

A new barn owl (Aves: Strigidae) from the early Miocene of Germany, with comments on the fossil history of the Tytoninae

Jiří Mlíkovský

Institute of Geology and Paleontology, Charles University, Albertov 6, CZ-128 43 Praha 2, Czech Republic

Summary

A previously unknown, very large barn owl, *Basityto rummeli* is described from the early Miocene of Grafenmühle 21 in Bavaria, Germany. This raises the number of tytonine genera known from the early Miocene to three. *Necrobyas* is known only from France, *Prosybris* from France and Austria, and *Basityto* so far only from Germany.

Further taxonomic conclusions are as follows: *Palaeotyto cadurcensis* Mourer-Chauviré, *Palaeobyas cracrafti* Mourer-Chauviré, and *Tyto edwardsi* (Gaillard) are excluded from the Tytoninae. Six species are synonymized: *Necrobyas rossignoli* Milne-Edwards with *Necrobyas harpax* Milne-Edwards, *Necrobyas edwardsi* Gaillard with *Necrobyas arvernensis* (Milne-Edwards), *Necrobyas minimus* Mourer-Chauviré with *Prosybris antiqua* (Milne-Edwards), *Tyto campiterrae* Jánossy with *Tyto sanctialbani* (Lydekker), *Tyto robusta* Ballmann with *Tyto gigantea* Ballmann, and *Tyto melitensis* (Lydekker) with *Tyto alba* (Scopoli). *Necrobyas medius* Mourer-Chauviré was transferred to the genus *Prosybris*. In addition, *Strix ignota* "Milne-Edwards" and *Strix ignota* "Paris" emerge as not available for nomenclatural purposes.

Key words: Aves, Strigidae, Tytoninae, Paleogene, Neogene, Quaternary

Zusammenfassung

Eine neue Schleiereule (Aves: Strigidae) aus dem Untermiozän in Deutschland: mit Anmerkungen zur fossilen Geschichte der Tytoninae

Eine neue, sehr große Schleiereule, *Basityto rummeli*, wird aus dem Untermiozän von Grafenmühle 21 in Bayern beschrieben. Damit ist die Anzahl der aus dem Untermiozän bekannten Schleiereulengattungen auf drei gestiegen. *Necrobyas* ist bisher nur aus Frankreich, *Prosybris* aus Frankreich und Österreich, und *Basityto* aus Bayern bekannt. Weitere taxonomische Ergebnisse sind wie folgt: *Palaeotyto cadurcensis* Mourer-Chauviré, *Palaeobyas cracrafti* Mourer-Chauviré und *Tyto edwardsi* (Gaillard) wurden aus den Tytoninae entfernt. Sechs Arten wurden synonymisiert: *Necrobyas rossignoli* Milne-Edwards mit *Necrobyas harpax* Milne-Edwards, *Necrobyas edwardsi* Gaillard mit *Necrobyas arvernensis* (Milne-Edwards), *Necrobyas minimus* Mourer-Chauviré mit *Prosybris antiqua* (Milne-Edwards), *Tyto campiterrae* Jánossy mit *Tyto sanctialbani* (Lydekker), *Tyto robusta* Ballmann mit *Tyto gigantea* Ballmann und *Tyto melitensis* (Lydekker) mit *Tyto alba* (Scopoli). *Necrobyas medius* Mourer-Chauviré wurde in die Gattung *Prosybris* überführt. Die Namen *Strix ignota* „Milne-Edwards“ und *Strix ignota* „Paris“ sind für nomenklatorische Zwecke nicht verfügbar.

Introduction

Modern barn owls (subfamily Tytoninae of the family Strigidae) are small to middle-sized owls, which inhabit a variety of biotopes around the world (Burton 1973, Eck & Busse 1973, Schneider 1977). The subfamily (treated as family by some authors) consists now only of two

genera (*Tyto* Billberg, 1828, and *Phodilus* Geoffroy-Saint-Hilaire, 1830), with 9 and 2 species (sensu Wolters 1975–1982), respectively. The fossil record of the Tytoninae, which includes also pigmy and gigantic forms, is quite rich and goes back to the late Eocene (Mourer-Chauviré 1987).

In the present paper I will describe a new barn

owl species from the early Miocene of Bavaria, Germany, and comment on the fossil history of the subfamily Tytoninae.

The stratigraphy follows Schmidt-Kittler (1987) for the Paleogene (Mammal Paleogene zones, MP), Mein (1990) for the Neogene (Mammal Neogene zones, MN), and Horáček & Ložek (1988) for the Quaternary (Quaternary biozones, Q). Museum acronyms are as follows: MNHN = Muséum National d'Histoire Naturelle, Paris, France; NHMW = Naturhistorisches Museum, Wien, Austria; and USNM = United States National Museum, Washington, D.C., USA.

Systematic Paleontology

Order Strigiformes Wagler, 1830

Family Strigidae Vigors, 1825

Subfamily Tytoninae Ridgway, 1914

Basityto, n. g.

Type: *Basityto rummeli*, n. sp.

Included species: Type species only.

Diagnosis: Very large barn owl. Humerus with high ectepicondyle, distal margin between external and internal condyle slightly deepened, ligamental furrow broad, deep, almost perpendicular to the axis of the bone, and distally opened.

Comparison: Holotypical humerus of *Basityto rummeli* agrees with the same element of the Tytoninae, and differs from that of other owls, in having a large and long ligamental furrow. It differs from the humeri of *Necrobyas* in having a higher ectepicondyle, and a slightly deepened distal margin between internal and external condylus; from the humeri of *Nocturnavis* in having a much broader ligamental furrow perpendicular to the axis of the bone; from *Tyto* and *Phodilus* in having a higher ectepicondyle, and a much broader ligamental furrow perpendicular to the axis of the bone. No direct comparison was possible with the humeri of *Prosybris* and *Selenornis*, because this element is not known for these two genera. Nevertheless, *Prosybris* was a genus of pigmy owls, and *Selenornis* was also much smaller than *Basityto*.

Etymology: Abbreviated from Greek βασιλευς, king, and *Tyto*, modern genus of barn owls. Alludes to the majestic size of the



Fig. 1. Holotype humerus of *Basityto rummeli* from the early Miocene of Bavaria (a), and humerus of a modern Barn Owl *Tyto alba* (b) in anconal view (55% of natural size)

Abb. 1. Der holotypische Humerus von *Basityto rummeli* aus dem Untermiozän Bayerns (a) und Humerus einer rezenten Schleiereule *Tyto alba* (b) in Medialansicht (55% der natürlichen Größe)

owl, which virtually made it the feathered king of Central European early Miocene.

Basityto rummeli, n. sp. (Fig. 1a, 2)

Holotype: Almost complete left humerus in two parts; coll. Rummel, uncatalogued.

Material: Holotype only.

Age and locality: Early Miocene, MN 2–3, of Grafenmühle 21, Bavaria, Germany (M. Rummel, in litt.). The locality is one of the many fossiliferous fissures in southern Germany (see Mlíkovský 1992, Mlíkovský & Hesse 1996).

Diagnosis: As for the genus.

Measurements: Greatest length (estimated) = 175 mm, greatest width of distal end = ca.



Fig. 2. Holotype humerus of *Basityto rummeli* from the early Miocene of Bavaria in plantar view (55% of natural size)

Abb. 2. Der holotypische Humerus von *Basityto rummeli* aus dem Untermiozän Bayerns in Lateralansicht (55% der natürlichen Größe)

26.5 mm, width $\times$ depth of shaft in the center = 13.1 $\times$ 11.2 mm.

Etymology: After Dr. Michael Rummel (Weissenburg), who collected the fossil, in recognition of his paleontological work on vertebrate remains from the Tertiary fissure deposits of Bavaria.

Remarks: *Basityto rummeli* is the largest continental barn owl known, being comparable in size to the gigantic island forms *Tyto riveroi* Arredondo, 1972b from the Quaternary of Cuba, and *Tyto gigantea* Ballmann, 1973 from the Pliocene of Gargano. It probably preyed upon small ungulates, which are abundant in south German fissure deposits, formed during the time when *Basityto rummeli* inhabited the region (see Heissig 1978).

Comments on some other fossil barn owls

Brodkorb (1971) listed 11 species of barn owl, to which Mourer-Chauviré (1987) added another ten. Below I present comments on some of these taxa.

Palaeotyto cadurcensis

Palaeotyto cadurcensis was described by Mourer-Chauviré (1987) in the monotypic genus *Palaeotyto* on the basis of a coracoid from an unknown locality within the Phosphorites du Quercy. Age of the species is unknown, and can lie anywhere between the middle Eocene and late Oligocene (Rémy et al. 1987, Mourer-Chauviré 1995, 1996). The coracoid of *Palaeotyto* differs from the same element of proper Tytoninae in the configuration of its head, and in the remarkable size of the coracoidal foramen. For further details of how the coracoid of *Palaeotyto* differs from the same element of *Necrobyas*, *Tyto* and *Phodilus*, the three most important barn owl genera, see Mourer-Chauviré (1987). Consequently, *Palaeotyto* should be removed from the Tytoninae.

Palaeobyas cracrafti

Palaeobyas cracrafti, the only species included in *Palaeobyas*, was described by Mourer-Chauviré (1987) on the basis of a single tarsometatarsus from an unknown locality within the Phosphorites du Quercy, which range in age from the middle Eocene to the late Oligocene (Rémy et al. 1987, Mourer-Chauviré 1995, 1996). The tarsometatarsus is very stout, trochleae are open in distal view, and external hypotarsal ridge is blunt. In these features *Palaeobyas* differs from the Tytoninae, and agrees with *Sophiornis* and *Berruornis*, which are placed in the family Sophiornithidae (Mourer-Chauviré 1987, 1994). Hence, *Palaeobyas* should be removed from the Tytoninae, and placed in the Sophiornithidae.

Necrobyas spp.

Mourer-Chauviré (1987) distinguished six species in the genus *Necrobyas*: *N. harpax* Milne-Edwards, 1892, *N. rossignoli* Milne-Edwards, 1892, *N. edwardsi* Gaillard, 1939,

N. medius Mourer-Chauviré, 1987, *N. minimus* Mourer-Chauviré, 1987, and *N. arvernensis* (Milne-Edwards, 1863). Of these, *Necrobyas medius* and *Necrobyas minimus* differ distinctly from *Necrobyas* in the morphology of their tarsometatarsi, and belong in the genus *Prosybris* (see below).

Before addressing the taxonomic status of the remaining four species, three technical comments are necessary: *Necrobyas harpax* was based by Milne-Edwards (1892) on a tarsometatarsus, to which an ulna and a humerus were assigned ("Je rapporte à . . ."). Hence, the tarsometatarsus is the holotype, while ulna and humerus are paratypes of the species. Inexplicably, Mourer-Chauviré (1987: 97) selected left tarsometatarsus (MNHN QU 15695) as a lectotype (sic!) of *Necrobyas harpax*. This action has no bearing on the nomenclatural or taxonomic status of the species. Moreover, measurements of this "lectotype" differ markedly from the measurements of the holotype given by Milne-Edwards (1892: 62), which are as follows: maximum length = 37 mm, proximal width = 8.5 mm, width of the shaft = 5 mm, and distal width = 10 mm. Among *Necrobyas* tarsometatarsi from early collections, which are deposited in MNHN, and could thus be at the disposal of Milne-Edwards, only the tarsometatarsus QU 15742 closely resembles Milne-Edwards' specimen in measurements (see Mourer-Chauviré 1987: 102). This specimen

should be deemed to be the holotype of *Necrobyas harpax*.

Necrobyas rossignoli was based by Milne-Edwards (1892: 63) on a single tarsometatarsus whose exact age he neglected to mention, from the deposits of the Phosphorites du Quercy, which range in age between the middle Eocene and late Oligocene (Mourer-Chauviré 1995, 1996, Rémy et al. 1987). Mourer-Chauviré (1987) decided that the species was late Eocene in age. This observation was based on a single, very fragmentary coracoid, of which only the shaft was measurable, which came from the late Eocene (MP 17) of Perrière in Quercy. Metrical comparison (Fig. 3) shows that this specimen differs from Oligocene coracoids of *Necrobyas* spp. in the shape of its shaft. Hence, I doubt that the specimen was correctly assigned to *Necrobyas*, let alone *Necrobyas rossignoli*. In consequence, there is no indication that *Necrobyas rossignoli* is a late Eocene species. Similarly, there is no indication that the genus *Necrobyas* existed before the Oligocene.

Necrobyas arvernensis was described by Milne-Edwards (1863) on the basis of a tarsometatarsus and a tibiotarsus from the early Miocene (MN 2) of Saint-Gérard-le-Puy in France. Most fossil owls were based on tarsometatarsi, while tibiotarsi are much less abundant. Hence, I select here the tarsometatarsus MNHN Av. 2834b as the lectotype of *Necrobyas arvernensis*. Herewith, the tibio-

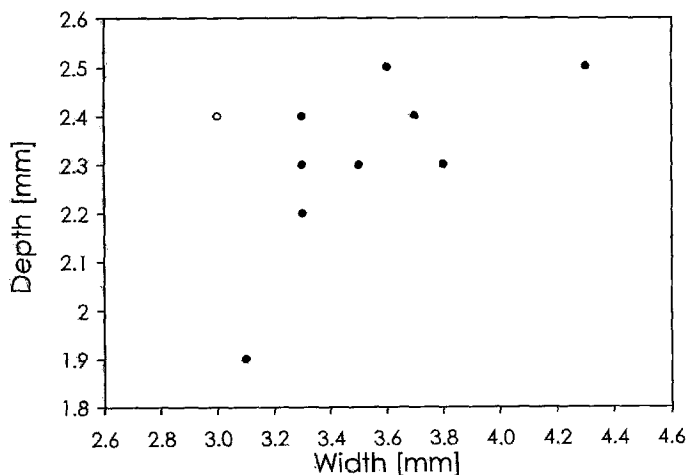


Fig. 3. Dimensions of *Necrobyas* coracoids, showing width and depth of shaft. Data are from Mourer-Chauviré (1987). Circle marks the coracoid from Perrière. See text for explanation

Abb. 3. Breite und Tiefe des Coracoidkörpers der Gattung *Necrobyas*. Die Angaben entstammen Mourer-Chauviré (1987). Der Kreis bezeichnet das Coracoid aus Perrière. Siehe Text für Erklärung

Fig. 4. Dimensions of *Necrobyas* tarsometatarsi, showing their maximum length and proximal width. Data are from Mourer-Chauviré (1987). 1 – holotype of *Necrobyas rossignoli*, 2 – holotype of *Necrobyas harpax*, 3 – holotype of *Necrobyas edwardsi*, 4 – lectotype of *Necrobyas arvernensis*

Abb. 4. Maximale Länge und proximale Breite der Tarsometatarsi von *Necrobyas*. Die Angaben entstammen Mourer-Chauviré (1987). 1 – Holotyp von *Necrobyas rossignoli*, 2 – Holotyp von *Necrobyas harpax*, 3 – Holotyp von *Necrobyas edwardsi*, 4 – Lektotyp von *Necrobyas arvernensis*

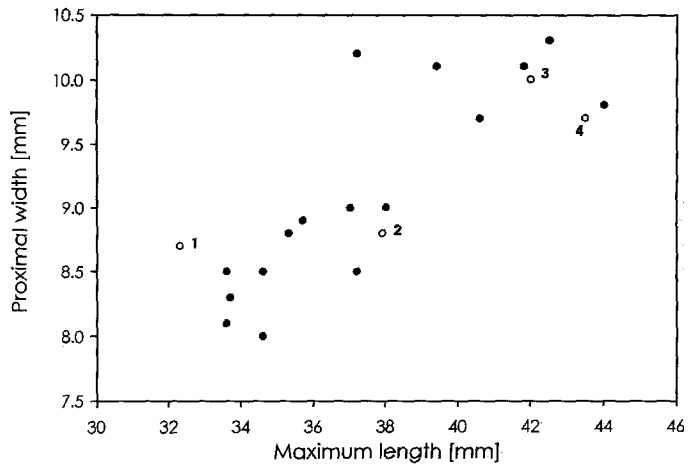
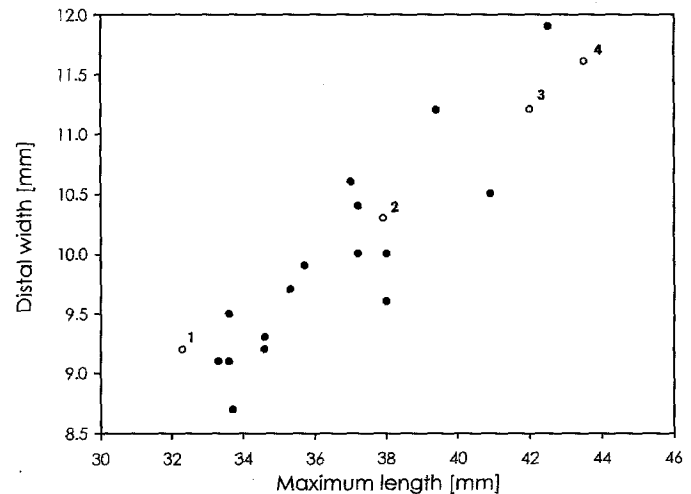


Fig. 5. Dimensions of *Necrobyas* tarsometatarsi, showing their maximum length and distal width. Data are from Mourer-Chauviré (1987). 1 – holotype of *Necrobyas rossignoli*, 2 – holotype of *Necrobyas harpax*, 3 – holotype of *Necrobyas edwardsi*, 4 – lectotype of *Necrobyas arvernensis*.

Abb. 5. Maximale Länge und distale Breite der Tarsometatarsi von *Necrobyas*. Die Angaben entstammen Mourer-Chauviré (1987). 1 – Holotyp von *Necrobyas rossignoli*, 2 – Holotyp von *Necrobyas harpax*, 3 – Holotyp von *Necrobyas edwardsi*, 4 – Lektotyp von *Necrobyas arvernensis*.



tarsus MNHN Av. 2834a becomes the paralectotype of the species.

All *Necrobyas* species were based on tarsometatarsi, and this element is by far the best represented in the collections. Metrical comparisons (Fig. 4 and 5) show that these tarsometatarsi fall into two distinct groups which differ in size, but not in shape. The group of smaller tarsometatarsi includes holotypes of *Necrobyas harpax* and *Necrobyas rossignoli*, while the group of larger tarsometatarsi includes the holotype of *Necrobyas edwardsi* and the lectotype of *Necrobyas arvernensis*. These two groups can be interpreted as paleospecies (Mlíkovský et al. 1985), which should bear the names *Necrobyas harpax* and *Necrobyas arvernensis*, respectively.

Accordingly, I synonymize here *Necrobyas rossignoli* Milne-Edwards, 1892 with *Necrobyas harpax* Milne-Edwards, 1892, and *Necrobyas edwardsi* Gaillard, 1939 with *Necrobyas arvernensis* Milne-Edwards, 1863. *Necrobyas harpax* was recorded only from the early Oligocene (MP 21-23), while *Necrobyas arvernensis* from the late Oligocene to the early Miocene (MP 28 – MN 2) of France. Subsequent research may show that *Necrobyas harpax* and *Necrobyas arvernensis* are chronospecies from a single phylogenetic lineage. If so, all these forms should be treated as a single species (cf. Haffer 1995).

Prosybris spp.

The genus *Prosybris* was created by Brodkorb (1970) for *Strix* [= *Tyto*] *antiqua*, described by Milne-Edwards (1869: 498) on the basis of a tarsometatarsus from the early Miocene (MN 2) of Saint-Gérard-le-Puy in France. The absence of an ossified supratendineal bridge clearly indicates that *Prosybris* was a barn owl which differed from *Tyto* in having shorter and more robust tarsometatarsi, and from *Necrobyas* in having slender and less robust tarsometatarsi. These three genera differ also in the proportions of their hind limbs, the relative lengths of femur, tibiotarsus and tarsometatarsus being approximately 1:1.7:1.2 in *Tyto*, 1:1.7:1.0 in *Prosybris*, and 1:1.3:0.7 in *Necrobyas*.

A flattened partial skeleton of a small bird from the early Miocene (MN 3–4) of Limberg in Lower Austria was described by Bachmayer (1980) as that of a falcon, but my reexamination of the specimen (NHMW 1977/1913) showed that it is a typical barn owl. Its tarsometatarsus agrees in size and shape with the same element of *Prosybris antiqua*, so that I assign here the specimen to this species. The measurements of the Limberg specimen are as follows: skull: length = 42 mm, width (flattened) = 33 mm; femur: greatest length = 33 mm, proximal width = 6.5 mm, distal width = 8.5 mm; tibiotarsus: greatest length = 55 mm, proximal width = 5.5 mm, distal width = 5 mm, width of shaft = 3 mm; tarsometatarsus: greatest length = 34 mm, proximal depth = 6.5 mm. Exact measurements could not be obtained, the presented values are thus rounded to 1 mm (lengths) and 0.5 mm (widths and depth), respectively. Note that these values differ more or less from those given by Bachmayer (1980), because he, apparently misled by the supposed similarity of the fossil with falcons, misinterpreted the shape and size of its bone ends.

Necrobyas minimus and *Necrobyas medius* were described by Mourer-Chauviré (1987) on the basis of distal parts of two tarsometatarsi from the Phosphorites du Quercy. These two tarsometatarsi differ from the same element of *Necrobyas* and agree with that of *Prosybris* in having its shaft more slender, and its external trochlea more flaring and more distant from the distal end of the medial trochlea. The holotype tarsometatarsus of *Necrobyas minimus* came

from Oligocene deposits of Fonbonne 1 in Quercy, for which no closer datation is available. It agrees in size and shape with the same element of *Prosybris antiqua* from the early Miocene (MN 2) of France. Hence, I synonymize here *Necrobyas minimus* Mourer-Chauviré, 1987 with *Strix* [= *Prosybris*] *antiqua* Milne-Edwards, 1869.

Prosybris medius was larger than *Prosybris antiqua*, and represents a second species of the genus. Unfortunately, its age is unknown, being anywhere between the middle Eocene and late Oligocene (cf. Rémy et al. 1987, Mourer-Chauviré 1995, 1996). Mourer-Chauviré (1987) assigned a distal end of a tibiotarsus from the early Oligocene (MP 23) of Itardies in Quercy to her *Necrobyas medius*. The specimen is severely damaged and not suitable for exact identification, although there is evidence that it has originated from a small owl (see Mourer-Chauviré 1987, pl. 2, fig. 21–22). There is thus no proof that *Prosybris* already existed in the early Oligocene (*contra* Mourer-Chauviré 1987).

Prosybris antiqua and *Prosybris medius* were pigmy barn owls, which have so far been recorded from the Oligocene (MP?) to the early Miocene (MN 3–4) of France and Austria.

Tyto sanctialbani

The modern genus *Tyto* appeared in Europe in the middle Miocene (MN 7). Miocene and Pliocene bones of *Tyto*, which were found in European deposits, fall into three groups, which can be identified as species (Mlíkovský et al. 1985). They should bear the following names: *Tyto sanctialbani* (Lydekker), *Tyto balearica* Mourer-Chauviré et al., and *Tyto gigantea* Ballmann.

Tyto sanctialbani was described by Lydekker (1893) on the basis of nine bones from the middle Miocene (MN 7–8) of La Grive-Saint-Alban in the Department of Isère, France. Further material of this species from the same complex locality was described by Ballmann (1969a). In the U.S. National Museum I identified additional material of this species from its type locality. The measurements are as follows: proximal width of left carpometa-carpus (USNM 205291) = 10.0 mm, distal width of left tibiotarsus (USNM 187665) = ca. 8.8 mm, proximal width of left tarsometatarsus (USNM

2170) = ca. 9 mm, distal width of left tarsometatarsi (USNM 187666 and 187667) = 10.8 mm and 10.9 mm.

I found further bones, which are clearly referable to *Tyto sanctialbani*, in the material from the late Miocene (MN 10) of Kohfidisch in Burgenland, Austria (see Mlíkovský 1996a for details on the locality). The material (deposited in NHMW) includes: fragments of left and right coracoids (not measurable), the proximal end of a left tibiotarsus (width = 10.1 mm), and the proximal end of a left tarsometatarsus (width = 10.1 mm).

Tyto campiterrae Jánossy, 1991 was based on a left tarsometatarsus from the late Miocene (MN 13) of Polgárdi 5 in Hungary. The only difference between *Tyto campiterrae* and *Tyto sanctialbani* mentioned by Jánossy (1991) was the smaller size of the former species. Unfortunately, he used for comparison measurements of a specimen from San Giovannino in Italy (following Ballmann 1973), which actually belongs to *Tyto balearica* (see below). Metrical comparisons of the holotype tarsometatarsus of *Tyto campiterrae* with the same element of *Tyto sanctialbani* are as follows: proximal width = 10.2–11.0 mm ($n = 8$) vs. ca. 9–10.1 mm ($n = 2$), distal width = 11.2–11.7 mm ($n = 5$) vs. 10.8–10.9 mm ($n = 2$) in *Tyto campiterrae* and *Tyto sanctialbani*, respectively. Hence, all these

bones fall in the same size class. In the absence of morphological differences I synonymize here *Tyto campiterrae* Jánossy, 1991 with *Strix* [= *Tyto*] *sanctialbani* Lydekker, 1893.

Ballmann (1973, 1976) reported on the record of *Tyto sanctialbani* from the Pliocene island (now peninsula) of Gargano in Italy (see Delle Cave 1996 for the age of the locality). The bones (partial coracoid, ulna, tibiotarsus, tarsometatarsus, and phalanges digitorum pedis) are larger and more robust than the same elements of *Tyto sanctialbani* (see measurements in Ballmann 1973, 1976), in which feature they agree with the same elements of *Tyto balearica*. There is no doubt that they should be referred to the latter species.

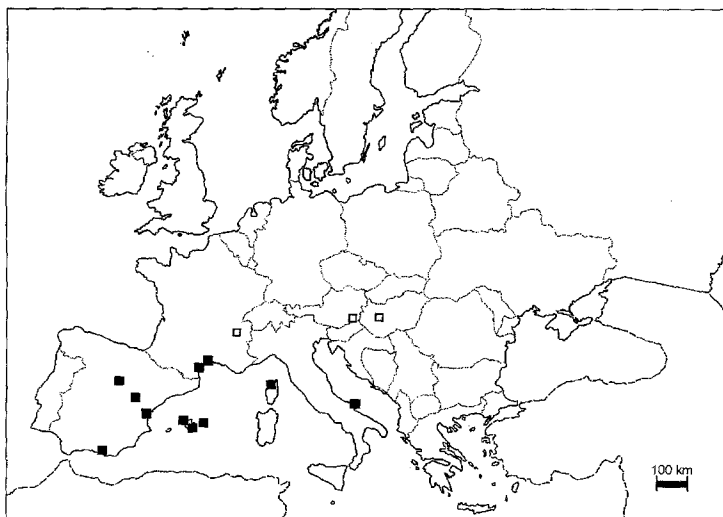
The evidence presented above extends both the temporal and geographic distribution of *Tyto sanctialbani*. The species is now known from the middle Miocene to the late Miocene of La Grive-Saint-Alban in France (MN 7–8), Kohfidisch in Austria (MN 10), and Polgárdi in Hungary (MN 13). *Tyto sanctialbani* was a barn owl of the size of the modern *Tyto alba*, and with similarly slender bones.

Tyto balearica

Tyto balearica was described from the latest Pliocene (MN 17) of Cova de Canet on the island of Mallorca (Mourer-Chauviré et al.

Fig. 6. Distribution of *Tyto sanctialbani* (□) and *Tyto balearica* (■) from the middle Miocene to the middle Pleistocene

Abb. 6. Verbreitung von *Tyto balearica* (□) und *Tyto sanctialbani* (■) im Zeitraum von Mittelmiozän bis Mittelpleistozän



1980). Subsequently it was found also in several late Pliocene to early Pleistocene localities on the nearby mainland in Spain and France (Mourer-Chauviré & Sanchez Marco 1988), in the late Miocene of Aljezar B in Spain (Cheneval & Adrover 1995), and in the middle Pleistocene of Castiglione 3 in Corsica (C. Mourer-Chauviré in Salotti et al. 1997). In addition, bones from the Pliocene of Gargano, assigned by Ballmann (1973, 1976) to *Tyto sanctialbani*, belong here (see above).

Tyto balearica was slightly larger than both *Tyto sanctialbani* and *Tyto alba*, and its bones were markedly more robust. Its known distribution ranges from the late Miocene (MN 12) to the middle Pleistocene (Q 3) of Spain, France and Italy (Fig. 6).

Tyto gigantea

Ballmann (1973) described from the Neogene island (now peninsula) of Gargano two new species of large barn owls: *Tyto robusta*, and *Tyto gigantea*. The "locality" is a complex of fissure deposits which differ in age, but all were believed to belong in the late Miocene, when Ballmann (1973, 1976) described the bones (Freudenthal 1971, 1976). However, subsequent research made it much more probable that the Gargano fauna is early Pliocene in age (see Delle Cave 1996).

Ballmann (1973, 1976) showed that the island was originally inhabited by a single barn owl species, erroneously identified by himself as *Tyto sanctialbani* (= *balearica*; see above). In younger deposits, the size of the barn owls from Gargano increased (Ballmann's *robusta*), but small (*balearica*) and very large (*gigantea*) forms were absent. In youngest deposits, the size of the barn owls from Gargano ranged from small to very large. Ballmann (1973, 1976) interpreted the latter observation as evidence of the contemporaneous presence of three barn owl species on Gargano during that time. Nevertheless, examination of fig. 8 in Ballmann (1976: 23) clearly shows that the size of barn owl bones from youngest deposits (particularly from San Giovannino) fall into two clusters. Bones from youngest deposits, identified by Ballmann (1973, 1976) as *robusta*, belonged in fact to large individuals of *Tyto ba-*

learica. This error is understandable, because Ballmann (1973, 1976) believed that the island was inhabited by slender-boned *Tyto sanctialbani*, whereas it was inhabited by a more robust *Tyto balearica*, the existence of which was not yet recognized in the mid 1970s.

The Pliocene history of barn owls on Gargano can be summarized as follows: originally, the island was inhabited by *Tyto balearica*, which was widespread in the western Mediterranean in that time (Fig. 6). Rodents and insectivores, which presumably was the main food of *Tyto balearica* on Gargano, evolved toward larger body size (see Freudenthal 1971, 1972, 1976), which forced their predator to increase its body size as well. At that time, the island was inhabited by but a single barn owl species, to which Ballmann (1973, 1976) applied the name *Tyto robusta*. Continuing increase in body size allowed subsequently *Tyto balearica* to resettle on the island. Interspecific competition between *Tyto balearica* and *Tyto robusta* forced the latter species to further increase its body size. The latter form, known only from youngest deposits was named by Ballmann (1973, 1976) *Tyto gigantea*. There is no evidence for the contemporaneous existence of *robusta* and *gigantea* (see above; contra Ballmann 1973, 1976). Taking into account that Gargano was a small island when these barn owls lived there, *robusta* and *gigantea* can be interpreted as temporary representatives of a single lineage of barn owls, evolving toward larger size. Such an evolution has been well documented on many Quarternary islands (see below). I agree with Haffer (1995) that the artificial delimitation of temporal portions of a lineage as chronospecies is meaningless. Hence, I synonymize here *Tyto robusta* Ballmann, 1973 with *Tyto gigantea* Ballmann, 1973.

Tyto melitensis

Tyto melitensis was described by Lydekker (1891) on the basis of a femur from the Quaternary (middle Pleistocene) deposits of Malta in the belief that it is "slightly longer and more slender" than the same element of modern *Tyto alba*, which it is not, as was already observed by Mourer-Chauviré et al. (1980). According to Lydekker (1891) length of the holotype femur

of *Tyto melitensis* is 54 mm, while it is 48.0–54.3 mm in European ($n = 28$, Cheneval & Adrover 1995, Mlíkovský unpub. data), 52.0–55.1 mm in African ($n = 2$), 51.4–56.1 mm in Asian ($n = 2$), and 58.5–63.4 mm in North American *Tyto alba* ($n = 11$). Width of the shaft is 4 mm in *Tyto melitensis* (Lykker 1891), while the corresponding dimension in the European *Tyto alba* is 3.9–4.3 mm ($n = 28$, Cheneval & Adrover 1995, Mlíkovský unpub. data). There is thus no reason to separate Maltese barn owls at the species level, and I synonymize here *Strix* [= *Tyto*] *melitensis* Lydekker, 1891 with the modern *Tyto alba* (Scopoli, 1769).

Strix edwardsi

Strix [= *Tyto*] *edwardsi* was described by Ennouchi (1930) from the middle Miocene (MN 7–8) of La Grive-Saint-Alban in France on the basis of distal part of a tibiotarsus, which was said to be smaller than the same element of *Strix* [= *Tyto*] *sanctialbani*, described by Lydekker (1893) from the same locality, the distal width of tibiotarsus being 10.6 mm in *Tyto sanctialbani*, and 7.2 mm in the holotype of *Tyto edwardsi*, respectively (Ennouchi 1930). As judged from the figures in Ennouchi (1930, pl. V., figs. 9–12), the holotype of *Strix edwardsi* differs from the same element of the Tytoninae, and agrees with that of the Striginae, in having: (1) transition between posterior margin of condyli and the shaft smooth, (2) internal condylus flattened, (3) anterior intercondylar fossa deep, and (4) posterior intercondylar fossa deep. Hence, the species must be removed from the Tytoninae in the Striginae. Strigine owls were abundant and diverse in the Miocene of Europe, but are in need of revision (Mlíkovský 1996b). Hence, I will not attempt here to fix the taxonomic position of *Strix edwardsi* within the Striginae.

Strix ignotus

Paris (1912: 287) and Lambrecht (1921: 97) listed among the fossil barn owls of France also *Strix* [= *Tyto*] *ignotus* Milne-Edwards, 1871 [= 1869], referring to p. 499 of Milne-Edwards' book. However, no such name appears on that page, nor elsewhere in Milne-Edwards' treatise, which caused much confusion. Lam-

brecht (1921: 97) inexplicably stated that *Strix ignota* Milne-Edwards is based on the distal portion of a tarsometatarsus from the middle Miocene of Sansan in France, figured in Milne-Edwards (1869, pl. 192, fig. 1–2). This specimen was referred by Milne-Edwards (1869: 499) to "*Strix* sp.", and the name *Strix ignota* does not appear even in the legend to Milne-Edwards' plate No. 192. Later, Lambrecht (1933: 613) attributed the name to Paris himself, stating that Paris applied this name to *Strix* sp. of Milne-Edwards ("1871": 499). Nevertheless, Lambrecht's (1933) approach cannot be accepted. Milne-Edwards (1869) devoted the upper part of his p. 499 to *Strix antiqua* (this chapter started on p. 498), and its lower part to *Strix* sp. Both of these taxa are correctly listed by Paris (1912: 287), which rules out the possibility that he applied *Strix ignota* to Milne-Edwards' *Strix* sp. (as believed by Lambrecht 1933, and Brodkorb 1971). Moreover, Paris (1912) labeled *Strix ignota* with Milne-Edwards' name, which indicates that he did not intend to name the species. Brodkorb (1971: 230) inexplicably stated that *Strix ignota* was created by Paris (1912) as a new name (!) for *Strix* sp. Milne-Edwards, 1871 [= 1869]. The latter does not include any species-group name, however, so that Brodkorb's interpretation is meaningless. Summarizing this evidence, it seems probable, that Paris (1912) simply listed *Strix ignota* in error. All in all, *Strix ignota* Milne-Edwards never did exist, and the name is not available for nomenclatural purposes with either Milne-Edwards' or Paris' name.

Varia

Genus *Palaeoglaux* with a single species *Palaeoglaux perrierensis* from the late Eocene of Perrière in France, which was described by Mourer-Chauviré (1987) as a barn owl, was removed from the family by Peters (1992).

Mlíkovský (1996b: 809) erroneously listed a barn owl record from the Oligocene of Libya. The record (a fragmentary humerus from Jebel Zelten) refers to a stork (see Mlíkovský, in press). The alleged barn owl record from Libya thus should be deleted from literature.

Alleged barn owls *Strix* [= *Tyto*] *sauzieri* Newton & Gadow, 1893 and *Strix* [= *Tyto*]

Table 1. Measurements of main fore limb bones of Tertiary barn owls [in mm]. For comparison, measurements of a single specimen of the modern *Tyto alba* (unsexed, Czech Republic) are given. L = maximum length (internal length in coracoid), PW = proximal width, DW = distal width. Asterisk (*) denotes estimated values. N is given in parentheses

Tab. 1. Maße der wichtigsten Vordergliedknochen tertiärer Schleiereulen [in mm]. Zum Vergleich sind die Maße einer rezenten Schleiereule *Tyto alba* (Geschlecht unbekannt, Tschechien) angegeben. L = größte Länge (mediale Länge beim Coracoid), PW = Proximalbreite, DW = Distalbreite. Geschätzte Angaben sind mit einem Stern (*) gekennzeichnet

	Coracoid			Humerus			Ulna			Carpometacarpus		
	L	PW	DW	L	PW	DW	L	PW	DW	L	PW	DW
<i>Tyto alba</i> ¹	32.0	84.1	13.4	94.0	8.3	6.6	44.2	9.5	6.2			
<i>Nocturnavis incerta</i> ²	—	91.0	16.6–18.0* (2)	—	—	—	—	—	—	—	—	—
<i>Necrobyas harpax</i> ²	27.4–30.1 (7)	74.0*	13.5	11.1–11.5* (3)	8.0	6.8	39.9	8.9	6.7			
<i>Necrobyas arvensis</i> ²	31.5–33.3* (2)	72.3	15.7	12.1–12.8 (3)	7.6*–8.3 (2)	7.1	42.9	9.3–10.3 (2)	6.7–6.8 (2)			
<i>Basityto rummeli</i> ¹	—	175*	—	26.5*	—	—	—	—	—	—	—	—
<i>Tyto sanctialbani</i> ^{1,3}	—	—	16.0	14.0–14.5 (3)	—	—	45.9–46.6 (2)	10.0–10.5 (3)	—	—	—	—
<i>Tyto balearica</i> ^{4,5,6}	38.1–45 (3)	102	16.8	15.7–17.1 (3)	9.7–10.4 (3)	6.9–7.2 (2)	—	—	—	—	—	—
<i>Tyto "robusta"</i> ⁶	—	—	26	24.0	14.5	12	—	—	—	—	—	—
<i>Tyto gigantea</i> ^{6,7}	70–74 (2)	185	—	—	—	16	98	22	15			

¹ Mlíkovský, orig., ² Mourer-Chauviré (1987), ³ Jánosy (1991), ⁴ Mourer-Chauviré et al. (1980), ⁵ Mourer-Chauviré & Sanchez Marco (1988), ⁶ Ballmann (1973), ⁷ Ballmann (1976)

Table 2. Measurements of main hind limb bones of Tertiary barn owls [in mm]. For comparison, measurements of a single specimen of the modern *Tyto alba* (unsexed, Czech Republic) are given. L = maximum length, PW = proximal width, DW = distal width. Asterisk (*) denotes estimated values. N is given in parentheses

Tab. 2. Maße der wichtigsten Hintergliedknochen tertiärer Schleiereulen [in mm]. Zum Vergleich sind die Maße einer rezenten Schleiereule *Tyto alba* (Geschlecht unbekannt, Tschechien) angegeben. L = größte Länge, PW = Proximalbreite, DW = Distalbreite. Geschätzte Angaben sind mit einem Stern (*) gekennzeichnet

	Femur			Tibiotarsus			Tarsometatarsus		
	L	PW	DW	L	PW	DW	L	PW	DW
<i>Tyto alba</i> ¹	51.7	9.5	9.9	86.4	9.1	8.9	61.4	8.8	9.6
<i>Selenornis henrici</i> ²	—	—	—	—	—	8.2	—	—	—
<i>Necrobyas harpax</i> ²	47.0*	8.7	8.7	—	—	7.9–8.9 (3)	32.3–38.0 (15)	8.0–9.0 (14)	8.7–10.6 (16)
<i>Necrobyas arvensis</i> ²	51.7–53.6 (4)	9.9–10.7 (5)	9.9–10.2 (5)	77.9	—	8.8–10.0 (4)	39.4–44.0* (8)	8.8–10.3 (7)	10.4–11.9 (7)
<i>Prosybris media</i> ²	—	—	—	—	—	—	—	—	7.8
<i>Prosybris antiqua</i> ^{1,2}	33	6.5*	8.5*	55	5.5*	5*	34	—	6.6
<i>Tyto sanctibani</i> ^{1,3,4}	55*–57.0 (4)	9.4–11.7 (5)	10*–11.2 (4)	—	10.1	8.8*–11.7 (4)	64.5–65.7 (2)	9*–12.5 (10)	10.8–11.7 (7)
<i>Tyto balearica</i> ^{5,6,7}	61* (2)	10.2	11.6	—	—	12	—	10.5–12.1 (3)	11.3–14.4 (4)
<i>Tyto "robusta"</i> ^{7,8}	—	15–16 (2)	—	—	14–17 (2)	15	—	15–16 (4)	—
<i>Tyto gigantea</i> ^{7,8}	115 (juv.)	26	28	195*	22	20	129	22*	23–28 (3)

¹ Mlíkovský, orig., ² Mourer-Chauviré 1987, ³ Jánosy 1991, ⁴ Cheneval & Adrover 1995, ⁵ Mourer-Chauviré et al. 1980, ⁶ Mourer-Chauviré & Sanchez Marco 1988, ⁷ Ballmann 1973, ⁸ Ballmann 1976

Tyto sanctialbani (MN 7–13 of France and Germany), *Tyto balearica* (MN 12–Q3 of Spain, France and Italy), and *Tyto gigantea* (early? Pliocene of Gargano island in the Adriatic Sea). In addition, an undescribed barn owl was found in the deposits of Love Bone Bed in Florida (Becker 1987), which correspond in age to MN 10. This is the oldest (and the only Tertiary) record of a tytonine owl outside of Europe.

In Quaternary continental deposits, only modern species of the genus *Tyto* have been found (Lambrecht 1933, Brodkorb 1971, and more recent studies), starting with *Tyto alba* from the earliest Pleistocene (Q 1) of Oldovai Gorge in Tanzania (Brodkorb & Mourer-Chauviré 1984). On the other hand, various endemic *Tyto* species, sometimes rather large, have been described from several oceanic and epicontinental islands, including New Caledonia (*Tyto letocarti* Balouet and Olson, 1989), Puerto Rico (*Tyto cavatica* Wetmore, 1920), Haiti (*Tyto ositologa* Wetmore, 1922; see also Olson & Hilgartner 1982), Bahamas (*Tyto pollens* Wetmore, 1937; see also Olson & Hilgartner 1982), and Cuba (*Tyto noeli* Arredondo, 1972a, and *Tyto riveroi* Arredondo, 1972b; see also Arredondo 1976).

Today, only two genera of barn owls survive. *Tyto* is ubiquitous, while *Phodilus* is limited to the forests of central Africa and south-east Asia. Morphologically, *Phodilus* bears many features of the Paleogene barn owls (cf. Mourer-Chauviré 1987) and it can be hypothesized that it is phylogenetically nearer to these owls than to *Tyto*. Its antiquity is supported also by its disjunctive neoendemic distribution.

Acknowledgements

The barn owl humerus from Grafenmühle was placed at my disposal by its collector Michael Rummel (Weissenburg). In addition, I was allowed to study bones of fossil barn owls in the Naturhistorisches Museum in Wien, Austria (Heinz Kollmann, Ortwin Schultz & Gudrun Daxner-Höck), and in the United States National Museum in Washington, D.C. (Storrs L. Olson). The drawings were prepared by Jan Hošek (Tnová). Comments of two anonymous referees helped to clarify the text. My thanks are due to all of these people. My studies in the United States National Museum in Washington, D.C. were conducted when I was a short-term fellow of the Smithsonian Institution in January/February 1997. My trips to Vienna were supported by the Naturhistorisches Museum Wien.

References

- Arredondo, O. (1972a): Nueva especie de ave fósil (Strigiformes: Tytonidae) del Pleistoceno superior de Cuba. Bol. Soc. venezol. Cienc. nat. 29: 415–431.
- Arredondo, O. (1972b): Especie nueva de lechuza (Strigiformes: Tytonidae) del Pleistoceno cubano. Bol. Soc. venezol. Cienc. nat. 30: 129–140.
- Arredondo, O. (1976): The great predatory birds of the Pleistocene of Cuba. In: Olson, S.L. (ed.): Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. Smithsonian. Contrib. Paleobiol. 27: 169–187.
- Bachmayer, F. (1980): Ein fossiler Vogelrest aus den Diatomeen-Schiefern (Miozän, Otnangien) von Limberg, Niederösterreich. Ann. naturhist. Mus. Wien 83: 25–28.
- Ballmann, P. (1969a): Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. Zitteliana 1: 5–61.
- Ballmann, P. (1969b): Les oiseaux miocènes de La Grive-Saint-Alban (Isère). Géobios 2: 157–204.
- Ballmann, P. (1973): Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). Scripta geol. 17: 1–75.
- Ballmann, P. (1976): Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), zweiter Teil. Scripta geol. 38: 1–59.
- Balouet, J.C. & Olson, S.L. (1989): Fossil birds from late Quaternary deposits in New Caledonia. Smithsonian. Contrib. Zool. 469: 1–38.
- Becker, J.J. (1987): Neogene avian localities of North America. Washington, D.C.
- Brodkorb, P. (1970): Two fossil owls from the Aquitanian of France. Quart. J. Florida Acad. Sci. 32: 159–160.
- Brodkorb, P. (1971): Catalogue of fossil birds: Part 4 (Columbiformes through Piciformes). Bull. Florida State Mus. (Biol. Sci.) 15: 163–266.
- Brodkorb, P. & Mourer-Chauviré, C. (1984): Fossil owls from early Man sites of Olduvai Gorge, Tanzania. Ostrich 54: 17–27.
- Burton, J.A. (ed., 1973): Owls of the world. New York.
- Chandler, R.M. (1982): A reevaluation of the Pliocene owl *Lechusa stirtoni* Miller. Auk 99: 580–581.
- Cheneval, J. & Adrover, R. ("1993" = 1995): L'avi-faune du Miocène supérieur d'Aljezar B (Los Aljezares, Province de Teruel, Espagne). Systématique et paléoécologie. Paleontologia i Evolució 26–27: 133–144.
- Delle Cave, L. (1996): Tertiary avian localities of Italy. In: Mlíkovský, J. (ed.): Tertiary avian localities of Europe. Acta Univ. Carol. (Geologica) 39: 665–681.
- Eck, S. & Busse, H. (1973): Eulen (Aves, Strigidae). Wittenberg Lutherstadt.
- Ennouchi, E. (1930): Contribution à l'étude de la

- faune du Tortonien de la Grive-Saint-Alban (Isère). Paris.
- Freudenthal, M. (1971): Neogene vertebrates from the Gargano Peninsula, Italy. *Scripta geol.* 14: 1-19.
- Freudenthal, M. (1972): *Deinogalerix koenigswaldi* nov. gen., nov. spec., a giant insectivore from the Neogene of Italy. *Scripta geol.* 14: 1-19.
- Freudenthal, M. (1976): Rodent stratigraphy of some Miocene fissure fillings in Gargano. *Scripta geol.* 37: 1-23.
- Gaillard, C. (1908): Les oiseaux des Phosphorites du Quercy. *Ann. Univ. Lyon (n.s.)* 23: 1-178.
- Gaillard, C. (1939): Contribution à l'étude des oiseaux fossiles. *Nouv. Arch. Mus. Lyon* 15 (2): 1-100.
- Haffer, J. (1995): Species versus lineages. In: Peters, D.S. (ed.): *Acta palaeornithologica*. Courier Forschungsinst. Senckenberg 181: 303-309.
- Heissig, K. (1978): Fossilführende Spaltenfüllungen Süddeutschlands und die Ökologie ihrer oligozänen Huftiere. *Mitt. bayer. Staatssamml. Paläontol. hist. Geol.* 18: 237-288.
- Horáček, I. & Ložek, V. (1988): Palaeozoology and the mid-European Quaternary past: scope of the approach and selected results. Praha.
- Jánosy, D. (1991): Late Miocene bird remains from Polgárdi (W-Hungary). *Aquila* 98: 13-35.
- Lambrecht, K. (1921): Pars 12. Aves. In: Diener, C. (ed.): *Fossilium catalogus*. I. Animalia. Berlin.
- Lambrecht, K. (1933): *Handbuch der Palaeornithologie*. Berlin.
- Lydekker, R. (1891): Catalogue of the fossil birds in the British Museum (Natural History). London.
- Lydekker, R. (1893): On some bird remains from the Miocene of La Grive-Saint-Alban, Department of Isère, France. *Proc. zool. Soc. London* 1893: 517-522.
- Mein, P. (1990): Updating of MN zones. In: Lindsay, E.H., Fahlbusch, V. & Mein, P. (eds.): *European Neogene mammal chronology*: 73-90. New York.
- Miller, L. (1956): A collection of bird remains from the Pliocene of San Diego, California. *Proc. California Acad. Sci.* 28: 615-621.
- Milne-Edwards, A. (1863): Mémoire sur la distribution géologique des oiseaux fossiles et description de quelques espèces nouvelles. *Ann. Sci. nat.* (4) 20: 132-176.
- Milne-Edwards, A. (1869): Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Vol. 2. Paris: Victor Masson et Fils. (+ Atlas 1869-1871).
- Milne-Edwards, A. (1892): Sur les oiseaux fossiles des dépôts éocènes de phosphate de chaux du Sud de la France. *C.R. 2^e Congr. ornithol. internat.* 2: 60-80.
- Mlíkovský, J. (1992): The present state of knowledge of the Tertiary birds of Central Europe. In: Campbell, K.E. (ed.): *Papers in avian paleontology honoring Pierce Brodkorb*. *Nat. Hist. Mus. Los Angeles Co., Sci. Ser.* 36: 433-458.
- Mlíkovský, J. (1996a): Tertiary avian localities of Austria. In: Mlíkovský, J. (ed.): *Tertiary avian localities of Europe*. *Acta Univ. Carol. (Geologica)* 39: 529-533.
- Mlíkovský, J. (1996b): Tertiary avian faunas of Europe. In: Mlíkovský, J. (ed.): *Tertiary avian localities of Europe*. *Acta Univ. Carol. (Geologica)* 39: 777-818.
- Mlíkovský, J. (in press): Early Miocene birds of Jebel Zelten, Libya. *Acta Univ. Carol. (Geologica)*.
- Mlíkovský, J., Bělka, L. & Zemek, K. (1985): Morphogenesis and the problem of morphospecies. In: Mlíkovský, J. & Novák, V.J.A. (eds.): *Evolution and morphogenesis*: 201-211. Praha.
- Mlíkovský, J. & Hesse, A. (1996): Tertiary avian localities of Germany. In: Mlíkovský, J. (ed.): *Tertiary avian localities of Europe*. *Acta Univ. Carol. (Geologica)* 39: 619-647.
- Mourer-Chauviré, C. (1987): Les Strigiformes (Aves) des Phosphorites du Quercy (France): systématique, biostratigraphie et paléobiogéographie. In: Mourer-Chauviré, C. (ed.): *L'évolution des oiseaux d'après le témoignage des fossiles*. *Docum. Lab. Géol. Lyon* 99: 89-135.
- Mourer-Chauviré, C. (1994): A large owl from the Palaeocene of France. *Palaeontology* 37: 339-348.
- Mourer-Chauviré, C. (1995): Dynamics of the avifauna during the Paleogene and the early Neogene of France. Settling of the recent fauna. *Acta zool. cracov.* 38: 325-342.
- Mourer-Chauviré, C. (1996): Paleogene avian localities of France. In: Mlíkovský, J. (ed.): *Tertiary avian localities of Europe*. *Acta Univ. Carol.* 39: 567-598.
- Mourer-Chauviré, C. & Sanchez Marco, A. (1988): Présence de *Tyto balearica* (Aves, Strigiformes) dans des gisements continentaux du Pliocene de France et d'Espagne. *Géobios* 21: 639-644.
- Mourer-Chauviré, C., J.A. Alcover, S. Moya & J. Pons (1980): Une nouvelle forme insulaire d'effraie géante, *Tyto balearica* n. sp., (Aves, Strigiformes), du Plio-Pleistocène des Balears. *Géobios* 13: 803-811.
- Mourer-Chauviré, C., Bour, R., Moutou, F. & Ribes, S. (1994): *Mascarenotus* nov. gen. (Aves, Strigiformes), genre endémique éteint des Mascareignes et *M. grucheti* n. sp., espèce éteinte de La Réunion. *C. R. Acad. Sci. Paris (II)* 318: 1699-1706.
- Newton, E. & Gadow, H. (1893): On additional bones of the dodo and other extinct birds of Mauritius obtained by Mr. Théodore Sauzier. *Trans. Zool. Soc. London* 13: 281-302.
- Olson, S.L. & Hilgarter, W.B. (1982): Fossil and subfossil birds from the Bahamas. In: Olson, S.L. (ed.): *Fossil vertebrates from the Bahamas*. *Smithson. Contrib. Paleobiol.* 48: 22-60.
- Paris, P. (1912): Oiseaux fossiles de France. *Rev. franç. Ornithol.* 37: 283-298.
- Peters, D.S. (1992): A new species of owl (Aves: Strigiformes) from the middle Eocene Messel oil

- shale. In: Campbell, K.E. (ed.): Papers in avian paleontology honoring Pierce Brodkorb. Nat. Hist. Mus. Los Angeles Co., Sci. Ser. 36: 161-169.
- Pomerol, C. & Premoli-Silva, I. (eds., 1986): Terminal Eocene events. Amsterdam.
- Rémy, J.A., Crochet, J.Y., Sigé, B., Sudre, J., de Bonis, L., Vianey-Liaud, M., Godinot, M., Hartenberger, J.L., Lange-Badré, B. & Comte, B. (1987): Biochronologie des Phosphorites du Quercy: Mise à jour des listes faunistiques et nouveaux gisements de mammifères fossiles. In: Schmidt-Kittler, N. (ed.): International symposium on mammalian stratigraphy and paleoecology of the European Paleogene. Münchner geowiss. Abh. (A) 10: 169-188.
- Rich, P.V. & Bohaska, D. (1976): The world's oldest owl: a new strigiform from the Paleocene of southwestern Colorado. In: Olson, S.L. (ed.): Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore. Smithsonian Contrib. Paleobiol. 27: 87-93.
- Rich, P.V. & Bohaska, D. (1981): The Ogygoptingidae, a new family of owls from the Paleocene of North America. *Alcheringa* 5: 95-102.
- Rothschild, W. (1907): Extinct birds. London.
- Salotti, M., Bailon, S., Bonifay, M.-F., Courtois, J.-Y., Dubois, J.-N., Ferrandini, J., Ferrandini, M., La Milza, L.-C., Mourer-Chauviré, C., Popelard, J.-B., Quinif, Y., Réal-Testud, A.-M., Miniconi, C., Pereira, E. & Persiani, C. (1997): Castiglione 3, un nouveau remplissage fossilifère d'âge Pléistocène moyen dans le karst de la région d'Oletta (Haute-Corse). *C.R. Acad. Sci. Paris (IIa)* 324: 67-74.
- Schmidt-Kittler, N. (1987): European reference levels and correlation tables. In: Schmidt-Kittler, N. (ed.): International symposium on mammalian stratigraphy and paleoecology of the European Paleogene. Münchner geowiss. Abh. (A) 10: 13-19.
- Schneider, W. (1977): Schleiereulen (Tytonidae). Wittenberg Lutherstadt.
- Wetmore, A. (1920): Five new species of birds from cave deposits in Porto Rico. *Proc. biol. Soc. Washington* 33: 77-82.
- Wetmore, A. (1922): Remains of birds from caves in the Republic of Haiti. *Smithson. misc. Coll.* 74 (4): 1-4.
- Wetmore, A. (1937): Bird remains from cave deposits on Great Exuma Island in the Bahamas. *Bull. Mus. comp. Zool.* 80: 427-441.
- Wolters, H.E. (1975-1982): *Die Vogelarten der Erde*. Hamburg.
- Bubo incertus* Milne-Edwards, 1892: 33.
- Nocturnavis incerta* (Milne-Edwards): Mourer-Chauviré 1987: 108 (new combination).
- Selenornis henrici* (Milne-Edwards) [status uncertain]
- Otus Henrici* Milne-Edwards, 1892: 63.
- Asio Henrici* (Milne-Edwards): Gaillard 1908: 36 (new combination).
- Asio henrici* (Milne-Edwards): Paris 1912: 287 (spelling emended)
- Selenornis henrici* (Milne-Edwards): Mourer-Chauviré 1987: 113 (new combination).
- Necrobyas harpax* Milne-Edwards
- Necrobyas harpax* Milne-Edwards, 1892: 61.
- Necrobyas Rossignoli* Milne-Edwards, 1892: 63 (here synonymized).
- Necrobyas rossignoli* Milne-Edwards: Paris 1912: 287 (spelling emended)
- Necrobyas arvernensis* (Milne-Edwards)
- Bubo arvernensis* Milne-Edwards, 1863: 458.
- Necrobyas Edwardsi* Gaillard, 1939: 8 (here synonymized).
- Paratyto arvernensis* (Milne-Edwards): Brodkorb 1970: 159 (new combination).
- Necrobyas edwardsi* Gaillard: Brodkorb 1971: 220 (spelling emended)
- Necrobyas arvernensis* (Milne-Edwards): Mourer-Chauviré 1987: 91 (new combination).
- Prosybris media* (Mourer-Chauviré)
- Necrobyas medius* Mourer-Chauviré, 1987: 104.
- Prosybris media* (Mourer-Chauviré): Mlíkovský, this paper (new combination).
- Prosybris antiqua* (Milne-Edwards)
- Strix antiqua* Milne-Edwards, 1869: 498.
- Prosybris antiqua* (Milne-Edwards): Brodkorb 1970: 159 (new combination).
- Necrobyas minimus* Mourer-Chauviré, 1987: 105 (here synonymized)
- Tyto sanctialbani* Lydekker
- Strix sancti-albani* Lydekker, 1893: 518.
- Strix sancti albani* Lydekker: Ennouchi 1930: 66 (spelling emended).
- Strix Sancti-albani* Lydekker: Gaillard 1939: 82 (spelling emended)
- Tyto sanctialbani* (Lydekker): Ballmann 1969b: 191 (new combination and spelling emended).
- Tyto campiterrae* Jánossy, 1991: 25 (here synonymized).
- Tyto balearica* Mourer-Chauviré et al.
- Tyto balearica* Mourer-Chauviré, Alcover, Moya & Pons, 1980: 804.
- Tyto gigantea* Ballmann
- Tyto gigantea* Ballmann, 1973: 37.
- Tyto robusta* Ballmann, 1973: 33 (here synonymized).

Accepted: 03 February 1998

Appendix. Systematic list of Tertiary barn owls (subfamily Tytoninae)

Nocturnavis incerta (Milne-Edwards)