 1976

Gallus beremendensis Jánossy, 1976b:34, fig. 8/5.

HOLOTYPE. Right humerus; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Beremend 5 (116).

Gallus steinheimensis
Fraas 1908

Gallus steinheimensis E. Fraas in Engel, 1908:567 (*nomen nudum*).

REMARKS. Brodkorb (1978:222) attributed this species to Theodor Fraas (probably *lapsus calami*), but Engel (1908) wrote E. Fraas, which apparently means Eberhard Fraas, son of Oskar Fraas.

Alectoris bavarica
Ballmann 1969

Alectoris bavarica Ballmann, 1969:36, pl. 1, fig. 4a, b.

HOLOTYPE. Left tarsometatarsus; BSP 18110.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Francolinus subfrancolinus
Jánossy 1976b

Francolinus subfrancolinus Jánossy, 1976b:36, fig. 8/3.

HOLOTYPE. Left carpometacarpus, lacking os metacarpale minus; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Francolinus capeki wenzensis
Jánossy 1974

Francolinus capeki wenzensis Jánossy, 1974b:540, pl. 23, figs. 7, 8.

Francolinus wenzensis [sic]: Jánossy, 1981:380 (new rank).

SYNTYPES. Thirty-four bones and bone fragments, listed in Jánossy (1974b:540).

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Węże 1 (101).

REMARKS. *Francolinus capeki wenzensis* was described as a temporal and geographical subspecies of *F. capeki* Lambrecht 1933, from the lower Pleistocene (Biharian) of northwest Rumania. The taxonomic position of these birds should be reevaluated because they differ markedly from modern francolins in lacking a spur on the tarsometatarsus.

Francolinus capeki villanyiensis
Jánossy 1974

Francolinus capeki villanyiensis Jánossy, 1974b:540, pl. 23, figs. 1–6.

Francolinus capeki villanyiensis: Mlíkovský, this paper (spelling emended).

SYNTYPES. 226 bones and bone fragments, listed in Jánossy (1974b:540).

HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 1 (107).

REMARKS. The subspecific name was spelled with a long-sign above the *a* in the original description. As this is not allowed by Article 32 of the International Code of Zoological Nomenclature (ICZN, 1985), I here emend the spelling to *villanyiensis*.

Francolinus capeki villanyiensis was described as a temporal subspecies of *Francolinus capeki* Lambrecht 1933, younger than *Francolinus capeki wenzensis* Jánossy (1974b).

Francolinus minor
Jánossy 1974

Francolinus (Lambrechtia) minor Jánossy, 1974b:547, unfigured.

HOLOTYPE. Left carpometacarpus, lacking os metacarpale minus; IZK, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielice Królewskie 2 (108).

Order Gruiformes Bonaparte 1854

Family Messelornithidae

Hesse 1988

Messelornis cristata Hesse 1988

Messelornis cristata Hesse, 1988:90, figs. 15–17.

HOLOTYPE. Complete skeleton in three plates; NFS ME 807a–c.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Gruidae Vigors 1825

Pliogrus germanicus

Lambrecht 1933

Pliogrus germanicus Lambrecht, 1933:522, fig. 156.

Palaelodus germanicus: Fischer and Stephan, 1971:576 (new combination).

HOLOTYPE. Distal end of left tibiotarsus; ZGIB, uncatalogued.

HORIZON AND LOCALITY. Upper Miocene (MN 9) of Eppelsheim (94).

REMARKS. Fischer and Stephan (1971) transferred this species to the flamingo genus *Palaelodus* Milne-Edwards 1863 and hypothesized that it might even be synonymous with *Palaelodus ambiguus* Milne-Edwards 1871 from the Lower Miocene (MN 2) of France. The species is in need of reexamination.

Family Rallidae Vigors 1825

Pararallus hassenkampii

Martini 1967

Pararallus hassenkampii Martini, 1967a:8, unfigured (*nomen nudum*).

Pararallus hassenkampii Martini, 1967b:289, text-fig. 1, pl. 29, figs. 1, 2.

HOLOTYPE. Distal end of left tarsometatarsus with associated proximal phalanges digitum I–IV (in a slab and counter-slab); GPIW F 1237 and F 1238.

HORIZON AND LOCALITY. Lower Oligocene of Sieblos (13).

REMARKS. This is apparently not a rail (Cracraft, 1973; Olson, 1977), but its affinities have not yet been clarified.

Microrallus fejfari Švec 1983

Microrallus fejfari Švec, 1983:37, fig. 1a.

HOLOTYPE. Distal end of left humerus; DP FNSP 4818.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

Porzana estramosi Jánossy 1979

Porzana estramosi Jánossy, 1979:20, fig. 4/8.

HOLOTYPE. Fragmentary distal end of left tarsometatarsus; GIB V.78120.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Osztramos 9 (104).

REMARKS. Jánossy (1979) placed this species in the modern rallid genus *Porzana* Vieillot 1816 solely on the basis of its small size. This is clearly insufficient. The diagnosis and the description

Table 1. Leg proportions [tibiotarsus length : tarsometatarsus length (tt:tmt)] in *Otis affinis* and modern genera of bustards.

	Number of species (individuals)	tt:tmt
<i>Otis affinis</i>	1 (1)	1.42 ^a
<i>Otis</i>	2 (4)	1.36–1.50
<i>Chlamydotis</i>	1 (2)	1.29–1.36
<i>Eupodotis</i>	6 (9)	1.21–1.38
<i>Ardeotis</i>	1 (1)	1.25
<i>Neotis</i>	2 (2)	1.22–1.25

^a My estimation based on the figure of the holotype in Lambrecht (1933: 529). Other values were recalculated from Verheyen (1957) and Jánossy (1972).

of the species do not include any usable morphological details, and because the figure is indistinct, *Porzana estramosi* should be treated as *Aves incertae sedis* until the holotype is restudied.

Family Phorusrhacidae

Ameghino 1899

Aenigmavis sapea Peters 1987

Aenigmavis sapea Peters, 1987a:73, figs. 1–12.

HOLOTYPE. Partial skeleton in a slab; UM, uncatalogued.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Otidae Gray 1840

Otis affinis Lydekker 1891

Otis affinis Lydekker, 1891:168, unfigured.

Chlamydotis affinis: Brodkorb, 1967:174 (new combination).

HOLOTYPE. Crushed postcranial skeleton in a slab; BMNH 36745. See Lambrecht (1933:fig. 157b) for its illustration.

HORIZON AND LOCALITY. Middle Miocene (MN 7) of Steinheim (87), according to Ammon (1918) who considered Lydekker's (1891) note that the holotype originated from the Lower Miocene (MN 3) of nearby Schnaitheim incorrect.

REMARKS. Brodkorb (1967) placed this species in the modern genus *Chlamydotis* Lesson 1839, possibly on the basis of Lydekker's (1891) erroneous remarks that the fossil has the exact proportions of *Otis* (= *Chlamydotis*) *undulata* (Jacquin 1784). Actually, the leg proportions of *Otis affinis* differ markedly from those of *Chlamydotis undulata* and agree best with those of *Otis* Linnaeus 1758 (Table 1). Thus, until the holotype is restudied, the species is best treated as a member of the latter genus.

Order Diatrymiformes

Matthew and Granger 1917

Family Diatrymidae

Matthew and Granger 1917

Diatryma geiselensis

Fischer 1978

Diatryma geiselensis Fischer, 1978:134, unfigured.

HOLOTYPE. Right scapulocoracoid; GM ?/Dia.2. See Fischer (1962:fig. 2) for an illustration of the holotype.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. This species deserves, as do all diatrymas, a modern revision (cf. Olson, 1985).

Order Charadriiformes

Huxley 1867

Family Scolopacidae Vigors 1825

Totanus praecursor Laube 1901

Totanus praecursor Laube, 1901:66, fig. 14.

HOLOTYPE. Pelvic impression; location unknown. The holotype is not in the Dresden Museum, where it should perhaps have been deposited (Lambrecht, 1933:538), but never was (S. Eck, in litt., 1987). Neither is it in the National Museum in Praha (J. Beneš, pers. comm., 1985), nor in the Regional Museum in Teplice (D. Ernygrová, pers. comm., 1986) where other bird remains from the same locality are deposited.

HORIZON AND LOCALITY. Lower Miocene (?MN 3) of Břešťany (59).

REMARKS. As the holotype appears to have been lost, and its figure in Laube (1901) is less than informative, I relegate *Totanus praecursor* to *Aves incertae sedis* until such time as the holotype is found and restudied.

Scolopax baranensis

Jánossy 1979

Scolopax baranensis Jánossy, 1979:23, unfigured.

HOLOTYPE. Proximal end of carpometacarpus (body side not given); NMB Vt.82.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

REMARKS. Jánossy's (1979) superficial and irrelevant description of this species makes it almost a *nomen nudum*. In any case, *Scolopax baranensis* belongs in *Aves incertae sedis* until its holotype is restudied.

Gallinago veterior Jánossy 1979

Gallinago veterior Jánossy, 1979:24, fig. 4/9.

HOLOTYPE. Nearly complete right coracoid; NMB Vt.81. Jánossy (1979) stated that the holotype is from the left side of the body, but the figure shows a right coracoid.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

REMARKS. *Gallinago veterior* is almost a *nomen nudum* because of the entirely useless diagnosis and nearly useless description given by Jánossy (1979). Until the holotype is restudied, the species is best referred to *Aves incertae sedis*.

Family Glareolidae Brehm 1831

Mioglareola gregaria

Ballmann 1979

Mioglareola gregaria Ballmann, 1979:68, text-fig. 3, pl. 1, figs. 3-5.

HOLOTYPE. Skull; BSP 1970 XVIII 851.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).

Glareola neogaena

Ballmann 1979

Glareola neogaena Ballmann, 1979:81, pl. 1, fig. 9; pl. 2, fig. 1.

HOLOTYPE. Right humerus; BSP 1970 XVIII 852.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).

Family Laridae Vigors 1825

Gaviota lipsiensis

Fischer 1983

Gaviota lipsiensis Fischer, 1983a:152, pl. XII, figs. 1, 2.

HOLOTYPE. Distal end of right humerus; MB Av.732.

HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Larus dolnicensis Švec 1980

Larus dolnicensis Švec, 1980:380, pl. 1, figs. 2, 3.

HOLOTYPE. Distal end of left humerus; DP FNSP 7344.

HORIZON AND LOCALITY. Lower Miocene (MN 4) of Dolnice 2 (67).

REMARKS. As already recognized by Olson (1985:182), this is not a gull, but a member of the family Glareolidae (Mlíkovský, pers. obs.). I have yet to ascertain its affinities within that family.

Family Alcidae Vigors 1825

Petalca austriaca

Mlíkovský 1987

Petalca austriaca Mlíkovský, 1987:136, text-figs. 4, 5, pls. 1, 2.

HOLOTYPE. Incomplete skeleton in a slab and counter-slab, including coracoids and all of the main wing bones; NMW 1980/25.

HORIZON AND LOCALITY. Upper Oligocene of Traun-Pucking (32).

Order Cuculiformes Wagler 1830

Family Cuculidae Vigors 1825

Cuculus csarnotanus

Jánossy 1979

Cuculus csarnotanus Jánossy, 1979:25, fig. 4/6.

HOLOTYPE. Distal end of left humerus; NMB Vt.80.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Csarnóta 2 (105).

Order Strigiformes Wagler 1830

Family Protostrigidae

Wetmore 1933

Oligostrix rupelensis

Fischer 1982

Oligostrix rupeliensis Fischer, 1982:152, unfigured (*nomen nudum*).

Oligostrix rupelensis Fischer, 1983b:483, figs. 1, 3, 5, 7, 9.

HOLOTYPE. Distal end of left tibiotarsus; MB Av. 730.

HORIZON AND LOCALITY. Middle Oligocene of Espenhain (21).

Family Strigidae Vigors 1825

Eoglaucidium pallas

Fisher 1987

Eoglaucidium pallas Fischer, 1987:138, figs. 1, 4.

HOLOTYPE. Right humerus; GM XXII/761.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. I am in the process of studying several more specimens (humeri, coracoids, scapulae) from the same horizon and locality that can clearly be referred to this species. This work is not complete, but it appears that the species may belong to the Coraciiformes and not the Strigiformes.

Bubo florianae Kretzoi 1957

Bubo (?) *florianae* Kretzoi, 1957:243, figs. 47–49.

HOLOTYPE. Phalanx 1 of pedal digit II; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Miocene (MN 10) of Csákvár (96).

Surnia robusta Jánossy 1977

Surnia robusta Jánossy, 1977:10, fig. 2a–d, 5/10.

HOLOTYPE. Left tarsometatarsus; NMB Vt.62.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Otus wintershofensis

Ballmann 1969

Otus wintershofensis Ballmann, 1969:39, pl. 1, fig. 11a, b.

HOLOTYPE. Distal end of right tibiotarsus; BSP 18121.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Athene noctua veta Jánossy 1974

Athene noctua veta Jánossy, 1974b:555, pl. 24, fig. 1.

Athene veta: Jánossy, 1979:19 (new rank).

HOLOTYPE. Humeral end of right [not left, as stated by Jánossy (1974b)] coracoid; IZK, uncatalogued. The specimen was not designated as holotype of *Athene noctua veta* by Jánossy (1974b); he generally does not select types for his new subspecies. I call it the holotype here because it is the only specimen upon which the taxon was based.

HORIZON AND LOCALITY. Upper Pliocene (MN 16) of Rębielec Królewskie 1 (107).

REMARKS. I have reexamined the holotype and find that it does not belong to the genus *Athene* Boie 1822, but to another modern strigiform genus, *Aegolius* Kaup 1829. The holotype coracoid differs from that of *Athene* and agrees with that of *Aegolius* in having the following: (1) head deflected more mediad

in ventral view, (2) head more robust in humeral view, (3) the border between impressio ligamenti acrocoracohumeralis and facies articularis humeralis indistinct (in *Athene* it is distinctly narrowed), and (4) foramen nervi supracoracoidei smaller. The latter character is the primary one in Jánossy's diagnosis of *Athene noctua veta*. Because there are no meaningful morphological or mensural character differences between the holotype coracoid fragment of *Athene noctua veta* (it is not measurable) and the same element of the extant *Aegolius funereus* (Linnaeus 1758), the only representative of the genus in the Palearctic, I here synonymize the *Athene noctua veta* Jánossy (1974) with the latter species.

Strix brevis Ballmann 1969

Strix brevis Ballmann, 1969:38, pl. 1, fig. 7a, b.

HOLOTYPE. Distal end of left humerus; BSP 18012.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

Order Apodiformes Peters 1940

Family Aegialornithidae

Lydekker 1891

Aegialornis szarskii Peters 1985

Aegialornis szarskii Peters, 1985:144, figs. 1, 4a, b.

Primapus szarskii: Mourer-Chauviré, 1988:372 (new combination).

HOLOTYPE. Nearly complete skeleton in a slab; NFS LNK-Me 301.

HORIZON AND LOCALITY. Middle Eocene of Messel (4).

Family Apodidae Hartert 1897

Chaetura baconica

Jánossy 1977

Chaetura baconica Jánossy, 1977:22, fig. 5/13.

HOLOTYPE. Right ulna; NMB Vt.64.

HORIZON AND LOCALITY. Upper Miocene (MN 11–12) of Sümeg (98).

Order Coraciiformes

Forbes 1884

Family Bucerotidae Vigors 1825

Geiseloceros robustus

Lambrecht 1935

Geiseloceros robustus Lambrecht, 1935:365, pl. 2.

HOLOTYPE. Partial skeleton in a slab, including more or less complete left and right coracoids, right scapula, left and right humeri, right ulna, right radius, right carpometacarpus, phalanx 1 of right digitus major, and phalanx of right digitus minor; GM 5884.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. The wing proportions of *Geiseloceros robustus* (ulna shorter than humerus) make it highly improbable that this species is a hornbill (Olson, 1985), all of which possess ulnae

markedly longer than humeri (Verheyen, 1955). The true systematic position of this species remains uncertain, although Houde (in Olson, 1985) suggested that it may possibly be identical with *Eocathartes robustus* Lambrecht 1935, an alleged vulture described from the same horizon and locality.

Order Piciformes
Meyer and Wolf 1810

Family *incertae sedis*

Zygodactylus ignotus
Ballmann 1969

Zygodactylus ignotus Ballmann, 1969:52, pl. 2, fig. 13a, b.

HOLOTYPE. Distal end of right tarsometatarsus; BSP 18164.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

REMARKS. Brodkorb (1971:257) created a new family, Zygodactylidae, for this species. Its affinities, however, still appear to be unclear (Olson, 1985:121–22).

Family Capitonidae
Bonaparte 1840

Capitonides europeus
Ballmann 1969

Capitonides europeus Ballmann, 1969:44, pl. 2, fig. 1a, b.

HOLOTYPE. Right carpometacarpus; BSP 18162.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Wintershof (West) (56).

REMARKS. In spite of a thorough original description, the genus *Capitonides* Ballmann 1969, which is based on *C. europeus*, was never properly diagnosed. To the contrary, Ballmann (1983) stressed its similarities to the modern genus *Trachyphonus* Vieillot 1816. The possibility that *Capitonides* is synonymous with *Trachyphonus* should be evaluated (but see Prum, 1988).

Capitonides protractus
Ballmann 1983

Capitonides protractus Ballmann, 1983:46, figs. 2/5–6, 3a–d.

HOLOTYPE. Right tarsometatarsus; BSP 1970 XVIII.

HORIZON AND LOCALITY. Middle Miocene (MN 6) of Steinberg, Nördlinger Ries (82).

REMARKS. See *Capitonides europeus* for the generic status of this species.

Family Picidae Vigors 1825

Dendrocopos praemedius
Jánossy 1974

Dendrocopos praemedius Jánossy, 1974a:237, unfigured.

HOLOTYPE. Right carpometacarpus; GIB, uncatalogued.

HORIZON AND LOCALITY. Upper Pliocene (MN 17) of Villány 3 (115).

Order Passeriformes
Linnaeus 1758

Family *incertae sedis*

Protornis glarniensis
Meyer 1844

Osteornis scolopacinus Gervais, 1844:39, unfigured (*nomen nudum*).

Protornis glarniensis Meyer, 1844:338, unfigured.

Protornis glarniensis Anonymous, 1844:v, unfigured (*nomen nudum*).

Protornis glaronensis Meyer, 1856:92, pl. XV, fig. 12 (unjustified emendation of *Protornis glarniensis* and consequently its objective synonym).

HOLOTYPE. Incomplete skeleton in a slab and counter-slab; MZ, uncatalogued.

HORIZON AND LOCALITY. Lower Oligocene of Matt (12).

REMARKS. This species was originally described as a passerine bird (*sensu lato*) by Meyer (1839b, 1844, 1856). It was later transferred to the Alcedinidae (Peyer, 1957; Storer, 1960; Brodkorb, 1971) but has more recently been placed with the Momotidae (Olson, 1976).

Protornis blumeri Heer 1865

Protornis blumeri Heer, 1865:236, fig. 143 (reprinted in Peyer, 1957:fig. 25).

HOLOTYPE. Partial skeleton impression in a slab; location unknown.

HORIZON AND LOCALITY. Lower Oligocene of Matt (12).

REMARKS. After studying the figure and description of this fossil by Heer (1865), I can only agree with Olson (1976:117) that *Protornis blumeri* "... should be relegated to the category of Aves incertae sedis ..." until its holotype is located and restudied.

Family Timaliidae Gray 1841

Turdoides borealis
Jánossy 1979

Turdoides borealis Jánossy, 1979:27, fig. 4/7.

HOLOTYPE. Proximal part of left humerus; GIB V.78119.

HORIZON AND LOCALITY. Lower Pliocene (MN 15) of Osztramos 1 (103).

REMARKS. This species is based upon a badly eroded, fragmentary humerus that is unsuitable for identification. Moreover, even if Jánossy (1979) correctly assigned the fossil to the turdoidine timalias, its generic affiliation is doubtful because he compared it with only 3 of the 38 extant genera of this subfamily (*sensu* Wolters, 1975–1982). I consider *Turdoides borealis* as Aves incertae sedis until its holotype is restudied.

Aves incertae sedis

Eleutherornis helveticus
Schaub 1940

Eleutherornis helveticus Schaub, 1940a:283, figs. 1–4.

HOLOTYPE. Anterior portion of a pelvis; NHMB Eh 781.

HORIZON AND LOCALITY. Middle Eocene of Egerkin-gen (6).

REMARKS. Schaub (1940a) conjectured that this may have been a ratite bird (*sensu lato*). Wetmore (1951) created a separate family, the Eleutherornithidae, for it, which he considered closely related to the Struthionidae (see also Brodkorb, 1963; Cracraft, 1974). Although this arrangement may prove to be correct, it seems advisable to consider *Eleutherornis helveticus* as *incertae sedis* until its holotype is restudied and compared with other giant Paleocene and Eocene birds, such as *Gastornis* Hébert 1855, the diatrymas, and phorusrhacids (cf. Houde, 1986; Houde and Haubold, 1987).

Saurornis matthesi
Fischer 1967

Saurornis matthesi Fischer, 1967:603, pl. I.

HOLOTYPE. Distal end of coossified ulna and radius (originally described as proximal end of tarsometatarsus); GM 1956/Saur. 1.

HORIZON AND LOCALITY. Middle Eocene of Geisel Valley (5).

REMARKS. This species, originally described as avian, was later transferred to Mammalia, more specifically to the perisodactylid genus *Lophiodon* (Fischer, 1987).

Ornithoidichnites badensis
Boehm 1896

Ornithoidichnites badensis Boehm, 1896:238, text-fig. 1, pl. I. *Ichnium badense*: Boehm, 1898:206 (new combination).

HOLOTYPE. Two footprints (left and right) of a single individual; location unknown. Boehm (1896) originally mentioned a series of 10 footprints, which led Brodkorb (1978:221) to consider all of them to be the holotype of *Ornithoidichnites badensis*. However, only two of these footprints were described in detail by Boehm (1896), and from his later article (Boehm, 1898), it is clear that only those two represent the holotype.

HORIZON AND LOCALITY. Upper Oligocene of Bellingen (27).

REMARKS. These footprints, originally described as avian, are actually those of a tapir (Boehm, 1898; see also Abel, 1935). Lambrecht (1933:665) and Brodkorb (1978:221) overlooked Boehm's (1898) correction and continued to list *Ornithoidichnites badensis* as avian.

Ichnoorder Avipedia Vjalov 1966

Family *incertae sedis*

Ornithotarnocia lambrechtii
Kordos 1983

Ornithotarnocia lambrechtii Kordos, 1983:269, fig. 1.

HOLOTYPE. Two footprints (left and right) of a single individual; GIB V.12721.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

REMARKS. These footprints were first described and figured by Lambrecht (1912b, 1933).

Aviadactyla media Kordos 1983

Aviadactyla media Kordos, 1983:276, fig. 6.

HOLOTYPE. Two footprints (left and right) of a single individual; GIB V.12729.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

Tetraornithopedia tasnadii
Kordos 1983

Tetraornithopedia tasnadii Kordos, 1983:279, fig. 7.

HOLOTYPE. Footprint (?left); CHI, uncatalogued.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

Passeripedia ipolyensis
Kordos 1983

Passeripedia ipolyensis Kordos, 1983:280, fig. 8.

HOLOTYPE. Footprint (?right); GIB, uncatalogued.

HORIZON AND LOCALITY. Lower Miocene (MN 3) of Ipolytarnóc (60).

TERTIARY AVIAN LOCALITIES
OF CENTRAL EUROPE

The following list contains all Central European localities known to me from which Tertiary birds have been recorded (Figs. 2, 3). Although no important locality appears to have been overlooked, the completeness of the list cannot be ascertained because bird finds are often just mentioned in papers on other animal groups, or even plants, and these notes are extremely difficult to detect.

The localities are listed by age. Their synonyms (in parentheses), stratigraphic and geographic position, and avian fossils recovered from each are given. The last data are, where possible, based upon revised results.

I have followed the latest administrative divisioning of the countries in describing the geographical position of the mentioned localities. I have deliberately termed the higher administrative units "districts" and the lower ones "counties"; where one-level divisioning was sufficient, the units were referred to as "provinces." The respective vernacular terms are "Land" and "Kreis" in Germany, "województwo" in Poland, "kraj" and "okres" in Czechoslovakia, "megye" in Hungary, "Land" and "Bezirk" in Austria, and "Kanton" in Switzerland. No Tertiary bird-yielding localities are known from Liechtenstein. Considerable changes in administrative divisioning of Central Europe followed both World Wars and 1989 revolutions, so many of the relevant terms applied in earlier works are outdated.

PALEOCENE

No Paleocene birds have been described from Central Europe thus far, although Walbeck (1) has yielded noticeable numbers of well-preserved avian fossils.

(1) WALBECK, Haldensleben County, Magdeburg District, Germany. Upper Paleocene (Tobien, 1986a). Numerous bird bones, including those of *Gastornis* (Weigelt, 1939, 1942).

Eocene

Of the eight localities listed below, important avifaunal collections have come only from Messel (4) and Geisel Valley (5).

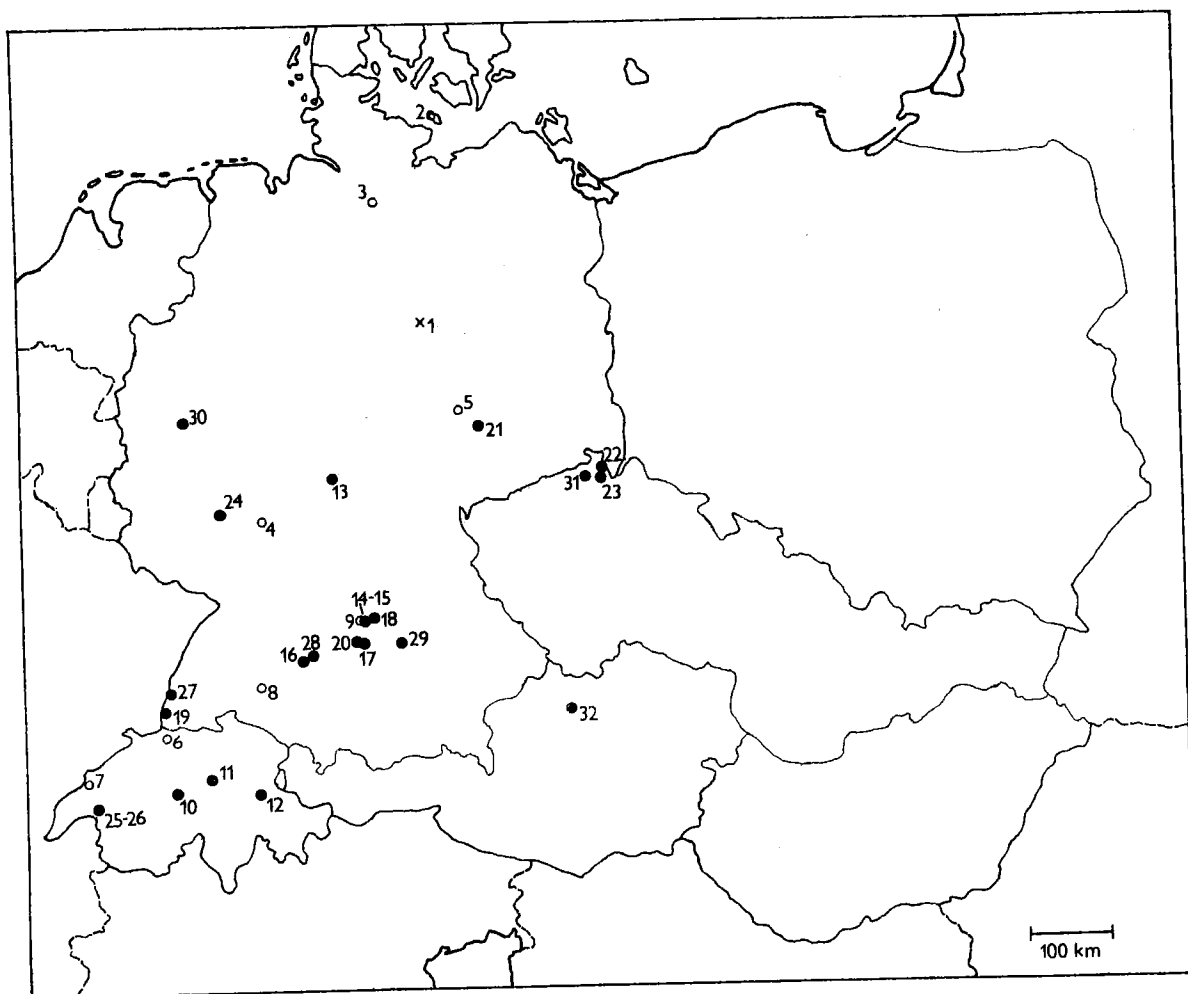


Figure 2. Map of Central Europe with distribution of its Paleogene avian localities. x, Paleocene; o, Eocene; •, Oligocene. Numbering of localities agrees with that in text. Order of localities approximates their decreasing age.

(2) KATHARINENHOF, Fehmarn County, District Schleswig-Holstein, Germany. Lower Eocene (Tobien, 1986a). Three brain casts, indeterminate bird bone fragments (Hoch, 1975).

(3) HAVIGHORST (Havighorst bei Reinbek), Stormarn County, District Schleswig-Holstein, Germany. Lower Eocene (Tobien, 1986a). Feather imprints (Illies, 1941, 1942).

(4) MESSEL, Darmstadt County, District Hessen, Germany. Middle Eocene (Franzen and Haubold, 1986). Diverse avifauna, of which only a small part has been described. It includes ibises, diatrymas, messelrails, and crested swifts (Wittich, 1899; Berg, 1965; Hoch, 1980; Peters, 1983, 1985, 1987a, 1987b; Hesse, 1988). Type locality of *Juncitarsus merkei*, *Rhynchoaeites meselensis*, *Plumumida lutetialis*, *Messelornis cristata*, and *Aegialornis szarskii*.

(5) GEISEL VALLEY (Geiseltal), Merseburg County, Halle an der Saale District, Germany. Middle Eocene (Krumbiegel et al., 1983; Franzen and Haubold, 1986). Diverse avifauna, including palaeognathous birds, galliforms, ibises, diatrymas, flamingos, falcons, owls, swifts, and coraciiform and piciform birds. (Lambrecht, 1928, 1935; Heller, 1932; Bachofen-Echt, 1936; Fischer, 1962, 1967, 1978, 1987; Houde, 1986; Houde and Haubold, 1987; Peters, 1989). Type locality of *Saurornis mat-*

thesi, *Eocathartes robustus*, *Diatryma geiselensis*, *Palaeogrus geiseltalensis*, *Palaeotis weigelti*, *Geiseloceros robustus*, and *Eoglaucidium pallas*.

(6) EGERKINGEN, Solothurn Province, Switzerland. Middle Eocene (Russell et al., 1982). Various bone fragments of a giant (?ratite) bird (Schaub, 1929, 1940a, 1940b). Type locality of *Eleutherornis helveticus*.

(7) CHAMBLON, Vaud Province, Switzerland. Middle Eocene (Russell et al., 1982). Thenius (1959) mentioned bird fossils from this locality.

(8) FROHNSTETTEN (Fronstetten), Sigmaringen County, District Baden-Württemberg, Germany. Upper Eocene (Thenius, 1959). Bird bones mentioned by Meyer (1852), Quenstedt (1853), and Lambrecht (1933:929).

(9) MÖHREN 19, Donauwörth County, District Bayern, Germany. Upper Eocene (Russell et al., 1982). Bird remains mentioned by Heissig (1978).

OLIGOCENE

Most of the 25 localities listed below are fissure fillings in the Jura Mountains of Switzerland and southwestern Germany. All

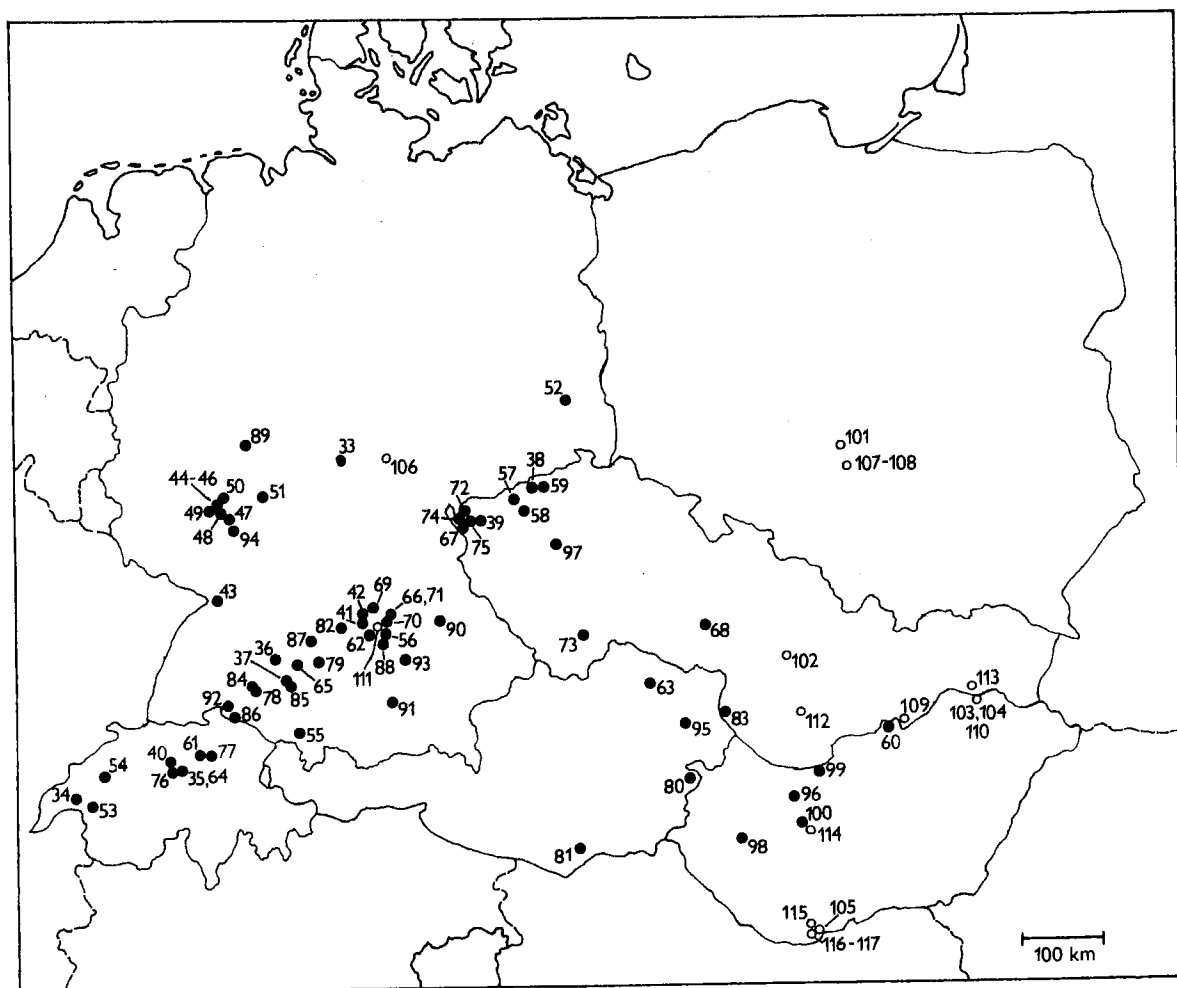


Figure 3. Map of Central Europe with distribution of its Neogene avian localities. ●, Miocene; ○, Pliocene. Numbering of localities agrees with that in text. Order of localities approximates their decreasing age.

have yielded only a few bird bones, mostly of terrestrial birds. Espenhain (21) and Traun-Pucking (32), however, have produced fossils of marine birds.

(9a) HŁUDNO, Krosno Province, Poland. Oligocene (Kotlarczyk and Jerzmańska, 1976). Leg remains of a bird, attributed to the Passeriformes (Bocheński and Szymczak, 1979).

(10) LAMMSCHLUCHT/FLÜHLI, Luzern Province, Switzerland. Lower Oligocene (cf. Weidmann and Reichel, 1979). Bird footprints, attributed to the family Rallidae (de Clercq and Holst, 1971).

(11) GOLDAU, Schwyz Province, Switzerland. Lower Oligocene (cf. Weidmann and Reichel, 1979). Bird footprints (Bräm, 1954).

(12) MATT (Engi-Matt, Engi), Glarus Province, Switzerland. Lower Oligocene (Kozur, 1984). Bones of motmots (Escher, 1839; Meyer, 1839b, 1856; Heer, 1865; Peyer, 1949, 1957; Stüssi, 1958; Baumann, 1958; Olson, 1976). Type locality of *Protornis glarniensis* and *Protornis blumeri*.

(13) SIEBLOS (Sieblos über Fulda), Fulda County, District Hessen, Germany. Lower Oligocene (Martini and Tobien, 1984). Two partial hindlimbs of birds, both probably indeterminate (Hassenkamp, 1858:207; Martini, 1967a, 1967b; Martini and Tobien, 1984). Type locality of *Pararallus hassenkampii*.

(14) MÖHREN 13, Donauwörth County, District Bayern, Germany. Lower Oligocene (Russell et al., 1982). A few bird bones mentioned by Heissig (1973).

(15) MÖHREN 6, Donauwörth County, District Bayern, Germany. Lower Oligocene (Heissig, 1970). A bird tarsometatarsus was recorded by Heissig (1970).

(16) HERRLINGEN/BLAU, Ulm County, District Baden-Württemberg, Germany. Lower Oligocene (Palmowski and Wachendorf, 1966). An ulna of a rail was noted by Immelmann (in Palmowski and Wachendorf, 1966).

(17) OPPERTSHOFEN 2, Donauwörth County, District Bayern, Germany. Lower Oligocene (Dehm, 1978). A few bones of small birds reported by Dehm (1978).

(18) WEISENBURG 9 (Weissenburg in Bayern), Weissenburg County, District Bayern, Germany. Lower Oligocene (Dehm, 1978). Undetermined bird fossils reported by Dehm (1978).

(19) KLEINKEMS (Klein-Kems), Lörrach County, District Baden-Württemberg, Germany. Middle Oligocene (Thenius, 1959). Feather imprints (Mieg et al., 1892:379, Lambrecht, 1933: 665).

(20) BURGMAGERBEIN 3, Dillingen an der Donau County, District Bayern, Germany. Middle Oligocene (Dehm, 1978). A few bones of small birds reported by Dehm (1978).

(21) ESPENHAIN, Borna County, Leipzig District, Germany. Middle Oligocene (Fischer, 1982). Fischer (1982, 1983a, 1983b, 1985) reported a small marine avifauna. Type locality of *Dimeoedoides minimus*, *Gaviota lipsiensis*, and *Oligostrix rupe-lensis*.

(22) VARNSDORF (Warnsdorf), Děčín County, District Severní Čechy, Czechoslovakia. Middle Oligocene (Konzalová, 1981; Kvaček, in litt.). Remains of an indeterminate heron (Bayer, 1882, 1883; Mlíkovský and Švec, 1989). Type locality of *Anas basaltica*.

(23) SKALICE (Skalitz), Litoměřice County, District Severní Čechy, Czechoslovakia. Middle Oligocene (Konzalová, 1981; Kvaček, in litt.). Indeterminate bird remains (Bayer, 1882, 1883; Mlíkovský and Švec, 1989). Type locality of *Anas skalicensis*.

(24) FLÖRSHEIM, Main-Taunus County, District Hessen, Germany. Upper Oligocene (Kuss, 1963). Lambrecht (1933:671) mentioned badly preserved bird remains.

(25) CHAUDERON/GRANDVAUX, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Footprints, attributed to the Rallidae and Anseridae (Weidmann and Reichel, 1979).

(26) LES ROCHES/EPESES, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Footprints, attributed to a small wader and a ?songbird (Weidmann and Reichel, 1979).

(26a) CRAU COULET/EPESES, Vaud Province, Switzerland. Upper Oligocene (Weidmann and Reichel, 1979). Two footprints, attributed to a wader (Weidmann and Reichel, 1979).

(27) BELLINGEN, Müllheim County, District Baden-Württemberg, Germany. Upper Oligocene (Brodkorb, 1978). No bird remains (Boehm, 1896, 1898). Type locality of *Ornithoidichnites badensis*.

(28) TOMERDINGEN, Ulm County, District Baden-Württemberg, Germany. Upper Oligocene (cf. Thenius, 1959). A bird bone, said to belong to *Palaeortyx ocyptera* Milne-Edwards 1892 (Seemann and Berckhemer, 1930; Lambrecht, 1933:671).

(29) GAIMERSHEIM, Ingolstadt County, District Bayern, Germany. Upper Oligocene (Ballmann, 1970). Ballmann (1970) reported an indeterminate turaco, family Musophagidae.

(30) ROTT, Monschau County, District Nordrhein-Westfalen, Germany. Upper Oligocene (Thenius, 1959). Feather imprints (Meyer, 1859, 1867).

(31) BECHLEJOVICE, Děčín County, District Severní Čechy, Czechoslovakia. Upper Oligocene (Č. Bůžek, pers. comm.). A feather imprint (Špinar, 1986:95, fig. 88c). The alleged bird bone from this locality illustrated by Špinar (1986:95, fig. 88d) is not bone at all (Mlíkovský, unpubl. obs.).

(32) TRAUN-PUCKING, Linz-Land County, District Oberösterreich, Austria. Upper Oligocene (J. Kovar in Mlíkovský, 1987). Partial skeleton of an auk (Mlíkovský, 1987). Type locality of *Petralca austriaca*.

MIocene

Miocene birds have been collected from more localities of Central Europe than all other Tertiary birds combined. Geographically, they are concentrated in the western part of Central Europe, being almost absent from its eastern part. Of the 79 localities listed here, only a few have yielded significant numbers of fossils. The complex of Aquitanian (MN 2) localities of the Mainz Basin (44–50) is completely comparable to the classic MN 2 locality of Saint-Gérard-le-Puy in France and represents the most northern and most eastern locality of the MN 2 age that has furnished

a large avifauna. Of particular interest are the Early to Middle Miocene localities of the Cheb Basin (67, 71), both of which have yielded moderate freshwater avifaunas whose identification will result in the first data on avifaunal changes at the Early to Middle Miocene transition. Of the other Middle Miocene localities, Nördlinger Ries (82) is of top quality. On the other hand, all of the Late Miocene localities have yielded just a few bird bones.

In addition to the following listed localities, Meyer (1867) mentioned a feather imprint from the Miocene of Höhgau, and Lambrecht (1933:687) mentioned a bird egg from the Miocene of Heiligenstadt and a feather imprint from the Miocene of Saltzenhausen. I was unable to identify these localities, nor verify their age, so I have excluded them from the following list.

(33) KALTENNORDHEIM (Tanne), Bad Salzungen County, Cottbus District, Germany. ?Miocene (cf. Lambrecht, 1933). Schlotheim (1820:26) reported a leg bone, said to be similar to that of *Fulica* sp.

(34) LAUSANNE, Vaud Province, Switzerland. Miocene (cf. Lambrecht, 1933). Remains of bird eggs (Gaudin, 1854).

(35) EMMENWEID, Luzern Province, Switzerland. Miocene (cf. Lambrecht, 1933). Bird eggs (Bachmann, 1878).

(36) BÖTTINGEN, Münsingen County, District Baden-Württemberg, Germany. Miocene (cf. Lambrecht, 1933). Feather imprints of a large bird, compared to those of *Aquila* sp. (Zeuner, 1931:360–61).

(37) SCHEMMERBERG, Biberbach an der Riss County, District Baden-Württemberg, Germany. Miocene (cf. Lambrecht, 1933). A few bird bones (Probst, 1879:244; Lambrecht, 1933:681).

(38) SKYŘICE (Skiritz), Most County, District Severní Čechy, Czechoslovakia. Lower Miocene (Č. Bůžek, pers. comm.). Remains of whistling-ducks (*Mionetta Livezey* and Martin 1988) (Laube, 1910).

(39) SOKOLOV, Sokolov County, District Severní Čechy, Czechoslovakia. Lower Miocene (P. Čtyrský, pers. comm.). Indeterminate remains of a bird leg (Mlíkovský, unpubl. obs.).

(40) FISCHBACH-RÜMLING, Luzern Province, Switzerland. Lower Miocene, MN 2 (cf. Weidmann and Reichel, 1979). Footprints, attributed to waders (Gasser, 1966; Weidmann and Reichel, 1979).

(41) TREUCHTLINGEN 2, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 2 (cf. Dehm, 1978). Undetermined bird remains (Dehm, 1978).

(42) WEISENBURG 6, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 2 (Schleich, 1985). Undetermined bird remains (Dehm, 1978).

(43) BÜCHELBERG, Gernersheim County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Bird remains, including those of *Palaelodus* (Kuss, 1960).

(44) WEISENAU (Weissenau, Mainz-Weissenau), Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Kuss, 1963). Remains of approximately 70 bones and 2 eggs, representing at least 12 avian species (Meyer, 1839c, 1843; Becker, 1849).

(45) BUDENHEIM, Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (Nordsieck, 1982). Bird remains (Lambrecht, 1933:670).

(46) OPPENHEIM, Mainz County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Rothausen, 1966). Bird skull, originally attributed to *Palaelodus* (Rothausen, 1966), to which it does not belong (Olson and Feduccia, 1980; Mlíkovský, 1988). Its identity remains uncertain.

- (47) MOMBACH, Bernkastel County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Lambrecht, 1933). Bones of a "cormorant" (Hoeninghaus, 1839).
- (48) INGELHEIM, Bingen County, District Rheinland-Pfalz, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Remains of a heron (Lambrecht, 1933:670).
- (49) KASTEL-BRUCH (Wiesbaden-Kastel), Wiesbaden County, District Hessen, Germany. Lower Miocene, MN 2 (cf. Thenius, 1959). Bird remains (Lambrecht, 1933).
- (50) WIESBADEN, Wiesbaden County, District Hessen, Germany. Lower Miocene, MN 2 (Nordsieck, 1982). A few bird eggs and bones, including those of waterfowl and flamingos (*Palaelodus*) (Meyer, 1839; Lambrecht, 1931, 1933; Rothausen, 1966; Eikamp, 1979). Type locality of *Cygnavus senckenbergi*.
- (51) RAVOLZHAUSEN, Hanau County, District Hessen, Germany. Lower Miocene, MN 2 (cf. Martini, 1974). Small freshwater bird fauna, including cormorants, flamingos, waterfowl, waders, and hawks (Martini, 1974; Eikamp, 1980).
- (52) SENFTENBERG, Senftenberg County, District Cottbus, Germany. Lower Miocene, MN 2 (cf. Lambrecht, 1933). A feather imprint (Menzel, 1906).
- (53) FLON MORAND, Vaud Province, Switzerland. Lower Miocene, MN 3 (cf. Weidmann and Reichel, 1979). Footprints, attributed to Laridae and Scolopacidae (Weidmann and Reichel, 1979).
- (54) LES USSEMENTS, Vaud Province, Switzerland. Lower Miocene, MN 3 (cf. Weidmann and Reichel, 1979). Footprints, attributed to Scolopacidae and Charadriidae (Weidmann and Reichel, 1979).
- (54a) AUGINE 7, Vaud Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Small avian footprints (Berger, 1985).
- (54b) MAFFLON 1, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).
- (54c) LIEFFRENS 5, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).
- (54d) BRÉ 8, Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Avian footprints, tentatively attributed to *Lymnocyrtus* (Berger, 1985).
- (54e) HEITENRIED 7 (Sodbach-Heitenried), Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Two types of avian footprints (Berger, 1985).
- (54f) BURG (Burggraben), Fribourg Province, Switzerland. Lower Miocene, MN 3 (Berger, 1985). Unidentified avian footprints (Berger, 1985).
- (55) HARBATSHOFEN (Harbatzhofen), Lindau County, District Bayern, Germany. Lower Miocene, MN 3 (cf. Erb, 1923). Indeterminate bird humerus (Haushalter, 1855; Brodkorb, 1980). Type locality of *Ardeacites molassicus*.
- (56) WINTERSHOF (WEST), Eichstätt County, District Bayern, Germany. Lower Miocene, MN 3 (Kretzoi, 1985). Diverse fauna of land birds, including gamefowl, hawks, owls, barbets, wood-hoopoes, zygodactylids, and many unidentified passerines (Dehm, 1937; Ballmann, 1969). Type locality of *Palaeortyx intermedia*, *Alectoris bavarica*, *Taoperdix miocaena*, *Otus wintershofensis*, *Strix brevis*, *Zygodactylus ignotus*, and *Capitonides europeus*.
- (57) AHNÍKOV, Chomutov County, District Severní Čechy, Czechoslovakia. Lower Miocene, MN 3 (P. Čtyrský, pers. comm.). Distal end of a humerus of a passerine bird (Mlíkovský, unpubl. obs.).*
- (58) TUCHOŘICE, Louny County, District Severní Čechy, Czechoslovakia. Lower Miocene, MN 3 (O. Fejfar, pers. comm.). Two endocranial casts of an accipitrid hawk and pedal phalanges of raptors (Mlíkovský, 1980; unpubl. obs.).
- (59) BŘEŠTANY (Preschen), Teplice County, District Severní Čechy, Czechoslovakia. Has not existed since 1962. Lower Miocene, MN ? (Č. Bůžek, pers. comm.). Small freshwater avifauna, including cormorants, herons, and storks (Laube, 1901, 1909). Type locality of *Cygnus bilineatus* and *Totanus praecursor*.
- (60) IPOLYTARNÓC, Nógrád Province, Hungary. Lower Miocene, MN 3 (Kordos, 1987). Four kinds of bird footprints (Lambrecht, 1912b, 1933:675; Kordos, 1983). Type locality of *Ornithotarnocia lambrechtii*, *Aviadactyla media*, *Tetraornithopodia tasnadii*, and *Passeripedia ipolyensis*.
- (61) WALDHALDE/SIHL, Zug Province, Switzerland. Lower Miocene, MN 3-4 (cf. Kordos, 1983). Bird footprints, attributed to the Cursoriinae and Charadriinae (Speck, 1945).
- (62) SOLNHOFEN, Weissenburg County, District Bayern, Germany. Lower Miocene, MN 3-4 (cf. Dehm, 1935). Undetermined bird bones (Dehm, 1935).
- (63) LIMBERG, Hollabrunn County, District Niederösterreich, Austria. Lower Miocene, MN 4 (cf. Bachmayer, 1980). Partial skeleton of *Falco* sp. (Bachmayer, 1980). Klipstein (*vide* Bonaparte, 1856:781) mentioned numerous birds from this locality.
- (64) RENGGBACH, Luzern Province, Switzerland. Lower Miocene, MN 4 (cf. Weidmann and Reichel, 1979). Footprints, attributed to the Scolopacidae and Recurvirostridae (Weidmann and Reichel, 1979).
- (65) KIRCHBERG, Ulm County, District Baden-Württemberg, Germany. Lower Miocene, MN 4 (cf. Cicha, 1970). A few bird bones (Probst, 1879:255; Lambrecht, 1933:681).
- (66) ERKERTSHOFEN 1, Hilpoltstein County, District Bayern, Germany. Lower Miocene, MN 4 (cf. Fahlbusch, 1966). Bones of small birds (Dehm, 1978).
- (67) DOLNICE, Cheb County, District Západočechy, Czechoslovakia. Lower Miocene, MN 4 (Fejfar and Roček, 1988). Diverse freshwater avifauna. Identified so far are loons, grebes, waterfowl, cormorants, flamingos, and gamefowl (Švec, 1980, 1981, 1982, 1983, 1984, 1985; Švec and Mlíkovský, 1986; P. Švec, pers. comm.). Type locality of *Gavia egeriana*, *Mio-baptus walteri*, *Microrallus fejfari*, and *Larus dolnicensis*. Note that records of *Querquedula*, *Nettion*, and *Anas* (Švec, 1981) are erroneous (Mlíkovský and Švec, unpubl. obs.).
- (68) OŘECHOV, Brno-venkov County, District Jižní Morava, Czechoslovakia. Lower Miocene, MN 4 (P. Čtyrský, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).
- (69) RAITENBUCH 2, Weissenburg County, District Bayern, Germany. Lower/Middle Miocene, MN 4-5 (cf. Heissig, 1978). Bird remains (Heissig, 1978).
- (70) PETERSBUCH 2, Hilpoltstein County, District Bayern, Germany. Lower/Middle Miocene, MN 4-5 (cf. Heissig, 1978). Bird remains (Heissig, 1978).
- (71) ERKERTSHOFEN 2, Hilpoltstein County, District Bayern, Germany. Lower/Middle Miocene, MN 4-5 (cf. Heissig, 1978). Remains of the family Strigidae (Heissig, 1978).
- (72) ZELENÁ, Cheb County, District Západočechy, Czechoslovakia. Lower/Middle Miocene, MN 4-5 (Č. Bůžek, pers. comm.). Two feather imprints (Mlíkovský and Švec, unpubl. obs.).
- (72a) RANDECKER MAAR, Kirchheim County, District Baden-Württemberg, Germany. Middle Miocene, MN ? (Westphal, 1963; Bleich, 1988). Unidentified feather imprints and coproliths of birds (Westphal, 1963).

- (73) LIŠOV, České Budějovice County, District Jižní Čechy, Czechoslovakia. Middle Miocene, MN 8 (O. Fejfar, pers. comm.). Cervical vertebra of a flamingo (Mlíkovský, unpubl. obs.).
- (74) FRANTIŠKOVY LÁZNĚ, Cheb County, District Západočechy, Czechoslovakia. Middle Miocene, MN 5 (O. Fejfar, pers. comm.). Moderate number of bird bones, of which *Dendrocygnini* and flamingos (*Palaelodus*) have been identified so far (Mlíkovský, unpubl. obs.).
- (75) MOKŘINA (Krottensee), Cheb County, District Západočechy, Czechoslovakia. Middle Miocene, MN 5 (cf. Obrhelová and Obrhel, 1984). Feather imprints (Novák, 1877:77–79, pl. II, fig. 13; pl. III, fig. 8). Novák (1877:77) mentioned that A.E. Reuss (1811–1873) had collected bird bones from this locality, but their whereabouts were already unknown in Novák's time.
- (76) SULZIGTOBEL/WERTHENSTEIN, Luzern Province, Switzerland. Middle Miocene, MN 5–6 (cf. Bolliger et al., 1988; Č. Bůžek, pers. comm.). Undetermined bird footprints (Weidmann and Reichel, 1979).
- (77) RISITOBEL/STÄFA, Zürich Province, Switzerland. Middle Miocene, MN 5–6 (Bolliger et al., 1988). Undetermined bird footprints (Weidmann and Reichel, 1979).
- (78) HEGGBACH, Biberbach an der Riss County, District Baden-Württemberg, Germany. Middle Miocene, MN 5–6 (Zöbele, 1983). A few bird bones (Probst, 1879:262).
- (79) GÜNZBURG, Günzburg County, District Bayern, Germany. Middle Miocene, MN 5–6 (Zöbele, 1983). Bird remains (Rühl, 1896).
- (79a) PRZEWORNO 1, Walbrzych Province, Poland. Middle Miocene, MN 5–6 (Nadachowski et al., 1989). Four bones of *Miophasianus* (Bocheński, 1987).
- (80) WEINGRABEN, Oberpullendorf County, District Burgenland, Austria. Middle Miocene, MN 5–6 (cf. Bachmayer, 1964). Feather imprints, attributed to grebes, ?cormorants, herons, and ducks (Bachmayer, 1964).
- (81) SCHÖNWEG, Wolfsberg County, District Kärnten, Austria. Middle Miocene, MN 5–6. An egg, attributed to *Pandion* sp. (Rauscher, 1984).
- (81a) ST. MARGARETHEN, St. Margarethen County, District Burgenland, Austria. Middle Miocene, MN 5–6 (O. Schultz, pers. comm.). Partial skeleton of a species of *Gavia* (Mlíkovský, unpubl. obs.).
- (82) NÖRDLINGER RIES, Nördlingen County, District Bayern, Germany. Includes the following fossil bird producing sites: Adlersberg, Goldberg, Hahnenberg, Kleinsorheim (Klein-Sorheim), Lierheim, Steinberg (Spitzberg), and Wallerstein. Middle Miocene, MN 6 (Heizmann and Fahlbusch, 1983). Rich avifauna that has not yet been adequately described. Reported so far are taxa of the Pelecanidae, Ciconiidae, Phoenicopteridae, Anseridae, Rallidae, Charadriidae, Scolopacidae, Glareolidae, Psittacidae, Coliidae, Capitonidae, and Passeriformes (Fraas, 1879; Lambrecht, 1933:677; Seemann, 1941; Ballmann, 1979, 1983; Heizmann and Fahlbusch, 1983; Mlíkovský, 1988). Type locality of *Pelecanus intermedius*, *Pelecanus fraasi*, *Anas risgoviensis*, *Mioglareola gregaria*, *Glareola neogaena*, and *Capitonides protractus*.
- (83) DĚVÍNSKÁ NOVÁ VES (Neudorf), Bratislava County, Bratislava District, Czechoslovakia. Middle Miocene, MN 6 (Kordos, 1987). Švec (1986) described from this locality two bone fragments of *Miophasianus*, but a larger number of bird bones are known from this site (Thenius, 1959:85; H. Zapfe fide O. Schultz, in litt., 1988; Mlíkovský, unpubl. obs.).
- (84) STORZINGEN (not Stotzingen, as written in Lambrecht, 1933), Sigmaringen County, District Baden-Württemberg, Germany. Middle Miocene, MN 6–7 (cf. Probst, 1879). A few bird bones (Probst, 1879:244).
- (85) BALTRINGEN, Biberbach an der Riss County, District Baden-Württemberg, Germany. Middle Miocene, MN 6–7 (cf. Probst, 1879). A few bird bones (Probst, 1879:244).
- (86) ÖHNINGEN (Oehningen, Öningen, Oeningen, Steyn, Stein, Stein am Rhein), Konstanz County, District Baden-Württemberg, Germany. Middle Miocene, MN 7 (Tobien, 1986b). Only waterfowl and gamefowl (indet.) have been mentioned from this locality so far, but more avian fossils from this site are apparently scattered over various central and western European museums (Scheuchzer, 1708; Karg, 1805; Meyer, 1838, 1839a, 1845, 1864, 1865; Heer, 1865:408). Type locality of *Anas oeningensis* and *Anas meyerii*.
- (87) STEINHEIM (Steinheim am Albuch), Heidenheim an der Brenz County, District Baden-Württemberg, Germany. Middle Miocene, MN 7 (Jung and Mayr, 1980). Small, mainly freshwater avifauna, including pelicans, waterfowl, ibises, flamingos, rails, bustards, and gamefowl (Fraas, 1870, 1879; Lydekker, 1891; Lambrecht, 1933:677–78). Type locality of *Ardea similis*, *Palaelodus steinheimensis*, *Anas atava*, *Anas cygniformis*, and *Otis affinis*.
- (88) ATTENFELD, Neuburg an der Donau County, District Bayern, Germany. Middle Miocene, MN 7 (cf. Thenius, 1959). Small avifauna, including waterfowl, gamefowl, and passerines (Lambrecht, 1933:687).
- (89) CLIMBACH 1, Giessen County, District Hessen, Germany. Middle Miocene, MN 7 (cf. Thenius, 1959). Dieffenbach (1853:685) mentioned "many bird bones" from this locality (see also Engelhardt and Schottler, 1914:328).
- (90) DECHBETTEN, Regensburg County, District Bayern, Germany. Middle Miocene, MN 7–8 (cf. Steininger et al., 1987). Small avifauna, including cormorants and gamefowl (Ammon, 1918). Type locality of *Phalacrocorax praecarbo*, *Botaurites avitus*, *Ardea brunhuberi*, *Phasianus augustus*, and *Gallus longaevus*.
- (91) AUMEISTER, München County, District Bayern, Germany. Middle/Upper Miocene, MN 8–9 (O. Fejfar, pers. comm.). Small freshwater avifauna, including herons and waterfowl (Stromer, 1928:4; Lambrecht, 1933). Type locality of *Anas isarensis*.
- (92) HÖWENEGG, Donaueschingen County, District Baden-Württemberg, Germany. Upper Miocene, MN 9 (Tobien, 1986b). A bird bone (Jörg, 1957:120).
- (93) SANDELZHAUSEN, Mainburg County, District Bayern, Germany. Upper Miocene, MN ?9 (cf. Fahlbusch and Gall, 1970). Bird bones (Fahlbusch and Gall, 1970).
- (94) EPELSHEIM, Alzey County, District Rheinland-Pfalz, Germany. Upper Miocene, MN 9 (Fejfar and Heinrich, 1987). A duck and a crane were recorded from here (Lambrecht, 1933), but both records are doubtful. Type locality of *Anas eppelsheimensis* and *Pligrus germanicus*.
- (95) VÖSENDORF (Brunn-Vösendorf), Mödling County, District Niederösterreich, Austria. Upper Miocene, MN 10 (Steininger et al., 1987). Two bird bones, including one of *Palaeocryptonyx* sp. (Thenius, 1954).
- (96) CSÁKVÁR, Fejér Province, Hungary. Upper Miocene, MN 10 (Fejfar and Heinrich, 1987). Small avifauna, including swans, cranes, and owls (Lambrecht, 1929; Kretzoi, 1957). Type locality of *Cygnus csakvarensis* and *Bubo florianae*.
- (96a) GÖTZENDORF (Götzendorf an der Leitha, Mannersdorf), Mannersdorf am Leithagebirge County, District Niederösterreich, Austria. Upper Miocene, MN 10 (Bachmayer and

Wilson, 1984; Rabeder, 1989) or MN 11 (cf. Lueger, 1981). Small freshwater avifauna, including *Anhinga* and *Dendronessa* (Mlíkovský, 1991).

(97) SUCHOMASTY 3, Beroun County, District Střední Čechy, Czechoslovakia. Upper Miocene, MN 11 (I. Horáček, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).

(98) SÜMEG, Veszprém Province, Hungary. Upper Miocene, MN 11 (Kordos, 1987) or MN 12 (Fejfar and Heinrich, 1987). A few bird bones, including those of *Palaeortyx* and a swift (?*Chaetura*) (Jánossy, 1976b, 1977). Type locality of *Chaetura baconica*.

(99) TARDOSBÁNYA, Komárom Province, Hungary. Upper Miocene, MN 12 (Kordos, 1987). Bones of *Palaeortyx* (Jánossy, 1976b).

(100) POLGÁRDI, Fejér Province, Hungary. Upper Miocene, MN 13 (Fejfar and Heinrich, 1987; Kordos, 1987). Moderate number of bird bones, including those of gamefowl, bustards, rails, waders, owls, and passerines (Lambrecht, 1912b; Jánossy, 1976b, 1979). Type locality of *Anas albae*.

PLIOCENE

None of the 19 localities listed below has yielded significant numbers of bird bones except Rębielice Królewskie 1 (107) and Villány 3 (115). The Pliocene localities are concentrated in the eastern part of Central Europe, the opposite of the Miocene localities.

(101) WĘŻE 1, Sieradz Province, Poland. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1987). Small avifauna, comprising gamefowl only (Jánossy, 1974b). Type locality of *Tetrao conjugens* and *Francolinus capeki wenzensis*.

(102) IVANOVCE, Trenčín County, District Západné Slovensko, Czechoslovakia. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1985). Bone remains of undetermined passerines (P. Švec in Fejfar and Heinrich, 1985).

(103) OSZTRAMOS 1 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Lower Pliocene, MN 15 (cf. Jánossy, 1986). A few bird bones (Jánossy, 1976b, 1979). Type locality of *Turdoides borealis*.

(104) OSZTRAMOS 9 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Lower Pliocene, MN 15 (cf. Fejfar and Heinrich, 1983). Type locality of *Porzana estramosi* (Jánossy, 1979).

(105) CSARNÓTA 2, Baranya Province, Hungary. Lower Pliocene, MN 15 (Fejfar and Heinrich, 1987). Moderate avifauna, including gamefowl, rails, waders, cuckoos, owls, and passerines (Jánossy, 1976a, 1976b, 1977). Type locality of *Tetrao macropus*, *Scolopax baranensis*, *Gallinago veterior*, and *Cuculus csarnotanus*.

(105a) GUNDERSHEIM, Worms County, District Rheinhessen, Germany. Lower Pliocene, MN 15? (I. Horáček, pers. comm.). A carpometacarpus, attributed to *Turdus* sp. (Heller, 1936).

(106) RIPPERSRODA 1, Arnstadt County, Erfurt District, Germany. Middle Pliocene, MN 15–16 (O. Fejfar, pers. comm.; see also Mai et al., 1963; Velitzelos and Gregor, 1987). Fossils of an eagle-owl and passerines (Giebel, 1860). Type locality of *Ardea lignitum*.

(107) RĘBIELICE KRÓLEWSKIE 1, Częstochowa Province, Poland. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Diverse avifauna, including gamefowl, owls, hawks, cranes, waders, and passerines (Jánossy, 1974b). Type locality of *Lagopus*

lagopus atavus, *Francolinus capeki villanyiensis*, and *Athene noctua veta*.

(108) RĘBIELICE KRÓLEWSKIE 2, Częstochowa Province, Poland. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Only gamefowl recorded so far (Jánossy, 1974b). Type locality of *Francolinus minor*.

(109) HAJNÁČKA (Ajnácskö), Rimavská Sobota County, District Východné Slovensko, Czechoslovakia. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1985). Fossils of waterfowl (*Mergus* sp.) (P. Švec in Fejfar and Heinrich, 1985).

(110) OSZTRAMOS 7 (Estramos), Borsod-Abaúj-Zemplén Province, Hungary. Upper Pliocene, MN 16 (Fejfar and Heinrich, 1987). Small terrestrial avifauna, including gamefowl and owls (Jánossy, 1976b, 1977, 1986).

(111) SCHERNFELD, Eichstätt County, District Bayern, Germany. Upper Pliocene, MN 17 (Fejfar and Heinrich, 1985). Undetermined bird bones (Dehm, 1962).

(111a) KIELNIKI 3B, Częstochowa Province, Poland. Upper Pliocene, MN 17 (Nadachowski et al., 1989). A single bone of *Lagopus* (Bocheński, 1989).

(112) KOLÍŇANY 2, Nitra County, District Západné Slovensko, Czechoslovakia. Upper Pliocene, MN 17 (I. Horáček, pers. comm.). A few bird bones (Mlíkovský, unpubl. obs.).

(113) VČELÁRE 3 (Méhész), Košice-vidiek County, District Východné Slovensko, Czechoslovakia. Upper Pliocene, MN 17 (Horáček, 1985). A few bird bones (Horáček, 1985).

(114) KISLÁNG, Fejér Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). A few bird bones, including those of *Struthio* sp. and *Anas* (Kretzoi, 1954, 1955; Jánossy, 1986). Type locality of *Struthio pannonicus*.

(115) VILLÁNY 3, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). Moderate-sized avifauna, including grebes, waterfowl, gamefowl, bustards, hawks, owls, pigeons, woodpeckers, and passerines (Jánossy, 1976a, 1976b, 1977, 1979, 1980; Mlíkovský, 1981, 1982). Type locality of *Anas submajor*, *Francolinus subfrancolinus*, *Surnia robusta*, and *Dendrocopos praemedius*.

(116) BEREMEND 5, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). Small avifauna, including gamefowl, rails, swifts, and passerines (Jánossy, 1976b, 1977). Type locality of *Gallus beremendensis*.

(117) BEREMEND 11, Baranya Province, Hungary. Upper Pliocene, MN 17 (cf. Jánossy, 1986). A few bird bones, including those of *Francolinus* sp., *Falco* sp., and undetermined passerines (Jánossy, 1986).

SUMMARY

A review of the present state of knowledge of the Tertiary birds of Central Europe shows that fossils of Tertiary birds are known from at least 132 localities within the region. These localities range in age from the Late Paleocene to the latest Pliocene. Fossil birds have been adequately described from just a few of these localities. The most important localities appear to be Walbeck (Late Paleocene), Messel (Middle Eocene), Wintershof-West (MN 3), Dolnice (MN 4), Nördlinger Ries (MN 6), Polgárdi (MN 13), Rębielice Królewskie 1 (MN 16), and Villány 3 (MN 17). Best documented are the Early and Middle Miocene birds of Central Europe.

At least 94 species group names were first given to the Tertiary birds of Central Europe, of which six are *nomina nuda*, 2 are based upon non-avian material, 21 were shown to be misidentified as to the family within the class Aves, 9 were shown to

be misidentified as to the genus within families, 1 was synonymized within genus, and 13 are to be currently regarded as having uncertain taxonomic position. Forty-eight, or 54 percent, of these species group names were not listed in Brodkorb's catalogue of fossil birds (Brodkorb, 1963, 1964, 1967, 1971, 1978). Data on the original description, holotypes, and their location (if known) and the age and locality from which each species or subspecies was found are given. The data for the taxa listed in Brodkorb's catalogues were checked, corrected in some cases, and sometimes supplemented.

At least 32 genus group names were first given to the Tertiary birds of Central Europe, of which 2 are *nomina nuda*, 10 were shown to be misclassified as to the family, 1 was synonymized within family, and 4 are to be currently regarded as having uncertain taxonomic position. Eighteen, or 56 percent, of these genus group names were not listed in Brodkorb's catalogue of fossil birds.

New taxonomic conclusions are as follows: (1) *Cygnus csakvarensis* belongs in the genus *Olor*; (2) *Anas isarensis* is an indeterminate member of the tribe Aythyini; (3) *Anas atava* belongs in the genus *Cygnus*; (4) *Anas eppelsheimensis* is Anseridae incertae sedis; (5) *Athene noctua veta* is synonymous with the modern *Aegolius funereus*; (6) *Ardea lignitum* is synonymous with the modern *Bubo bubo*; and (7) *Eleutherornis helveticus*, *Anas risgoviensis*, *Anas meyerii*, *Totanus praecursor*, *Scolopax baranensis*, *Gallinago veterior*, and *Turdoides borealis* should be considered Aves incertae sedis until their types are restudied.

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APPENDIX 1

List of family group names based upon Tertiary birds of Central Europe. Type genera are given in parentheses and the original taxonomic level is indicated.

- Capitonidae Prum 1988 (*Capitonides* Ballmann 1969)—family.
- Diomedeoidea Fischer 1985 (*Diomedeoidea* Fischer 1985)—family.
- Eleutherornithidae Wetmore 1951 (*Eleutherornis* Schaub 1940)—family.
- Messelornithidae Hesse 1988 (*Messelornis* Hesse 1988)—family.
- Palaeotidae Houde and Haubold 1987 (*Palaeotis* Lambrecht 1928)—subfamily.
- Petralidae Mlíkovský 1987 (*Petralca* Mlíkovský 1987)—subfamily.
- Zygodactylidae Brodkorb 1971 (*Zygodactylus* Ballmann 1969)—family.

APPENDIX 2

List of genus group names based upon Tertiary birds of Central Europe. Type species are given in parentheses.

- Aenigmavis* Peters 1987 (*Aenigmavis sapea* Peters 1987).
- Ardeacites* Haushalter 1855 (*Ardeacites molassicus* Haushalter 1855).
- Aviadactyla* Kordos 1983 (*Aviadactyla media* Kordos 1983)—ichnogenus.
- Botaurites* Ammon 1918 (*Botaurites avitus* Ammon 1918 = *Graculus intermedius* Milne-Edwards 1867).
- Capitonides* Ballmann 1969 (*Capitonides europeus* Ballmann 1969).
- Cygnanser* Kretzoi 1957 (*Cygnus csakvarensis* Lambrecht 1933).
- Cygnavus* Lambrecht 1931 (*Cygnavus senckenbergi* Lambrecht 1931).
- Diomedeoidea* Fischer 1985 (*Diomedeoidea minimus* Fischer 1985).
- Eleutherornis* Schaub 1940 (*Eleutherornis helveticus* Schaub 1940).
- Eocathartes* Lambrecht 1935 (*Eocathartes robustus* Lambrecht 1935).
- Eoglaucidium* Fischer 1987 (*Eoglaucidium pallas* Fischer 1987).
- Geiseloceros* Lambrecht 1935 (*Geiseloceros robustus* Lambrecht 1935).
- Lambrechtia* Jánossy 1974. [Type species neither designated nor indicated, hence a *nomen nudum* according to provisions of Article 13b of the International Code of Zoological Nomenclature (ICZN, 1985).]
- Messelornis* Hesse 1988 (*Messelornis cristata* Hesse 1988).
- Microrallus* Švec 1983 (*Microrallus fejfari* Švec 1983).
- Miobaptus* Švec 1982 (*Miobaptus walteri* Švec 1983).
- Miogallus* Lambrecht 1933 (*Gallus longaevis* Ammon 1918).
- Mioglareola* Ballmann 1979 (*Mioglareola gregaria* Ballmann 1979).
- Oligostrix* Fischer 1982 (*Oligostrix rupeliensis* Fischer 1982 = *nomen nudum*)—*nomen nudum*.
- Oligostrix* Fischer 1983 (*Oligostrix rupelensis* Fischer 1983).
- Ornithotarnocia* Kordos 1983 (*Ornithotarnocia lambrechtii* Kordos 1983)—ichnogenus.
- Osteornis* Gervais 1844 (*Osteornis scolopacinus* Gervais 1844 = *nomen nudum*)—*nomen nudum*.
- Pachystruthio* Kretzoi 1954 (*Struthio panonicus* Kretzoi 1954 = *Struthiolithus chersonensis* Brandt 1873).
- Palaeogrusr* Lambrecht 1935 (*Palaeogrusr geiseltalensis* Lambrecht 1935).
- Palaeotis* Lambrecht 1928 (*Palaeotis weigelti* Lambrecht 1928).
- Passeripedia* Kordos 1983 (*Passeripedia ipolyensis* Kordos 1983)—ichnogenus.
- Petralca* Mlíkovský 1987 (*Petralca austriaca* Mlíkovský 1987).
- Pliogrusr* Lambrecht 1933 (*Pliogrusr germanicus* Lambrecht 1933).
- Plumumida* Hoch 1980 (*Plumumida lutetialis* Hoch 1980 = *Rhynchaetes messelensis* Wittich 1899).
- Protornis* Meyer 1844 (*Protornis glarniensis* Meyer 1844).
- Rhynchaetes* Wittich 1899 (*Rhynchaetes messelensis* Wittich 1899).
- Tetraornithopedia* Kordos 1983 (*Tetraornithopedia tasnadii* Kordos 1983)—ichnogenus.
- Zygodactylus* Ballmann 1969 (*Zygodactylus ignotus* Ballmann 1969).