

Two new owls (Aves: Strigidae) from the early Miocene of the Czech Republic, with comments on the fossil history of the subfamily Striginae

Dvě nové sovy (Aves: Strigidae) ze staršího miocénu České republiky, s poznámkami o fosilní historii podčeledi Striginae

MLÍKOVSKÝ J.

Dipl.-Biol. Jiří Mlíkovský, CSc., Institute of Geology and Paleontology, Charles University, Albertov 6, 128 43 Praha 2, Czech Republic; e-mail mlík@post.cz

ABSTRACT. Two new strigine owls were described from the early Miocene (MN 3) of Merkur in the northwestern Czech Republic: *Mioglaux debellatrix*, and *Intulula tinnipara*. Both were placed in new genera, belonging to the tribe Strigini. Further taxonomic conclusions are as follows: *Bubo poirrieri* MILNE-EDWARDS was transferred to the newly described genus *Mioglaux* MLÍKOVSKÝ. *Strix brevis* BALLMANN was transferred to the Surniini, but its generic position was not clarified. *Otus wintershofensis* BALLMANN and *Strix* [auct., non LINNAEUS] *edwardsi* ENNOUCHI were transferred to the genus *Strix* LINNAEUS. *Strix collongensis* BALLMANN was placed in a new genus *Alasio*, belonging to the tribe Asionini. *Bubo longaeus* UMANS'KAJA was transferred to the genus *Asio* BRISSON. *Bubo florianae* KRETZOI was relegated to the category of nomina dubia. All three basic groups of strigine owls were recorded from the early Miocene onwards: Strigini from MN 2, and Surniini and Asionini from MN 3.

INTRODUCTION

Neogene deposits of Europe (MLÍKOVSKÝ 1996a) and North America (BECKER 1987) yielded numerous remains of owls (family Strigidae). All of these remains seem to belong to the modern subfamilies Tytoninae and Striginae. Recent revisions are available for the Tytoninae (MOURER-CHAUVIRÉ 1987, MLÍKOVSKÝ 1998a), but no such review of the Striginae was published thus far. Below, I describe rich finds of owl bones from the early Miocene locality Merkur in northwestern Bohemia (Czech Republic), and additional material from the middle Miocene localities Františkovy Lázně in western Bohemia (Czech Republic) and Petersbuch 39 in Bavaria (Germany), and comment on the taxonomic status of previously described strigine species.

I follow the classification of strigine owls provided by FORD (1976) throughout this paper. Unlike Ford, however, I prefer to lump his Tytonidae and Strigidae in a single family (see MLÍKOVSKÝ 1998a). Consequently, I lower here the rank of all his suprageneric taxa as follows: his families = my subfamilies, his subfamilies = my tribes, his tribes = my groups of genera (e.g. his Otini = my *Otus* group). FORD's (1967: 90) classification of the Striginae is rewritten here as follows:

Strigini: (1) *Otus*, *Pyrroglaux*, *Gymnoglaux*, *Mimizuku*, *Lophostrix*, *Jubula*; (2) *Bubo* (incl. *Ketupa blakistoni*), *Ketupa*, *Pseudoptynx*, *Scotopelia*, *Nyctea*; (3) *Strix* (incl. *Ciccaba*), *Pulsatrix*;

Surniini: (1) *Surnia*, *Glaucidium*, *Micrathene*, *Athene* (incl. *Speotyto*); (2) *Ninox*, *Uroglaux*, *Sceloglaux*; (3) *Aegolius*;

Asionini: *Asio* (incl. *Rhinoptynx*, *Pseudoscops*), *Nesasio*.

The stratigraphy follows SCHMIDT-KITTLER (1987) for the Paleogene (Mammal Paleogene zones, MP), and MEIN (1990) for the Neogene (Mammal Neogene zones, MN). The age of European and North American localities was taken from MLÍKOVSKÝ (1996a) and BECKER (1987), respectively. In the latter case, MN-zones were inferred using the data on absolute age, and on the correlation with nannoplankton zones (see STEININGER & RÖGL 1984, STEININGER et al. 1989, 1996).

Order Strigiformes WAGLER, 1830

Family Strigidae LEACH, 1819

Mioglaux n. g.

Type: *Mioglaux debellatrix* n. sp.

Included species: *Mioglaux debellatrix* n. sp., *Mioglaux poirrieri* (MILNE-EDWARDS).

Diagnosis: Medium large owls from the tribe Strigini. Tarsometatarsus short and robust, with broad rims of shaft, and with the external calcaneal ridge bent posteriorly. Tibiotarsus with the groove for ligamentum obliquum deep

Comparison: According to the morphology of the tarsometatarsus (see below under *Bubo poirrieri*), the genus is referable to the Strigini. Ulna and radius tend to be more robust when compared with the same element of similarly sized Striginae. The coracoid is similar to the same element of the Strigini in general shape. It is almost non-pneumatic (as in *Ketupa*) with a small pneumatic foramen hidden under the rim of the furcular facet, has a deep triosseal canal, and its head is not inclined in comparison with the axis of the shaft. Coracoidal fenestra is large. The intermuscular line on femur is similar to that found on the same element of *Bubo* and *Ketupa*. The tarsometatarsus is slender. Within the Strigini, *Mioglaux* is probably most closely allied to the modern genus *Strix* (incl. *Ciccaba*).

Etymology: Abbreviated from Miocene, the time period when this owl lived, and glaux, one of the Greek words for an owl. The name is feminine in gender.

Remarks: The genus was recorded in the early Miocene (MN 2) of France, and in the early Miocene (MN 3) of the Czech Republic so far.

Mioglaux debellatrix n. sp.

Holotype: Distal end of right tibiotarsus (Figs. 1, 2); coll. O. FEJFAR (Praha), uncatalogued.

Material: Distal end of right tibiotarsus (holotype), proximal part of right femur (tentatively assigned), left tarsometatarsus lacking distal end, fragmentary distal end of right tarsometatarsus. Referred specimen from Františkovy Lázně: fragmentary distal end of left tarsometatarsus.

Age and locality: Early Miocene of Merkur, Chomutov County, North Bohemia, Czech Republic (FEJFAR and KVAČEK 1993, MLÍKOVSKÝ 1996b).

Diagnosis: A *Mioglaux* owl, smaller than *M. poirrieri*.

Comparison: See data on the genus. The femoral fragment is rather nondescript, but was found on the same site as the holotypical tibiotarsus, and belongs to a strigine owl of the same size class as *Mioglaux debellatrix*.

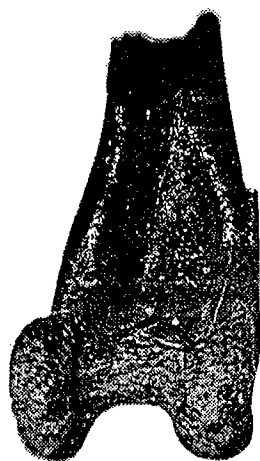


Fig. 1 - Distal end of tibiotalus of *Mioglaux debellatrix* from the early Miocene of Merkur, Czech Republic (holotype).
Obr. 1 - Distální konec tibiotalu druhu *Mioglaux debellatrix* ze staršího miocénu Merkuru, Česko (holotyp).

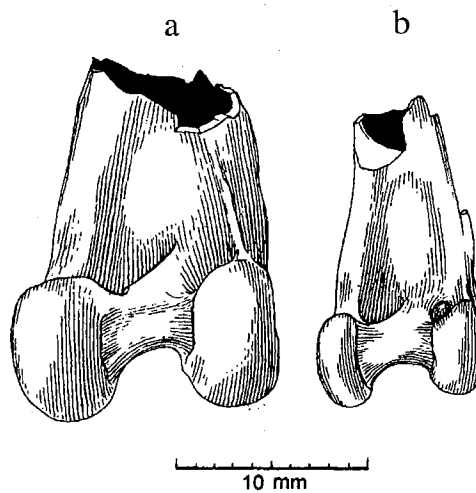


Fig. 2 - Distal ends of owl tibiotali from the early Miocene of Merkur, Czech Republic. a - *Mioglaux poirrieri* (referred specimen), b - *Mioglaux debellatrix* (holotype).
Obr. 2 - Distální konce dvou sovích tibiotalů ze staršího miocénu Merkuru, Česko. a - *Mioglaux poirrieri* (přirazená kost), b - *Mioglaux debellatrix* (holotyp).

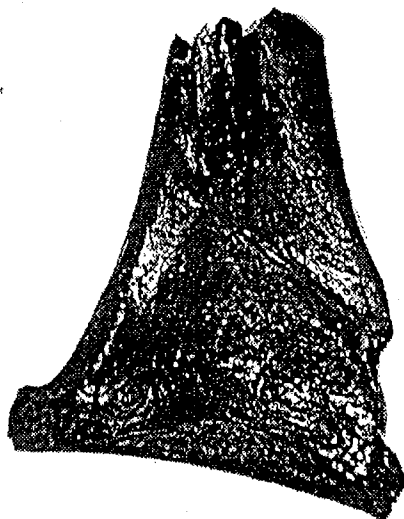


Fig. 3 - Sternal end of an owl coracoid from the early Miocene of Merkur, Czech Republic, tentatively referred to *Mioglaux debellatrix*.
Obr. 3 - Sternální konec korakoidu sovy ze staršího miocénu Merkuru, Česko, snad náležící druhu *Mioglaux debellatrix*.



Fig. 4 - Proximal end of tarsometatarsus of *Intulula tinnipara* from the early Miocene of Merkur, Czech Republic (holotype).
Obr. 4 - Proximální konec tarsometatarsu druhu *Intulula tinnipara* ze staršího miocénu Merkuru, Česko.

A fragmentary distal part of tarsometatarsus was found in the middle Miocene (MN 5) locality Františkovy Lázně. It belongs to an owl from the tribe Strigini, and agrees in size with the same element of *Mioglaux debellator*, to which I tentatively refer it.

Measurements: Holotypical tibiotarsus: distal width = 8.4 mm, depth of internal trochlea 6.9 mm; Femur: proximal width = ca. 9.5 mm; Tarsometatarsus: proximal width = 9.4 mm, minimum width of shaft = 5.2 mm, maximum width across trochleae for digiti II-III = 7.6 mm, maximum width across trochleae for digiti III-IV (specimen from Františkovy Lázně) = 8.0 mm.

Etymology: From Latin *debellatrix*, meaning victor or conqueror. The name is selected in allusion of the evolutionary victory of strigine owls, represented by the genus *Mioglaux*, over the tytonine owls in the early Miocene of Europe (see below, and MLÍKOVSKÝ 1998a). The name is a noun in apposition.

Remarks: The species was recorded only from the early Miocene (MN 3) of Merkur thus far. It represents the youngest record for the genus *Mioglaux*.

The locality Merkur yielded also a partial coracoid (not measurable; Fig. 3), that may belong to *Mioglaux debellatrix*, but appears to have originated from an individual somewhat larger than was that yielding the holotypical tibiotarsus. Whether the sexual size dimorphism can account for the difference, or whether the specimen represents another species, cannot be solved on the basis of the available material.

Genus *Intulula* n. g.

Type: *Intulula tinnipara* n. sp.

Included species: Type species only.

Diagnosis: Small strigine owl, with slender tarsometatarsus, characterized by the insertion of musculus tibialis anticus projecting proximally under the bony loop.

Comparison: The holotypical tarsometatarsus of *Intulula tinnipara* is characterized by having (1) anterior rim of internal trochlea not protruding more anteriorly than the anterior rim of the external trochlea, (2) external calcaneal ridge bent posteriorly (not flaring externally), (3) bony loop broad, and (4) tubercle for musculus tibialis anticus displaced externally (it is placed in the axis of the bone in most modern genera of the Striginae). This combination of characters is typical for the Asionini. Within the latter tribe, the tarsometatarsus of *Intulula tinnipara* differs from the same element of *Nesasio* in being much more slender, and from that of *Rhinoptynx* and *Asio* in having the tubercle for musculus tibialis anticus slender, long, turning into a scar proximally, and projecting under the bony loop. No tarsometatarsus was available for study from the last asionine genus, *Pseudoscops*. However, the genus is currently limited to Jamaica in distribution (ECK and BUSSE 1973), and its occurrence in the early Miocene of Europe is improbable for zoogeographical reasons (cf. MLÍKOVSKÝ 1996).

Two other fossil asionine owls are known from the Miocene, incl. *Asio longaevus* (UMANS'KAJA) from the late Miocene of Ukraine, and *Alasio collongensis* (BALLMANN) from the early Miocene of Germany (see below). The former species belongs in the modern genus *Asio*, from which *Intulula* differs in details listed above. *Alasio collongensis* was much larger than *Intulula tinnipara*, and is characterized by a such modified coracoid, that I do not believe that the two forms can be congeneric. Nevertheless, direct comparison is

impossible, because *Alasio collongensis* is known only on the basis of a coracoid, while *Intulula tinnipara* on the basis of a tarsometatarsus.

Etymology: Abbreviated from Latin intrepidus = dauntless, and ulula = owl. Selected in allusion of the evolutionary dauntlessness of this tiny owl, with which it entered the early Miocene realm of tytonine owls in Europe. The name is feminine in gender.

Intulula tinnipara n. sp.

Holotype: Left tarsometatarsus lacking distal end (Fig. 4); coll. O. FEJFAR (Praha), uncatalogued.

Material: Holotype only.

Age and locality: Early Miocene of Merkur, Cheb County, West Bohemia, Czech Republic (FEJFAR & KVAČEK 1993, MLÍKOVSKÝ 1996b).

Diagnosis: As for the genus.

Comparison: See under genus.

Measurements: Proximal width = ca. 5.5 mm.

Etymology: Latin tinnipara = hooting. Selected in allusion of the courtship voices of strigine owls.

Remarks: This tiny owl was found only in the type locality as yet.

COMMENTS ON SOME OTHER TERTIARY STRIGINAE

BRODKORB (1971) listed in his Strigidae (i.e. Striginae in the sense of this paper) 15 Tertiary species of owls. Subsequently, four species were named, including *Athene veta* JANOSSY, 1974 from the late Pliocene of Poland, *Surnia robusta* JANOSSY, 1977 from the late Pliocene of Hungary, *Bubo longaevus* UMANS'KAJA, 1979 from the late Miocene of Ukraine, and *Eoglaucidium pallas* FISCHER, 1987 from the middle Eocene of Geiseltal in Germany. In addition, two Tertiary species were transferred to the Striginae from other family-group taxa: *Ardea lignitum* GIEBEL, 1860 from the Ardeidae (BRODKORB 1980), and *Strix* [= *Tyto*] *edwardsi* ENNOUCHI, 1930 from the Tytoninae (MLÍKOVSKÝ 1998a). Below, I will comment on some of these species.

Most strigine owls are represented in the fossil record by tibiotarsi and/or tarsometatarsi, while other elements are underrepresented. A summary of their measurements is given in Table 1.

Bubo poirrieri

Bubo poirrieri was described by MILNE-EDWARDS (1863: 158) on the basis of a tarsometatarsus from the early Miocene (MN 2a) of Saint-Gérard-le-Puy in France. The holotypical tarsometatarsus was figured by MILNE-EDWARDS (1869-1871, pl. 192, figs. 24-29). Hypotarsus consists of two calcaneal ridges in owls, of which the external one flares laterally in most Striginae, while it is bent posteriorly in *Strix* (incl. *Ciccaba*), *Asio*, and the fossil. The holotypical tarsometatarsus of *Bubo poirrieri* differs from the same element of *Asio*, and agrees with that of *Strix* in having: (1) internal calcaneal ridge short and broad in medial view, (2) internal calcaneal ridge located more medially, and (3) trochlea for digit III more protruding in comparison with the trochlea for digit II. The holotypical tarsometatarsus of *Bubo poirrieri* differs from the same element of *Strix*: (1) in being much more robust, and in having (2) posterior rims of the shaft more broad, and

(3) intermuscular lines on the internal rim much more pronounced. This combination of characters allows "*Bubo* *poirrieri*" to be allied with the *Strix* group within the Strigini, where it deserves separation at the genus level.

Table 1 - Measurements of tibiotarsi and tarsometatarsi of the Tertiary Striginae [mm]. L = maximum length, PW = proximal width, DW = distal width. Asterisk (*) denotes estimated values. Two asterisks (**) denote values estimated from published illustrations. N is given in parentheses.

Tab. 1 - Rozměry tibiotarsů a tarsometatarsů třetihorních Striginae [mm]. L = délka, PW = šířka proximální hlavičky, DW = šířka distální hlavičky. Hvězdička (*) označuje přibližné hodnoty. Dvě hvězdičky (**) znamenají, že hodnoty byly odečteny z publikovaných obrázků. N je uvedeno v závorkách.

	Tibiotarsus			Tarsometatarsus		
	L	PW	DW	L	PW	DW
" <i>Strix</i> " <i>dakota</i> ¹	-	-	-	-	-	8.3
<i>Mioglaux</i> <i>poirrieri</i> ^{2,3}	-	-	13.9	53.5	13	15
<i>Mioglaux</i> <i>debellatrix</i> ³	-	-	8.4	-	9.4	-
<i>Intulula</i> <i>tinnipara</i> ³	-	-	-	-	5.5*	-
<i>Strix</i> <i>wintershofensis</i> ^{3,4}	-	-	5.5	-	-	5.5
<i>Strix</i> <i>edwardsi</i> ^{3,5}	-	-	6.1-7.2 (2)	-	-	-
<i>Bubo</i> <i>perpastus</i> ⁵	-	-	15.5	-	-	-
" <i>Strix</i> " <i>brevis</i> ⁴	-	-	9.5	45	8	-
<i>Athene</i> <i>megalopeza</i> ⁶	-	-	-	-	-	7.6
<i>Surnia</i> <i>robusta</i> ⁷	-	-	-	37.2	12.6	12.6-15.0 (4)
<i>Asio</i> <i>longaevus</i> ⁸	125	16.7**	15.0**	-	-	16.5
<i>Asio</i> <i>brevipes</i> ⁹	-	-	-	-	-	9.5

¹MILLER 1944, ²MILNE-EDWARDS 1869, ³MLÍKOVSKÝ orig., ⁴BALLMANN 1969, ⁵BALLMANN 1976, ⁶FORD 1966, ⁷JÁNOSSY 1977, ⁸UMANS'KAJA 1979, ⁹FORD & MURRAY 1967

A fragmentary distal part of tarsometatarsus from the early Miocene (MN 3) of Merkur in the Czech Republic is identical with the holotypical tarsometatarsus of "*Bubo* *poirrieri*". I assign it herewith to the latter species. The deposits of Merkur yielded 6 other bone fragments, all belonging to a strigine owl of the same size class as "*Bubo* *poirrieri*". The material includes the following elements: right coracoid with damaged sternal end (external length = ca. 45 mm), left coracoid lacking distal end, distal part of left ulna (distal width = 9.8 mm), proximal end of right radius (width x depth = 7.8 x 4.9 mm), left femur with damaged ends (width in the middle = 6.5 mm), proximal portion of shaft of left tibiotarsus, distal part of right tibiotarsus (width = 13.9 mm, depth of external trochlea = 11.6 mm, depth of internal trochlea = 11.4 mm; Fig. 2), fragmentary distal end of left tarsometatarsus, and complete phalanx 2 digiti II (maximum length = 27.0 mm).

Most of the elements from Merkur assigned to "*Bubo*" *poirrieri* are less diagnostic, but the tibiotarsus is morphologically identical to, though larger than, the same element of *Mioglaux debellatrix*. Hence, I transfer here *Bubo poirrieri* to the genus *Mioglaux* as *Mioglaux poirrieri* (MILNE-EDWARDS, 1863), new combination.

Strix dakota

Strix dakota was described by MILLER (1944: 95) on the basis of a tarsometatarsus without proximal end from the early Miocene (MN 3) of Flint Hill in South Dakota. I agree with FORD (1967) that it does not belong to the genus *Strix*, and - as judged from illustrations (MILLER 1944, fig 8a-b) - it does not even fit any of the known genera of owls. Unfortunately, the figures are not sufficient to allow for a closer discussion of the taxonomic position of this species. A possibility must even be taken into account, that the species does not belong to the Striginae, because several Oligocene and early Miocene barn owls (Tytoninae) had robust tarsometatarsi generally similar to that of *Strix dakota* (see MOURER-CHAUVIRÉ 1987, MLÍKOVSKÝ 1998a).

Strix brevis

BALLMANN (1969: 38) described this species on the basis of a humerus, lacking proximal end, from the early Miocene (MN 3) of Wintershof (West) in Germany. Humerus is a less diagnostic element within the Striginae. Nevertheless, the curvature of the humeral shaft is smooth in most owls, incl. *Strix*, while the bend is sharp in the Surniini. In the latter character, the holotypical humerus of *Strix brevis* agrees with the Surniini. Hence, *Strix brevis* must be removed from the genus *Strix*, but its identity within the Surniini cannot be ascertained on the basis of the two figures of the holotypical humerus in BALLMANN (1969, pl. 1, figs. 7a-b).

JÁNOSSY (1993) attributed several bone fragments from the middle Miocene (MN 9) of Rudabánya in Hungary tentatively to *Strix brevis*. If correctly assigned to the genus *Strix*, these remains cannot belong to "*Strix*" *brevis*, because the latter species belongs to another tribe within the Striginae.

Otus wintershofensis

Otus wintershofensis was described by BALLMANN (1969: 39) on the basis of distal part of a tibiotarsus from the early Miocene (MN 3) of Wintershof (West) in Germany. The holotypical tibiotarsus differs from the same element of Surniini in having: (1) distal end less symmetrical, i.e. internal condyle more excentric in comparison to the axis of the shaft, and (2) internal and external condylus less compressed proximo-distally. It differs markedly from the tibiotarsi of the Asionini in having the internal ligamental prominence indistinct. Hence, *Otus wintershofensis* is correctly assigned to the Strigini. Within the latter group, the holotypical tibiotarsus of *Otus wintershofensis* differs from the same element of *Otus* group in having: (1) intercodylar sulcus more excavated, and (2) the space between the condyli broader. It differs from the tibiotarsi of the *Bubo* group in having: (1) the distal end more symmetrical, (2) tendineal groove less excavated, (3) plantar groove less excavated, (4) rim of internal condyle not elevated. In all observable details, the holotypical tibiotarsus of *Otus wintershofensis* agrees with the same element of *Strix* (incl. *Ciccaba*). In absence of contrary evidence I transfer here *Otus wintershofensis* to the

modern genus *Strix* LINNAEUS, 1758 as *Strix wintershofensis* (BALLMANN, 1969), new combination. *Strix wintershofensis* was much smaller than any modern *Strix* species (distal width of the holotypical tibiotarsus = 5.5 mm, BALLMANN 1969).

A slender left tarsometatarsus lacking proximal end from Merkur (MN 3) belongs to a tiny representative of the genus *Strix*, that belonged to the same size class as *Strix wintershofensis*, to which I here refer the specimen. Its distal width is 5.5 mm.

Strix collongensis

BALLMANN (1972: 97) described *Strix collongensis* on the basis of a complete coracoid from the middle Miocene (MN 5) of Vieux de Collonges in France. The holotypical coracoid differs from the same element of the Strigini, and agrees with the other two subfamilies in having the head bent medially. It differs from the coracoids of the Surniini, and agrees with those of the Asionini in having: (1) robust (broad) shaft, and (2) pneumatic foramina hidden in a round, deep hollow below the furcular facet. The species is thus referable to the latter tribe, but not to *Asio*, from which it differs in having shaft very long in comparison with the head and the sternal wing of the coracoid. Because of this difference, I create here a new genus for the species:

Alasio n. g.

Type: *Strix collongensis* BALLMANN, 1972. Etymology: Abbreviated from Latin alacer = pugnacious, and asio = owl. Selected in allusion of the predatory habits of strigine owls. The name is feminine in gender. *Strix collongensis* BALLMANN, 1972 is the type species of *Alasio* n. g., and the only species currently included in it. It should be thus known as *Alasio collongensis* (BALLMANN, 1972), new combination. The known occurrence of *Alasio* is limited to the type locality of its type species.

No skeleton of *Nesasio* PETERS, 1937 was available for comparison. The species, now confined to the Solomon Islands in the Pacific Ocean, was originally thought to be derived from *Asio* (PETERS 1937), but OLSON (1995) argued that it may be a relict of an early asionine radiation. If so, its presence in the early Miocene of Europe would be possible (cf. MLÍKOVSKÝ 1996c). However, the bird has robust hindlimb bones (see OLSON 1995), and it is thus less probable, that it would have a relatively prolonged anterior part of the skeleton, incl. coracoid, and that it could be similar to *Alasio*.

Strix edwardsi

ENNOUCHI (1930: 66) described *Strix edwardsi* on the basis of a complete tibiotarsus from the middle Miocene (MN 7-8) of La Grive-Saint-Alban in France. The figures (ENNOUCHI 1930, pl. 5, figs. 9-12) show a tarsometatarsus morphologically similar to the same element of *Strix* (incl. *Ciccaba*). Nevertheless, ENNOUCHI (1930) used the generic name *Strix* auct. in the sense of the current *Tyto* BILLBERG, 1828 (barn owls; cf. MATHEWS 1912), while the similarity described in the present paper refers to *Strix* LINNAEUS, 1758 (true owls). Hence, I transfer here *edwardsi* from *Strix* auct. (non LINNAEUS, 1758) to *Strix* LINNAEUS, 1758, where it will be known as *Strix edwardsi* (ENNOUCHI, 1930), new combination. *Strix edwardsi* was larger than *Strix wintershofensis* (BALLMANN, 1969) from the early Miocene (MN 3) of Germany. Distal width of holotypical tibiotarsi is 5.5 mm in *Strix wintersho-*

fensis (BALLMANN 1969), and 7.2 mm in *Strix edwardsi* (ENNOUCHI 1930), respectively. *Strix edwardsi* is apparently a valid species.

The distal fragment of a left tibiotarsus from Petersbuch 39 in Bavaria (MN 6) belongs in *Strix*, and I refer it here to this species, although it is somewhat smaller, its distal width being 6.1 mm. The Miocene record of genus *Strix* in Europe is limited to three localities, differing in age. All yielded scanty remains of a very small *Strix*. The data indicate that there was gradual increase in size in these forms, and it is thinkable that all belong to a single species, that underwent evolutionary increase in size. Distal widths of tibiotarsi were 5.5 mm (MN 3), 6.1 mm (MN 6), and 7.2 mm (MN 7-8), respectively. Nevertheless, this is nothing more than a speculation until more material is discovered. The form from MN 3 bears a name *Strix wintershofensis* (see above).

Bubo florianae

KRETZOI (1957: 243) described *Bubo* (?) *florianae* on the basis of a single pedal phalanx from the late Miocene (MN 11) of Csákvár in Hungary. As noted by himself (1957: 247), "such an incomplete find is not suitable at all to any closer comparison and even less suitable to serve as a basis for new taxonomic units." I absolutely agree. Although the specimen indeed seems to have belonged to an owl, I consider it indeterminate within the family. KRETZOI (1957) tentatively assigned the fossil to the genus *Bubo* on the basis of its large size, and for zoogeographical reasons. *Bubo florianae* KRETZOI, 1957 is a nomen dubium, being available for nomenclatural purposes, but having no bearing on the fossil history of owls.

Bubo longaevus

Bubo longaevus was described by UMANS'KAJA (1979: 779) on the basis of a complete tibiotarsus from the late Miocene (MN 11-13) of Čebotarevka in Ukraine. The bone is characterised by: (1) protruding external ligamental prominence, causing the rim of shaft between the prominence and external condyle to be concave in lateral view, and (2) distinct posterior wing of the external condyle. This is typical for *Asio* among strigine owls, the prominence being markedly less distinct in the remaining owls, incl. *Nesasio* and *Rhinoptynx* (see OLSON 1995), and *Bubo*. The bone is similar to the same element of *Asio*, so that *Bubo longaevus* must be transferred to the latter genus. Within the genus *Asio*, *longaevus* is distinctly larger than both modern Palearctic species: maximum length of tibiotarsus is 125 mm in *longaevus* (n = 1, UMANS'KAJA 1979), while it is 71.5-78.5 in *Asio otus* (n = 2), and 83.6 mm (n = 1) in *Asio flammeus* (my measurements). *Asio longaevus* (UMANS'KAJA, 1979), new combination, is apparently a valid species of *Asio*. It is known only from its type locality as yet.

Strix perpasta

BALLMANN (1976: 27) described *Strix? perpasta* on the basis of a tibiotarsus, lacking proximal end, from San Giovannino in Italy. The locality (and three other fissures, where additional material of this species was found - BALLMANN 1976) are located on the Gargano Peninsula, which was separated from the mainland as an island during the deposition of the remains (see BALLMANN 1973, 1976, DELLE CAVE 1996). The locality was believed to be late Miocene in age, when BALLMANN (1976) described the species, but subsequent

research showed, that it is probably younger, belonging in the early Pliocene (see DELLE CAVE 1996). The holotypical tibiotarsus of *Strix? perpasta* differs from the same element of *Strix* and agrees with that of *Bubo* (incl. *Ketupa* - see MEISE 1933, ECK & BUSSE 1973) in having: (1) internal condyle displaced medially, making the distal end of tibiotarsus more asymmetric, (2) well developed rim of the internal condyle (see Character 12 of BALLMANN 1976: 28), and (3) internal condyle rounded in medial view (it is oval in *Strix*). Hence, I transfer *Strix? perpasta* to the genus *Bubo* as *Bubo perpastus* (BALLMANN, 1976), new combination.

Eagle owls of the genus *Bubo* (incl. *Ketupa*) were recorded from the Plio-Pleistocene deposits of several Mediterranean islands (ALCOVER et al. 1992, TYRBERG 1998). *Bubo insularis* MOURER-CHAUVIRÉ & WEESIE, 1986 was described from the late Pleistocene of Corsica and Sardinia (MOURER-CHAUVIRÉ & WEESIE 1986, ALCOVER et al. 1992). The species was smaller than *Bubo perpastus*, having distal width of tibiotarsus 13.2-14.8 mm (n = 6, MOURER-CHAUVIRÉ & WEESIE 1986), while the same dimension = 15.5 mm in *Bubo perpastus* (n = 1, BALLMANN 1976). In addition, modern Brown Fish Owl *Bubo zeylonensis* (GMELIN, 1788) was recorded from Pleistocene deposits (exact age unknown) of the island of Crete (WEESIE 1987). Remains of the latter species were also reported from the earliest Pleistocene of 'Ubeidiya in Jordan Valley in Israel (TCHERNOV 1980). Both *Bubo insularis* and *Bubo perpastus* should be compared with the modern *Bubo zeylonicus* to confirm their species identity. The latter species is smaller than *Bubo bubo*, and is known to inhabit islands and rocky shores (CRAMP 1985).

Surnia robusta

Surnia robusta JÁNOSSY (1977: 10) was described on the basis of a complete tarsometatarsus from the late Pliocene (MN 17) of Villány 3 in Hungary. The figures of the holotype (JÁNOSSY 1977, figs. 2a-d) convincingly show a tarsometatarsus belonging to a representative of the genus *Surnia* DUMÉRIL, 1806. As documented by JÁNOSSY (1977), *Surnia robusta* was much larger than the modern Hawk Owl *Surnia ulula* (LINNAEUS, 1758), its holotypical tarsometatarsus being 37.2 mm long, while the same dimension of the modern *Surnia ulula* is 23-27 mm (n = 36). For further biometrical data see JÁNOSSY (1977: 13). *Surnia robusta* is known only from its type locality so far.

Varia

Of the remaining species listed by BRODKORB (1971) in his Strigidae, MOURER-CHAUVIRÉ (1987) transferred *Bubo incertus* MILNE-EDWARDS, 1892, *Necrobyas harpax* MILNE-EDWARDS, 1892, *Necrobyas rossignoli* MILNE-EDWARDS, 1892, *Necrobyas edwardsi* GAILLARD, 1938, and *Asio henrici* MILNE-EDWARDS, 1892 to the Tytonidae (see also MLÍKOVSKÝ 1998a). *Strigogyps minor* GAILLARD, 1938 was shown to belong to the Phorusrhacidae (MOURER-CHAUVIRÉ 1981, 1983), and *Strigogyps dubius* GAILLARD, 1908 was removed from the Strigiformes, although its affinities were not clarified (MOURER-CHAUVIRÉ 1987). All of these species were described from the Eo-Oligocene deposits of the Phosporites du Quercy in France.

Eoglaucidium pallas FISCHER, 1987 was described on the basis of a humerus from the middle Eocene (MP 13) of Geiseltal XX in Germany. The species was removed from the

Strigiformes by MLÍKOVSKÝ (1992: 443), who suggested that the species may belong in the Coraciiformes.

BAYAN (1873) attributed a feather imprint from the late Oligocene (MP 30) of Aix-en-Provence in France to *Strix* sp. Even if he is right in assigning the imprint to the family Strigidae, it is highly improbable that it belonged to *Strix*. There is no osteological evidence that the Striginae existed in Europe before MN 2, while the Tytoninae were diverse and common during that time period in that region (MOURER-CHAUVIRÉ 1987, MLÍKOVSKÝ 1998a), and the feather could thus belong to some representative from the latter subfamily.

Asio pigmaeus SEREBROVS'KYI, 1941 was described from the early Pliocene (MN 15) deposits of Odesa catacombs in Ukraine. Until its holotype is located and restudied, this species must be considered a meaningless name.

Ardea lignitum was described by GIEBEL (1860) on the basis of a partial femur from the middle Pliocene (MN 15-16) of Rippersroda 1 in Germany. BRODKORB (1980) showed that the specimen belongs to an owl from the genus *Bubo*, and MLÍKOVSKÝ (1992: 437) subsequently synonymized *Ardea lignitum* GIEBEL, 1860 with the modern Eagle Owl *Bubo bubo* (LINNAEUS, 1758).

Two strigine owls were described from the early Pliocene (MN 14-15) of North America: *Speotyto megalopeza* FORD, 1966 was based on the distal portion of a tarsometatarsus from Fox Canyon, Kansas, and *Asio brevipes* FORD & MURRAY, 1967 was based on a tarsometatarsus lacking proximal end from Hagerman, Idaho. I restudied their descriptions and illustrations, and consider both of them to be valid species.

JÁNOSSY (1974) described from the late Pliocene (MN 16) deposits of Rebielice Królewskie 1 in Poland a fossil subspecies of the modern Little Owl *Athene noctua veta*, elevating it later to the rank of species (JÁNOSSY 1977, 1981). MLÍKOVSKÝ (1992: 443) restudied the holotypical coracoid of this species, showing that it is inseparable from the coracoids of the modern Tengmalm's Owls *Aegolius funereus* (LINNAEUS, 1758), with which it was synonymized (see also MLÍKOVSKÝ 1998b).

Several Tertiary records of the Striginae were assigned only to genera. Due to the difficulties in identified postcranial elements of this subfamily (cf. SHUFELDT 1900, PYCRAFT 1903, VERHEYEN 1956, FORD 1967), I do not consider these remains identified with sufficient certainty. They are not considered in the discussion below, and not included in the Table 2.

FOSSIL HISTORY OF THE STRIGINAE

Taking into account all taxonomic changes mentioned above, the fossil history of the Striginae can be summarized as follows:

The record of owls goes back to the Paleocene (RICH & BOHASKA 1976, 1981, MOURER-CHAUVIRÉ 1994). In the Oligocene and early Miocene, barn owls from the subfamily Tytoninae flourished - in Europe at least (MLÍKOVSKÝ 1998a). On the other hand, the oldest representative of the subfamily Striginae was recorded only from the early Miocene (MN 2) of France (*Mioglaux poirrieri*). Shortly thereafter, in MN 3, an array of the Striginae appeared in Europe, incl. *Mioglaux debellatrix* and *Intulula tinnipara* from the Czech Republic, and *Strix wintershofensis* and "*Strix*" *brevis* from Germany. It is

possible that competition with the Striginae caused the decline and subsequent extinction of most of the Tytoninae in Europe in that time (cf. MLÍKOVSKÝ1998a). Outside of Europe, *Strix dakota* was described from the early Miocene (MN 3) of South Dakota (MILLER 1944), but its referral to the Striginae is uncertain (see above). In addition, OLSON (1985: 131) mentioned that "a fair number of specimens" belonging to owls is available from the Oligocene of Wyoming. These remains have not been described as yet, and it remains unknown to which subfamily within the Strigidae they belong.

Table 2 - Stratigraphical distribution of the Striginae during the Tertiary. MN zones were lumped into standard mammal ages (MEIN 1990).

Tab. 2 - Stratigrafické rozšíření zástupců podčeledi Striginae v třetihorách. MN-zóny jsou sloučeny do standardních úseků (MEIN 1990).

	MN						
	1-2	3-5	6-8	9-10	11-13	14-15	16-17
<i>Mioglaux</i>	●	●					
<i>Intulula</i>		●					
<i>Alasio</i>		●					
Surniini gen. indet.		●					
<i>Strix</i>		●	●				
<i>Asio</i>					●	●	
<i>Bubo</i>						●	
<i>Athene</i>						●	
<i>Aegolius</i>							●
<i>Surnia</i>							●

Subsequent record of the Striginae is rather rich, but most of the remains are still undescribed. It is noteworthy that, starting with the middle Miocene, only modern genera of the Striginae were found, whereas most of the early Miocene species belong in extinct genera. The Miocene species include *Strix edwardsi* from France (MN 7-8), and *Asio longaevus* from Ukraine (MN 11-13). The Pliocene record includes *Bubo perpastus* from Italy (MN 14-15), *Asio brevipes* from Idaho (MN 14-15), *Athene megalopeza* from Kansas and Idaho (MN 14-15), and *Surnia robusta* from Hungary (MN 17). The record is furnished with dubious species "*Bubo floriana*" from Hungary (MN 11), and "*Asio pigmaeus*" from Ukraine (MN 15). First modern species were recorded from the middle Pliocene: *Bubo bubo* in Germany (MN 15/16), and *Aegolius funereus* in Poland (MN 16).

The Quaternary record from continental deposits includes only representatives of modern genera (for a possible exception see OLSON 1984). Nevertheless, extinct genera of the Striginae were recorded from various oceanic islands, incl. Cuba (*Ornimegalonyx*; ARREDONDO 1958, 1976, 1982), Mascarene Islands (*Mascarenotus*; MOURER-CHAUVIRÉ et al. 1994), and Hawaii Islands (*Grallistrix*; OLSON & JAMES 1991).

FORD (1967) recognized three groups of strigine owls, incl. Strigini, Surniini, and Asionini (see above for the ranking of these taxa). Of them, the Strigini are known from MN 2 onwards, while Surniini and Asionini from MN 3. The Tertiary record of the Striginae can be summarized as follows (see also Tab. 2):

Strigini: *Mioglaux poirrieri* (MN 2, France), *Mioglaux debellator* (MN 3, Czech), *Intulula tinnipara* (MN 3, Czech), *Strix wintershofensis* (MN 3, Germany), *Strix edwardsi* (MN 6-8, France, Germany), *Bubo perpastus* (MN 14-15, Italy), rec. *Bubo bubo* (MN 15-16, Germany);

Surniini: "*Strix*" *brevis* (MN 3, Germany), *Athene megalopeza* (MN 14-15, Kansas, Idaho), *Surnia robusta* (MN 17, Hungary), rec. *Aegolius funereus* (MN 16, Poland);

Asionini: *Alasio collongensis* (MN 5, France), *Asio longaevus* (MN 11-13, Ukraine), *Asio brevipes* (MN 14-15, Idaho).

ACKNOWLEDGMENTS. Zdeněk DVORÁK (Bílina), Oldřich FEJFAR (Praha), and Michael RUMMEL (Weissenburg) kindly placed at my disposal avian bones from Merkur (ZD, OF), Františkovy Lázně (OF), and Petersbuch (MR). Zygmunt BOCHENSKI (Kraków) allowed me to study the holotype of *Athene veta*. Oldřich FEJFAR generously drew figure 2. Skeletons of modern owls were compared in the collections of the United States National Museum in Washington, D.C. (S. L. OLSON), Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences in Kraków (Z. BOCHENSKI), Paleontological Institute of the Russian Academy of Sciences (E. N. KUROČKIN & A. A. KARCHU), and in the author's collection in Praha. The manuscript benefited from comments by I. HORÁČEK (Praha). I thank all the named persons. Much of this work was conducted when I was short-term fellow of the Smithsonian Institution in Washington, D.C., in January/February 1997.

SOUHRN

V této práci je předložena revize fosilních nálezů podčeledi Striginae (puštíkovití), se zvláštním zřetelem ke staromiocénní lokalitě Merkur v severních Čechách, která je na nálezy těchto sov mimořádně bohatá. Z Merkuru popisují dva nové druhy puštíkovitých sov: *Mioglaux debellatrix* a *Intulula tinnipara*, oba v nových rodech. Další taxonomické závěry jsou tyto: *Bubo poirrieri* MILNE-EDWARDS byl přearozán do rodu *Mioglaux* MLÍKOVSKÝ. *Strix brevis* BALLMANN byl přearozán do tribu Surniini, ale jeho rodové postavení nebylo objasněno. Druhy *Otus wintershofensis* BALLMANN a *Strix* [auct., non LINNAEUS] *edwardsi* ENNOUCHI byly přearozány do rodu *Strix* LINNAEUS. *Strix collongensis* BALLMANN byl přearozán do nového rodu *Alasio* MLÍKOVSKÝ z tribu Asionini. *Bubo longaevus* UMANS'KAJA byl přearozán do rodu *Asio* BRISSON. *Bubo florianae* KRETZOI byl popsán na základě blíže neurčitelného materiálu (článek prstu nohy) a byl tedy přearozán do kategorie nomina dubia.

Historii podčeledi Striginae lze na základě dostupných dokladů zrekonstruovat takto [Stáří lokalit je vyjadřováno v tzv. MN-zónách ve smyslu MEINA 1990, který rozdělil mladší třetihory na 17 úseků. V rámci podčeledi jsou rozlišitelné 3 skupiny (FORD 1976), zde označované jako triby.]: Nejstarším doloženým zástupcem podčeledi Striginae je *Mioglaux poirrieri* MILNE-EDWARDS ze staršího miocénu (MN 2) Francie, který patří do tribu Strigini. Další třetihorní zástupci tohoto tribu jsou: *Mioglaux debellator* MLÍKOVSKÝ a *Intulula tinnipara* MLÍKOVSKÝ ze staršího miocénu (MN 3) Čech, *Strix wintershofensis* (BALLMANN) ze staršího miocénu (MN 3) Německa, *Strix edwardsi* (ENNOUCHI) ze středního miocénu (MN 6-8) Francie a Německa, a *Bubo perpastus* (BALLMANN) ze staršího pliocénu (MN 14-15) Itálie. Ze středního pliocénu Německa byl doložen i současný výr velký *Bubo bubo* (LINNAEUS).

Rovněž tribus Surniini je doložen už od staršího miocénu, ale jeho nálezy jsou daleko vzácnější, než nálezy tribu Strigini. Nejstarším nalezeným zástupcem tohoto tribu je "*Strix brevis*" BALLMANN ze staršího miocénu (MN 3) Německa. Další nálezy pocházejí až z pliocénu. Jedná se o druhy *Athene megalopeza* (FORD & MURRAY) ze staršího pliocénu Kansasu a Idaha, a *Surnia robusta* JÁNOSSY z mladšího pliocénu (MN 17) Maďarska. Z mladšího pliocénu (MN 16) Polska byl doložen i současný sýc rousný *Aegolius funereus* (LINNAEUS).

Tribus Asionini má rovněž stručný fosilní záznam. Nejstarším dokladem je *Alasio collongensis* (BALLMANN) ze středního miocénu (MN 5) Francie, následovaný druhy *Asio longaeus* (UMANSKAJA) ze svrchního miocénu (MN 11-13) Ukrajiny a *Asio brevipes* FORD ze staršího pliocénu (MN 14-15) Idaha.

Ve čtvrtohorách byly na kontinentech nalezeny pouze zbytky současných rodů. Na některých oceánských ostrovech však byla doložena existence dnes vyhynulých rodů puštíkovitých sov. Jedná se o Kubu (*Ornimegalonyx*), Maskarény (*Mascarenotus*) a Havajské ostrovy (*Grallistrix*).

REFERENCES

- ALCOVER, J. A., FLORIT, F., MOURER-CHAUVIRÉ, C. & WEESIE, P. D. M. 1992: The avifaunas of the isolated Mediterranean islands during the middle and late Pleistocene. - In: CAMPBELL, K. E. (ed.): *Studies in avian paleontology honoring Pierce Brodkorb*. - *Nat. Hist. Mus. Los Angeles, Sci. Ser.*, 36: 273-283.
- ARREDONDO, O. 1958: Aves gigantes de nuestro pasado prehistórico. - *El Cartero Cubano*, 17(7): 10-12.
- 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*. - *Smithson. Contrib. Paleobiol.*, 27: 169-187.
- ARREDONDO, O. 1982: Los Strigiformes fósiles del pleistoceno cubano. - *Bol. Soc. venezol. Cienc. nat.*, 140: 33-55.
- BALLMANN, P. 1969: Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. - *Zitteliana*, 1: 5-60.
- BALLMANN, P. 1972: Les oiseaux miocènes de Vieux-Collonges. - *Docum. Lab. Géol. Fac. Sci. Lyon*, 50: 93-101.
- 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.
- BAYAN, F. 1873: Sur les plumes d'oiseaux des gypses d'Aix. - *Bull. Soc. géol. France*, (3) 1: 386-387.
- BECKER, J. J. 1987: Neogene avian localities of North America. - *Smithsonian Institution Press, Washington, D.C.*
- BRODKORB, P. 1971: Catalogue of fossil birds: Part 4 (Columbiformes through Piciformes). - *Bull. Florida State Mus. (Biol. Sci.)*, 15: 163-266.
- BRODKORB, P. 1980: A new fossil heron (Aves: Ardeidae) from the Omo Basin of Ethiopia, with remarks on the position of some other species assigned to the Ardeidae. - In: CAMPBELL, K. E. (ed.): *Papers in avian paleontology honoring Hildegard Howard*. - *Nat. Hist. Mus. Los Angeles Co., Contrib. Sci.*, 330: 87-92.
- CRAMP, S. (ed.) 1985: The birds of the western Palearctic. Vol. 4. - *Oxford University Press, Oxford*.
- 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. - *A. Ziemsen Verlag, Wittenberg Lutherstadt*.
- ENNOUCHI, E. 1930: Contribution a l'étude de la faune du Tortonien de La Grive-St-Alban (Isère). - *Les Presses Modernes, Paris*.
- FEJFAR, O. & KVAČEK, Z. (1993): Tertiary basins in northwest Bohemia. - *Univerzita Karlova & Česká geologická společnost, Praha*.
- FISCHER, K. 1987: Eulenreste (*Eoglaucidium pallas* nov. gen., nov. sp., Strigiformes, Aves) aus der mitteleozänen Braunkohle des Geiseltales bei Halle (DDR). - *Ann. Orn.*, 11: 137-142.

- FORD, N. L. 1966: Fossil owls from the Rexroad fauna of the Upper Pliocene of Kansas. - *Condor*, 68: 472-475.
- FORD, N. L. 1967: A systematic study of the owls based on comparative osteology. - *Unpub. Ph.D. Thesis, University of Michigan*.
- FORD, N. L., & MURRAY, B. G. Jr. 1967: Fossil owls from the Hagerman local fauna (Upper Pliocene) of Idaho. - *Auk*, 84: 115-117.
- GAILLARD, C. 1939: Contribution à l'étude des oiseaux fossiles. - *Nouv. Arch. Mus. Lyon*, 15 (2): 1-100.
- GIEBEL, C. G. 1860: Zur Fauna der Braunkohlenformation von Rippersroda in Thüringen. - *Z. ges. Naturwiss.*, 16: 147-153.
- JÁNOSSY, D. 1974: Upper Pliocene and Lower Pleistocene bird remains from Poland. - *Acta zool. cracov.*, 19: 531-566.
- JÁNOSSY, D. 1977: Plio-Pleistocene bird remains from the Carpathian basin. III. Strigiformes, Falconiformes, Caprimulgiformes, Apodiformes. - *Aquila*, 84: 9-36.
- JÁNOSSY, D. 1981: Die altpleistozänen Vogelfaunen von Deutsch-Altenburg 2 und 4 (Niederösterreich). - *Beitr. Paläontol. Österreich*, 8: 375-391.
- JÁNOSSY, D. 1993: Bird remains from the Upper Miocene (MN 9) of Rudabánya (N-Hungary). - *Aquila*, 100: 53-70.
- KRETZOI, M. 1957: Madármaradványok a Csákvári Hipparion-faunából. - *Aquila*, 63-64: 239-248.
- MATHEWS, G. M. 1912: On the generic name of the Barn-owl. - *Austral avian Rec.*, 1: 104.
- MEIN, P. 1990: Updating of MN zones. - In: LINDSAY, E. H., FAHLBUSCH, V. & MEIN, P. (eds.): *European Neogene mammal chronology*. Plenum Press, New York: 73-90.
- MEISE, W. 1933: Zur Systematik der Fischeulen. - *Orn. Monatsber.*, 41: 169-173.
- MILLER, A. H. 1944: An avifauna from the Lower Miocene of South Dakota. - *Univ. California Publ., Bull. Dept. geol. Sci.*, 27: 85-99.
- MILNE-EDWARDS, A. 1863: Mémoire sur la distribution géologique des oiseaux fossiles et description de quelques espèces nouvelles. - *Ann. Sci. nat. (Zool.)*, (4) 20: 132-176.
- MILNE-EDWARDS, A. 1869-1871: Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux de la France. Vol. 2. - *G. Masson, Paris*.
- MILNE-EDWARDS, A. 1892: Sur les oiseaux fossiles des dépôts éocènes de phosphate de chaux du Sud de la France. - *C. R. 2e 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.): *Studies in avian paleontology honoring Pierce Brodkorb*. - *Nat. Hist. Mus. Los Angeles, Sci. Ser.*, 36: 433-458.
- MLÍKOVSKÝ, J. (ed.) 1996a: Tertiary avian localities of Europe. - *Acta Univ. Carol. (Geol.)*, 39: 519-848.
- MLÍKOVSKÝ, J. 1996b: Tertiary avian localities of the Czech Republic. - In: MLÍKOVSKÝ, J. (ed.): *Tertiary avian localities of Europe*. - *Acta Univ. Carol. (Geol.)*, 39: 551-557.
- MLÍKOVSKÝ, J. 1996c: Tertiary avian faunas of Europe: a review. - In: MLÍKOVSKÝ, J. (ed.): *Tertiary avian localities of Europe*. - *Acta Univ. Carol. (Geol.)*, 39: 777-818.
- MLÍKOVSKÝ, J. 1998a: A new barn owl (Aves: Strigidae) from the early Miocene of Germany, with comments on the fossil history of the Tytoninae. - *J. Orn.*, 139: 247-261.
- MLÍKOVSKÝ, J. 1998b: Early Pleistocene birds of Deutsch-Altenburg, Austria. - *Acta Soc. Sci. bohém.*, 62: 135-141.
- MOURER-CHAUVIRÉ, C. 1981: Première indication de la présence de Phorusrhacidae, famille d'oiseaux géants d'Amérique du Sud, dans le Tertiaire européen: Ameghinornis nov. gen. (Aves, Ralliformes) des Phosphorites du Quercy, France. - *Geobios*, 14: 637-647.
- MOURER-CHAUVIRÉ, C. 1983: Les Gruiformes (Aves) des Phosphorites du Quercy (France). 1. Sous-ordre Cariamae (Cariamidae et Phorusrhacidae). Systématique et biostratigraphie. - *Palaeo-vertebrata*, 13: 83-143.
- 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. & WEESIE, P. D. M. 1986: *Bubo insularis* n. sp., forme endémique insulaire de grand-duc (Aves, Strigiformes) du Pleistocène de Sardaigne et de Corse. - *Rev. Paléobiol.*, 5: 197-205.
- 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 (IIa)* 318: 1699-1706.

- OLSON, S. L. 1984: A very large enigmatic owl (Aves: Strigidae) from the late Pleistocene at Ladds, Georgia. - In: *GENOWAYS, H. H. & DAWSON, M. R. (eds.): Contributions in Quaternary vertebrate paleontology. - Carnegie Mus. nat. Hist., Spec. Publ., 8: 44-46.*
- OLSON, S. L. 1995: The genera of owls in the Asioninae. - *Bull. Brit. Orn. Club, 115: 35-39.*
- OLSON, S. L. & JAMES, H. F. 1991: Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes. - *Orn. Monogr., 45: 1-88.*
- PETERS, J. L. 1937: A new genus for *Pseudoptynx salomonensis* Hartert. - *J. Washington Acad. Sci., 27: 81-83.*
- PYCRAFT, W. P. 1903: A contribution towards our knowledge of the morphology of the owls. II. Osteology. - *Trans. Linn. Soc. London, (2) 9: 1-46.*
- 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 *Ogygoptyngidae*, a new family of owls from the Paleocene of North America. - *Alcheringa, 5: 95-102.*
- 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.*
- SEREBROVS'KYJ, P. V. 1941: Pticy iz pliocenovych otloženij Odessy. - *Dokl. AN SSSR, 33: 476-479.* [not seen]
- SHUFELDT, R. W. 1900: On the osteology of the Striges. - *J. Morphol., 17: 665-722.*
- STEININGER, F. F. & RÖGL, F. 1984: Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys. - In: *DIXON, J. E. & ROBERTSON, A. H. F. (eds.): The geological evolution of the eastern Mediterranean. Blackwell Scientific Publications, Oxford: 659-668.*
- STEININGER, F. F., BERNOR, R. L. & FAHLBUSCH, V. 1989: European Neogene marine/continental chronologic correlations. - In: *LINDSAY, E. H., FAHLBUSCH, V. & MEIN, P. (eds.): European Neogene mammal chronology. Plenum Press, New York: 15-46.*
- STEININGER, F. F., BERGGREN, W. B., KENT, D. V., BERNOR, R. L., SEN, S. & AGUSTI, J. 1996: Circum Mediterranean Neogene (Miocene and Pliocene) marine-continental correlations of European mammal units and zones. - In: *BERNOR, R. L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.): The evolution of the western Eurasian Neogene mammal faunas. Columbia University Press, New York: 7-46.*
- TCHERNOV, E. 1980: The Pleistocene birds of 'Ubeidiya, Jordan Valley. - *The Israel Academy of Sciences and Humanities, Jerusalem.*
- UMANS'KAJA, A. S. 1979: Novyj vid filina (*Bubo longaeus*) iz pozdneneogenovykh otloženij severnogo Pričernomor'ja USSR. - *Dokl. AN UkrSSS (B): 1979: 779-782.*
- VERHEYEN, R. 1956: Les Striges, les Trogones et les Caprimulgi dans la systématique moderne. - *Bull. Inst. roy. Sci. nat. Belgique, 32 (3): 1-31.*
- WEESIE, P. D. M. 1987: The Quaternary avifauna of Crete, Greece. - *Unpub. Ph.D. Thesis, State University of Utrecht.*

(Received 28.6.1998, accepted 15.9.1998)

