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A new barn owl (Aves: Strigiformes: Tytonidae) from the Middle Miocene of the Nördlinger Ries (Germany) with remarks on the history of the owls

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Abstract — We describe a new taxon of barn owl, *Miotyto montispetrosi* nov. gen. et spec. from the Middle Miocene (Astaracium, MN6) localities at Steinberg and Goldberg in the Nördlinger Ries (Southern Germany). A single individual from Steinberg is represented by well-preserved long bones of the limbs, the shoulder girdle and by phalanges of the wing and foot. The description lists almost 60 features used for the determination of the affinities of the fossil. Although *Miotyto montispetrosi* nov. spec. clearly belongs to the Tytonidae, it shows some characters intermediate with Strigidae. Some additional juvenile bones from Goldberg indicate that the species was breeding at the Middle Miocene Ries crater lake.

Key words: Tytonidae, *Miotyto montispetrosi* nov. spec., Steinberg, Goldberg

Introduction

Fossil Strigiformes are by no means rare, Kurochkin & Dyke (2011, Tab.1) list over 40 species representing over 20 genera – most of them extinct – for Europe alone. However, many of those taxa, especially from pre-Pleistocene times, are based on single or a few bones that are often fragmentary. Therefore, relatively complete and well-preserved fossil material, even if it is limited to postcranial elements, deserves special attention, the more so, if it can be attributed to a single individual, as in the present case (Fig. 2).

The current material comes from two localities, Steinberg and Goldberg, in the Nördlinger Ries of Southern Germany (Fig. 1). The Nördlinger Ries is an approximately 15 million years old meteorite impact crater, which forms at present a circular shallow depression, 22–24 km in diameter, that separates the Jurassic limestone plateaus of the Swabian and the Franconian Alb. Subsequent to the impact, the Ries crater was filled by a soda lake without outlet, in which spring mounds of calcareous tufa, the so called "travertine hills", rose at sources of sub-lacustrine spring water (Pache *et al.* 2001; Arp 2006).

The Steinberg (formerly called Spitzberg) and the Goldberg are two of these spring mounds.

Some of the spring mounds became temporary islands in the ancient lake. During the late freshwater stage of the Ries crater lake, vertebrate fossils accumulated in fissures and pockets on top of some of the hills such as the Goldberg spring mound (Arp 2006). A few specimens of the material presented here come from the locality Goldberg 9 described by Bolten (1977: 68–71). The processes of deposition and accumulation are unclear for the much richer fossil material of

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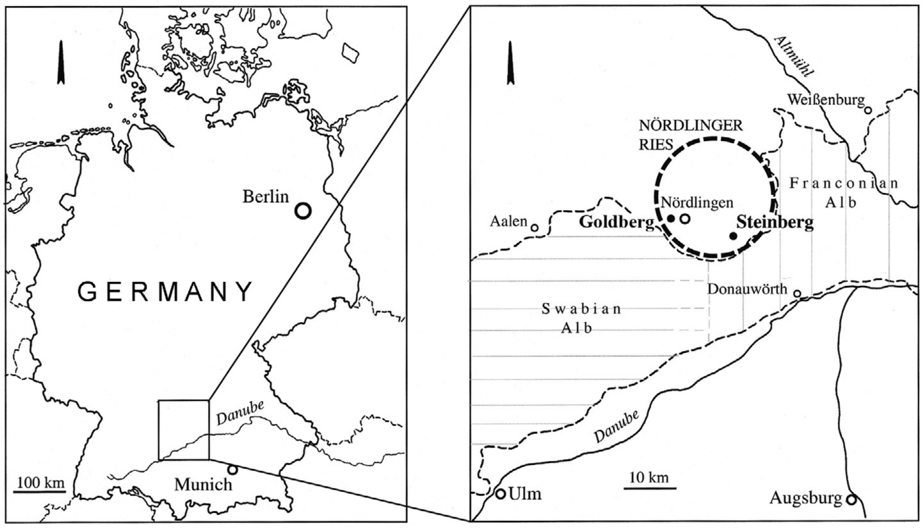

FIGURE 1. Map showing the geographical position of the Steinberg and Goldberg localities within the impact crater of the Nördlinger Ries.

the Steinberg locality. In 1969, a few loose blocks of fossiliferous calcareous tufa were found on the foot of the southwest slope of the Steinberg hill, which is situated on the ring structure in the southeast sector of the crater and whose basis consists predominantly of crystalline basement rocks (Bolten 1977). These loose fossiliferous blocks are also supposed to be the remnants of pocket or fissure, but their exact origin on the top of the Steinberg remains unknown (Heizmann & Fahlbusch 1983: 84). The calcareous tufa from both localities was treated with dilute acetic acid to recover the fossil bones and teeth.

Beside Strigiformes, the following bird taxa are represented by fossils from different localities in the Nördlinger Ries: Pelecanidae, Phalacrocoracidae, Palaelodidae, Anatidae, Rallidae, Charadriidae, Scolopacidae, Glareolidae, Phasianidae, Psittacidae, Coliidae, Apodidae, Capitonidae, and Passeriformes (Ballmann 1979, 1983, 2004; Heizmann & Hesse 1995, Lambrecht, 1933; Mayr & Göhlich 2004). Several of these taxa have not yet been described. The great variety makes the Nördlinger Ries one of the most important sites for Miocene birds in Europe.

On the basis of fossil micro-mammals, the fauna of Steinberg has been determined to be early Astaracium, Mammal Neogene Unit MN6, by Heizmann & Fahlbusch (1983). Besides Soricidae, Gliridae, Cricetidae especially Chiroptera are very rich in the Steinberg fauna; eight species of Chiroptera (Rachl 1983) represent about one third of all mammal species.

Mammals as well as birds from the Steinberg and Goldberg are all small forms, which makes regurgitation pellets by predatory or scavenging birds, especially owls, the most probable origin for these fossil accumulations.

Material and methods

The presented fossil material is kept in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG) under the collection numbers BSPG 1970 XVIII 861 to 897 (Steinberg) and BSPG 1966 XXXIV 3276 to 3279 (Goldberg). In the following text only the last digital number is given. The osteological terminology follows Baumel *et al.* 1993, and occasionally Ballmann (1969a, b). Measurements were taken after von den Driesch (1976). Estimated measurements of slightly damaged bones are given in parenthesis. The systematics of extant owls follows König & Weick (2008).

Recent species examined for comparison: Tytonidae. *Tyto alba*, *Phodilus badius*. Strigidae: *Strix aluco*, *S. uralensis*, *S. nebulosa*, *Asio otus*, *A. flammeus, Athene noctua*, *A. cunicularia*, *Aegolius funereus*, *Bubo scandiacus*, *Bubo bubo*, *Otus scops*, *Glaucidium passerinum, Ninox novaeseelandiae*. The specimens are kept at the ornithological department of the Naturhistorisches Museum Wien (NHMW). Some selected limb bones of *Phodilus badius* (specimen USNM 20310) were lent from the National Museum of Natural History (Smithsonian Institution) Washington, Division of birds (NMNH).

For systematic comparisons the following fossil species of Tytonidae were considered: Neogene Tytoninae: *Tyto campiterrae* Jánossy, 1991, *T. gigantea* Ballmann, 1973, *T. robusta* Ballmann, 1973, *T. sanctialbani* (Lydekker, 1893), *Prosybris antiqua* (Milne-Edwards, 1863). Paleogene and Neogene Necrobyinae. *Necrobyas arvernensis* (Milne-Edwards, 1863), *N. edwardsi* Gaillard, 1939, *N. harpax* Milne-Edwards, 1892, *N. rossignoli* Milne-Edwards, 1892, *N. medius* Mourer-Chauviré, 1987.

Following Louchart (2002), the species *Tyto balearica* Mourer-Chauviré, Alcover, Moya & Pons, 1980 can only be confirmed in post-Neogene, thus Pleistocene localities; all previous reports of Neogene findings referred to *Tyto balearica* belong to a different and not yet described tytonid species (Louchart 2002). *Basityto rummeli* Mlíkovský, 1998 from the Early Miocene of Grafenmühle 21 (MN2–3, southern Germany, Coll. Rummel (Weissenburg)) was determined to be a taxon outside Strigiformes by Mourer-Chauviré (2001). Although Mlíkovský (1998) had synonymized *T. campiterrae* with *T. sanctialbani*, we follow Pavia & Mourer-Chauviré (2011), who retain *T. campiterrae* as a separate species. Also *T. robusta* (see Tab. 3), which was taken into synonymy with *T. gigantea* by Mlíkovský (1998), is kept as a discrete species in this article.

The Mammal Neogene-Zones (MN-Zones) are used as defined by Mein (1999), the Neogene and Paleogene stratigraphy follows Hilgen *et al.* (2012) and Vandenberghe *et al*. (2012), respectively.

Osteological abbreviations: tmt: tarsometatarsus, tt: tibiotarsus, dext.: right, sin.: left, prox.: proximal(is), dist.: distal(is), dors.: dorsal(is).

Institutional abbreviations: BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich; NHMW: Naturhistorisches Museum Wien; NHMUK: Natural History Museum, London; USNM: Smithsonian Institution National Museum of Natural History, Washington.

Systematic Paleontology

Order Strigiformes Wagler, 1830

The owls are a well circumscribed order of nocturnal birds of prey and their osteology assigns them to a ‘natural group’ *sensu* Milne-Edwards (1869–71). Up to now, paleontology has been unable to resolve their relationship with other orders but recent DNA studies, place owls in a clade with diurnal raptors (excluding falcons), which is a sister taxon to parrots and song birds (König & Weick 2008).

One of the oldest owls, *Ogygoptynx wetmorei*, was described by Rich & Bohaska (1976) from the Paleocene of Colorado and later placed into a separate family Ogygoptyngidae (Rich & Bohaska 1981). It is known from a fairly complete tarsometatarsus which shows a mosaic of tytonid and strigid features, but is too old to be at the branching point of the two families.

The oldest record of Strigiformes in Europe dates back to the Late Paleocene and belongs to the genus *Berruornis* Mourer-Chauviré, 1994 (Mayr 2009). The Eocene and Oligocene record of strigiforms is quite extensive but restricted to the northern hemisphere and comprises the extinct families Palaeoglaucidae, Sophiornithidae, Protostrigidae and the extant family Tytonidae (Fig. 12). All Neogene to Recent owls belong to two families, the Tytonidae (barn owls) and the Strigidae (typical owls), which together form the crown group Strigiformes (Mayr 2009).

Recent Strigiformes share a unique osteological character in the form of an ossified arch on the radius described by Bock & McEvey (1969). This structure was not found on the radius of *Palaeoglaux artophoron* (Peters, 1992) from the Middle Eocene of Messel.

The fossil record of the Tytonidae dates from a much earlier time than the earliest known Strigidae (Fig. 12) and will be discussed in more detail below.

The oldest Strigidae (typical owls) date back to the Early Miocene: MN2 of Saint-Gérand-le-Puy (France) and MN3 of Wintershof-West (Germany) (Fig. 12). Originally those fossils were placed in geographically widespread recent genera of similar size and shape. This does not look very likely at present and they have con-

FIGURE 2. Schematic figure of a barn owl skeleton indicating the preserved bones (black) from the Steinberg individual. Pedal phalanges and claws of uncertain digital affiliation are shaded in grey. Additional bones from the locality Goldberg, comprising a fragmentary coracoid, a femur, a distal tibiotarsus, and a juvenile tarsometatarsus, are not indicated.

sequently been moved to newly erected extinct genera (Mlíkovský 2002), but for which unfortunately diagnoses are virtually missing. Therefore these genera must be regarded as quite "modern-looking" typical owls with uncertain affinities.

The Strigidae are the most numerous and diverse family among extant owls and account for well over two hundred species in more than twenty genera (König & Weick 2008). They inhabit a wide geographical range and are nearly cosmopolitan except for Antarctica. They are especially speciose in the tropical forests but occupy a variety of habitats from deserts to swamps to sub-polar wooded areas and tundra with severe winter conditions (Burton 1973; Del Hoyo *et al.* 1999). In size the Strigidae range from very small (*Glaucidium*) to very large (*Bubo*) taxa. Their postcranial skeleton appears to be more adapted to the reduction of wing loading and to the seizing of prey than the skeleton of the Tytonidae. Weight reduction is expressed by the degree of pneumatization in the bones of their shoulder girdles (scapula and coracoid) and the great reduction of their furcula. Predatory capability is implied by robust leg bones that are sculpted to accommodate large muscles and tendons, e.g. in the supracondylar fossa of the distal tibiotarsus and in the sulcus extensorius on the proximal tarsometatarsus where only thin lamellae of bone remain between extensor and flexor sides in the Strigidae.

Ford (1967) examined the osteology of over 80 species of Strigiformes belonging to 30 genera including *Tyto* and *Phodilus*. According to him, the taxonomic subdivision of extant owls is mainly based on external morphology that is not always reflected in skeletal characteristics. Furthermore, osteologic features and distinctions between genera, based on postcranial elements of a few species, do not always hold when more species become available for comparison. Consequently, the allocation of a fossil owl in the taxonomic system remains difficult.

The skeletal differences between Strigidae and Tytonidae have been described not only by Ford (1967) but in many publications ranging from Lydekker (1893) to Louchart (2002).

Family Tytonidae Ridgway, 1914

Half of the 17 characters listed by Sibley & Ahlquist (1972) after Ridgway (1914) to differentiate between Strigidae and Tytonidae refer to external morphology and only two of the remainders are applicable to the fossil owl described here: The third toe in Tytonidae is as long as the second and the tarsometatarsus is without an bony loop (arcus extensorius).

The recent Tytonidae comprise two genera, of which *Phodilus* Geoffroy Saint-Hilaire, 1830 is clearly a relict limited to South and Southeast Asia, while the other genus, *Tyto* Billberg, 1828, which comprises 25 species, is widespread in its distribution but mainly within tropical and subtropical regions (König & Weick 2008). The type species, the Common Barn Owl, *Tyto alba* (Scopoli, 1769), comprises 10 subspecies and is the most widespread of all the owls. It is the only barn owl to reach the temperate regions of Europe and North America, where severe winters may decimate its populations (Voous 1962). Its geographical distribution reaches from Europe over Africa and Madagascar to Arabia, Asia Minor,

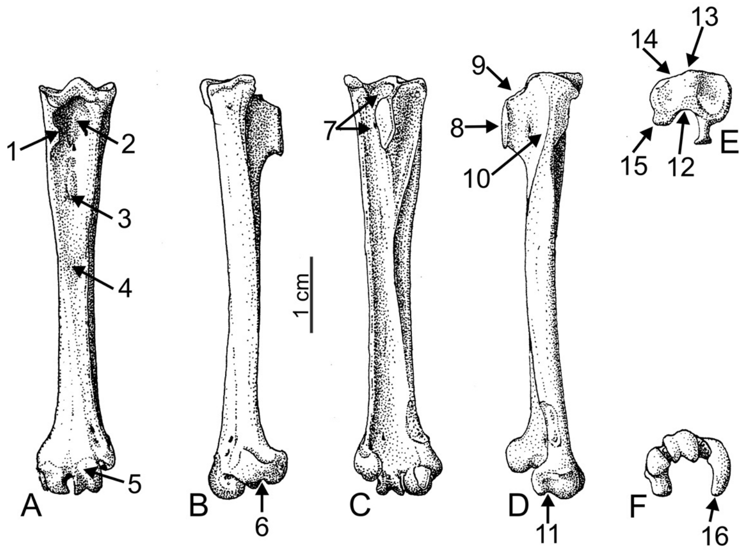

FIGURE 3. Holotype of *M. montispetrosi* nov. spec., tarsometatarsus sin. (1970 XVIII 867) from Steinberg. (numbers refer to the description in the text). **A**) dorsal, **B**) lateral, **C**) plantar, **D**) medial; **E**) proximal, **F**) distal.

India and Malaysia and south into Indonesia. The diet of the European barn owls consists mainly of small nocturnal mammals, like shrews, mice, and voles, but rats and even small rabbits are recorded as well as small birds, bats, frogs, small reptiles and large insects (Burton 1973; del Hoyo *et al.* 1999). The undigested parts including the bones are regurgitated as pellets.

The fossil record for *Tyto alba* goes back to the Early Pleistocene in Europe and to the Late Pliocene in Morocco (Pavia *et al*. 2012).

The origins of the family Tytonidae can be traced back to the Paleogene of France, where the fossil genus *Necrobyas* is documented from the Late Eocene (phosphorites du Quercy) (up to the Early Miocene of Saint-Gérand-le-Puy) (Fig. 12). *Necrobyas* shows similarities to *Tyto* and is usually placed within the Tytonidae (Mourer-Chauviré 1987). From the Oligocene of North America Olson (1985) mentions several undescribed complete skeletons of a small species of owl with a stout 'phodiline' tarsometatarsus without an ossified tendinal loop (arcus extensorius). In Europe the first clearly tytonine species is *Prosybris antiqua* originally described from the early Miocene (MN2) of Saint-Gérand-le-Puy (see Tab. 4), but according to Mlíkovský (1998) also known from early Oligocene of the phosphorites du Quercy. The fossil history of the genus *Tyto* has recently been summarized by Pavia & Mourer-Chauviré (2011).

***Miotyto* nov. gen.**

Type species: *Miotyto montispetrosi* nov. spec.

Included species: The type species only. But see "discussion and conclusion".

Etymology: *Miotyto: Mio*, abbreviated from Miocene, the epoch for which this barn owl is proven; combined to the existing genus name *Tyto* for most extant (and some fossil) barn owls. Feminine in gender.

Diagnosis: Middle-sized member of Tytonidae, about the size of the Recent *Tyto alba guttata*. Tarsometatarsus and coracoid relatively stout. Tarsometatarsus: vestigial arcus extensorius, tuberositas m. tibialis cranialis relatively low on shaft; sulcus extensorius deep, reaching to half the length of the shaft; sulcus of trochlea III extending proximally; crista hypotarsi long; tuberculum m. fibularis brevis directed plantolaterally. Scapula: acromion projecting dorso-laterally. Phalanx proximalis digiti majoris: cranial face flat, not concave. Femur: Cranial linea intermuscularis merges in a curve into crista trochanteris. Tibiotarsus: Lateral condyle slanted proximolaterally. Pedal phalanges: The indices of the lengths of phalanx II 1/phalanx III 1 and phalanx III 1/phalanx III 2 are intermediate between Tytonidae and Strigidae.

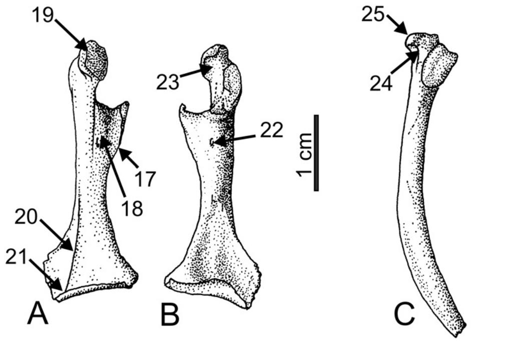

FIGURE 4. Coracoid dext. (1970 XVIII 872) (**A, B**) and scapula dext. (1970 XVIII 873) (**C**) of *M. montispetrosi* nov. spec. from Steinberg. **A**) ventral, **B**) dorsal, **C**) lateral.

***Miotyto montispetrosi* nov. spec.**
(Figs 3–11)

Holotype: left tarsometatarsus (BSPG 1970 XVIII 867) (Figs 3, 10H-I, 11C)

Paratypes (Figs 4–9, Fig. 10B, D, O, R, U, W, Fig. 11A, E): coracoid dext. (872), scapula dext. (873), humerus dext., dist. 2/3 (861), humerus dext., prox. end (862), ulna dext., prox. half (863), ulna sin., prox. end (871), ulna dext., dist half (874), os carpi ulnare dext. (876), os carpi ulnare sin. (877), phalanx prox. digiti majoris dext. (875), femur dext., prox. half (865), tt sin. (866), tt dext., dist. half (870), tmt dext. (868), os metatarsale I dext. (878), os metatarsale I sin. (879), phalanx I 1 dext. (880), phalanx I 1 dext. (881), phalanx II 1 dext. (882), phalanx II 1 sin. (883), phalanx II 2 dext. (884), phalanx III 1 dext. (885), phalanx III 1 sin. (886), phalanx III 2 dext. (887), phalanx III 2 sin. (888), phalanx III 3 or IV 4 dext.? (889), phalanx IV 1 dext. (890), phalanx IV 2 dext. (891), phalanx IV 3 dext. (892), phalanx III 3 or IV 4 dext (893), four phalanges terminales (claws) (894–897). Almost all of these bones including the holotype can be attributed to the same adult individual (Fig. 2). The only exceptions are the two specimens of pedal phalanx I 1 dext., one of which must represent a second individual.

Type locality: Steinberg (= Spitzberg, 496 m NN)), about 1 km northeast of the village Appetshofen in the Nördlinger Ries, Southern (Fig. 1). Loose blocks of calcareous tufa found on the SW slope of the Steinberg in the Jungwald forest Germany (N48°49′33″, E10°37′18″), topographic map 7129 Deiningen.

Type horizon: Fissure and pocket fillings in calcareous tufa (“travertine”), Middle Miocene, early Astaracium, MN6 (Heizmann & Fahlbusch 1983).

Differential diagnosis: Tarsometatarsus and coracoid shorter and stouter than in *Tyto* including fossil *T. sanctialbani, T. campiterrae* and *T. balearica* (see Tab. 4). *Miotyto montispetrosi* nov. spec. is distinctly smaller than *T. gigantea* and *T. robusta*, smaller than *T. balearica* and *T. campiterrae*, and distinctly larger than *Prosybris antiqua*. Similar in size to *T. sanctialbani*, but differing by the shorter and stouter tarsometatarsus with vestigial arcus extensorius, sulcus extensorius reaching less distally. Tuberculum m. fibularis brevis directed plantolaterally, whereas oriented plantarly in *Tyto* (*T. alba, T. sanctialbani, T. gigantea,* and *T. robusta*), in *Phodilus*, and in *Prosybris antiqua*. Linea intermuscularis cranialis on femur merging with crista trochanteris clearly below proximal end of femur, whereas linea intermuscularis cranialis reaches up to facies articularis antitrochanterica in *Tyto* (*T. alba, T. sanctialbani,* and *T. robusta*) and in *Phodilus.* Unlike the tibiotarsus of *T. alba* and *T. sanctialbani*, the apophysis of the crista cnemialis cranialis projects distally in *M. montispetrosi* nov. spec.. Index of length of phalanx II 1/phalanx III 1 smaller than in *Tyto*.

Tarsometatarsus relatively longer and more slender than in *Phodilus*. Relative distal width of humerus smaller and intumescentia humeri wider than in *Phodilus*. Unlike *Phodilus*, pedal phalanges IV 1 and IV 2 not fused in *M. montispetrosi* nov. spec..

Etymology: geographic name, *montispetrosi* from Latin mons, montis (= mountain) and petrosus (= stoney) = Steinberg (in German), as possessive noun in genitive case.

Additional referred material (Fig. 8C and D)**:** There are at least two more individuals represented by material from Goldberg (BSPG 1966 XXXIV…): Coracoid sin., fragmentary cranial half (3276), femur dext. (3277), tmt sin. (juvenile) (3278), tt sin., distal half (3279) (subadult).

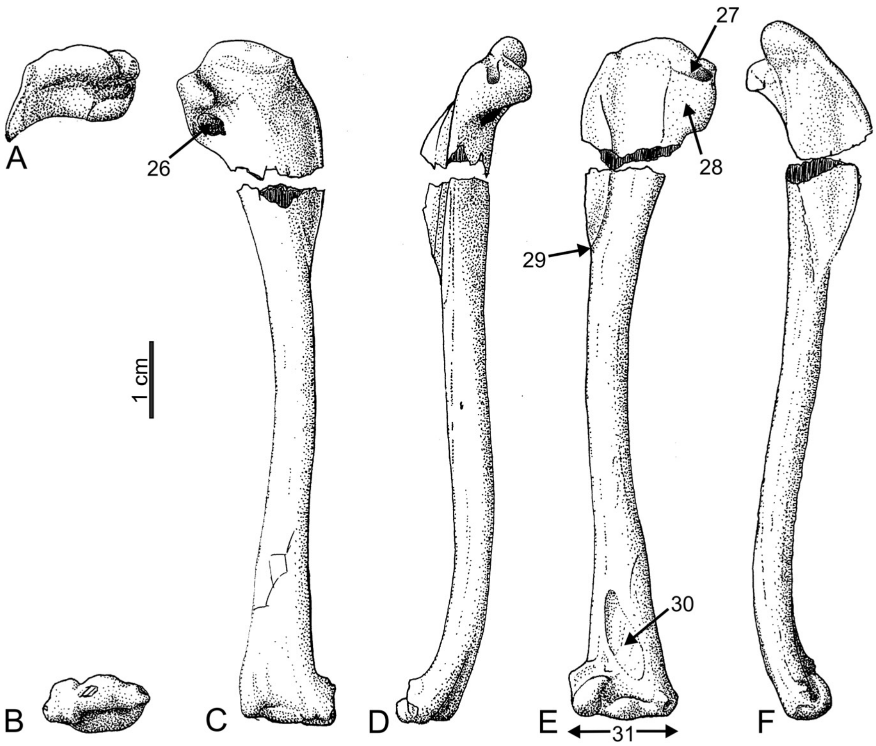

FIGURE 5. Humerus dext. (1970 XVIII 861+862) of *M. montispetrosi* nov. spec. from Steinberg. **A**) proximal, **B**) distal, **C**) caudal, **D**) ventral, **E**) cranial, **F**) dorsal.

Description

Measurements: For measurements of the holotype, paratypes and referred material see Tab. 1.

Holotype tarsometatarsus (Figs 3, 10H-I, 11C**):** Shape relatively stout and robust. Dorsal view: Arcus extensorius lacking, except vestigial pointed projection on medial side (1); fossa infracotylaris dorsalis equally deep on both sides (2); tuberositas m.tibialis cranialis positioned relatively low on shaft (3); sulcus extensorius deep and reaching to half the length of shaft (4); sulcus of trochlea III extending proximally (5). Lateral view: Distal margin of trochlea IV distinctly indented (6). Plantar view: Proximal part of sulcus flexorius moderately excavated (7). Medial view: Crista hypotarsi relatively long (8) starting proximally somewhat below articular surface and carrying no proximal projection (9); fossa parahypotarsalis medialis (= fossa m. flexoris hallucis brevis) cutting far dorsally into facies subcutanea medialis (10); ligamental fossa on trochlea II at distal margin (11). Proximal view: Sulcus flexorius wide and rounded (12); eminentia intercotylaris protruding slightly dorsally (13); no notch in dorsal margin (14); tuberculum m. fibularis brevis directed plantolaterally (15). Distal view: trochleae arranged in semicircle with trochlea IV projecting furthest in plantar direction (16).

Paratypes and referred material

Coracoid (Figs 4A–B, 10O): The coracoid is almost complete, damaged only at the lateral edge of the processus lateralis. A fragmentary cranial portion of a coracoid is preserved from the Goldberg locality.

Bone short and stout. Ventral view: Processus procoracoideus triangular in shape, with broad basis and slightly convex medial margin (17); sulcus supracoracoideus wide and rounded (18); processus acrocoracoideus rounded, knob-like (19); distinct linea intermuscularis ventralis (20) ends medially of angulus externus (21). Dorsal view: Foramen n. supracoracoidei present (22); acrocoracoid not pneumatized (23).

Scapula (Figs 4C, 10D): The scapula is complete except for the caudal tip.

Lateral view: acromion not pneumatized (24)

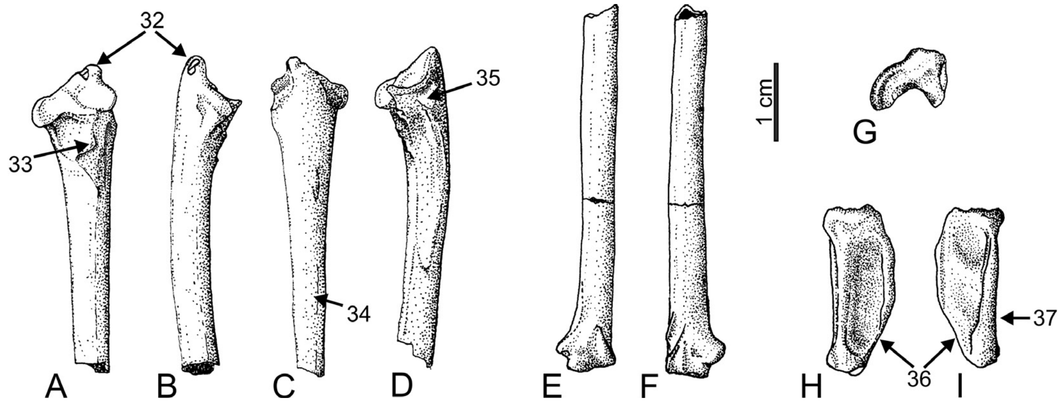

FIGURE 6. Proximal half of ulna dext. (1970 XVIII 863) (**A-D**) and distal half of ulna dext. (1970 XVIII 874+876) (**E, F**), os carpi ulnare dext. (1970 XVIII 876) (**G**), phalanx dig. majoris dext. (1970 XVIII 875) (**H, I**) of *M. montispetrosi* nov. spec. from Steinberg. **A**) cranial, **B**) dorsal, **C**) caudal, **D**) ventral, **E**) ventral, **F**) dorsal, **G**) cranial, **H**) ventral, **I**) dorsal.

and projecting dorso-laterally (25).

Humerus (Figs 5, 10B, 11A): The humerus is almost complete. Shaft sigmoidal in both cranio-caudal and dorsoventral direction.

Caudal view: No fossa pneumotricipitalis, opening of foramen pneumaticum level with surface (26).

Cranial view: Ventral end of strongly marked sulcus transversus almost reaching crista bicipitalis (27); intumescentia humeri well-marked and dorsally sharply delimited (28); length of crista deltopectoralis approximately one third of humerus (29); fossa m. brachialis large and well-marked (30); distal end ventrally enlarged (31).

Ulna (Fig. 6A-F): Two proximal and one distal halves of the ulna are preserved.

Cranial view: Olecranon short and blunt (32); tuberculum bicipitale well-marked and elongated (33). Caudal view: Papillae remigales visible but weakly developed (34). Ventral view: Flat, triangular tuberculum lig. collateralis ventralis cutting slightly under cotyla ventralis (35).

Left and right **os carpi ulnare** (Fig. 6G) are perfectly preserved but without conspicuous features.

Phalanx proximalis digiti majoris (Fig. 6H, I): One complete right element is preserved.

Ventral view: Caudal part blade-like, reaching pila cranialis in regular curve without angle or ligamental process (36). Dorsal view: Cranial face of pila cranialis flat (37).

Femur (Figs 7, 10W, 11E): Two right femora are available, one proximal half from the type locality and an almost complete one from Goldberg with slightly damaged distal end.

Shaft almost straight. Caudal view: well developed tuberculum as origin of the intermediate flexor muscles of the toes (38). Cranial view: Trochanter moderately surpassing caput femoris proximally (39); cranial linea intermuscularis simple, not bifurcate distally (40); linea proximally merging with crista trochanteris without reaching up to proximal margin (41).

Tibiotarsus (Fig. 8): Two left tibiotarsi are preserved; a complete one (adult) from the type locality, a distal half of a subadult specimen from the Goldberg locality.

Relatively stout and shaft slightly curved into medial concavity. Cranial view: apophysis interna ligamenti obliqui well-marked (42); spina fibulae fused with shaft (43); fusion well proximal of apophysis interna ligamenti obliqui (44); pons supratendineus lacking (45); groove proximal of area intercondylaris relatively shallow (46); lateral condyle slanted proximo-laterally (47). Medial view: Tiny tooth-like protuberance in proximal end of fossa plantaris (48); apophysis on crista cnemialis cranialis projecting distally (49); impressio ligamenti collateralis medialis well-marked (50); epicondylus medialis strongly protruding plantarly (51). Lateral view: Epicondylus lateralis strongly protruding plantarly (52).

Proximal view: Incisura tibialis deep and U-shaped (53). Distal view: Caudal rim of epicondylus medialis forming sharp edge (54).

Tarsometatarsus: In addition to the left holotype tmt a complete right tmt is preserved from the type locality. An additional juvenile left tmt

TABLE 1. Measurements (mm) of the type material for *Miotyto montispetrosi* nov. spec. from Steinberg and referred material from Goldberg. GL: greatest length, L: length, Wp: proximal width, Dp: proximal depth, Dgp: proximal diagonal (in the scapula cranial diagonal), Dgd: distal diagonal, WF: width of facies articularis basalis in coracoid, Ws: smallest width of shaft, Wd: distal width, Dd: distal depth, Wdg: maximal diagonal width of os carpi ulnare. *length medially, °width basally. Estimated measurements of slightly damaged bones are given in parenthesis.

		GL	L	Wp	Dp	Dgp	Ws	Wd	Dd	
Steinberg	BSPG 1970 XVIII									
coracoid dext.	872	(35)	(33)*					(13)°		WF: (12)
scapula dext.	873	(42)				9.6				
humerus dext., dist. 2/3	861						5.7	14.4		
humerus dext., prox. end	862			17.0						
reconstructed humerus: 861+862		*c*. 90								
ulna dext., prox. half	863			9.7		10.0	4.3			
ulna dext., dist half	874						4.4			Dgd: 7.5
ulna sin., prox. end	871			(9.5)		(10)				
os carpi ulnare dext.	876									Wdg: 8.2
os carpi ulnare sin.	877									Wdg: 8.1
phalanx digiti major. 1 dext.	875	20.1	20.0	7.2				4.4		
femur dext., prox. half	865			10.8	7.3		4.9			
tibiotarsus sin.	866	90.5	89.1			12.1	4.5	10.9	10.0	
tibiotarsus dext., dist half	870						4.9	11.0		
tarsometatarsus sin. (holotype)	867	55.1		10.4			5.5	11.8		
tarsometatarsus dext.	868	55.1		10.5			5.4	11.8		
os metacarpale I dext.	878		6.9					4.4		
os metacarpale I sin.	879		7.1					4.4		
phalanx I 1 dext.	880	12.7		4.6	5.0		3.0	3.5	3.9	
phalanx I 1 dext.	881	12.5		4.5	5.0		3.0	3.4	4.0	
phalanx II 1 dext.	882	13.0		7.0	6.3		3.8	4.5	5.2	
phalanx II 1 sin.	883	13.1		7.0	6.0		3.6	4.3	5.1	
phalanx II 2 dext.	884	17.6		5.0	5.1		4.0	4.2	4.1	
phalanx III 1 dext.	885	7.6		7.4	4.8		4.4	5.1		
phalanx III 1 sin.	886	7.6		7.3	5.1		4.3	5.2		
phalanx III 2 dext.	887	12.9		4.6			3.2	3.9	4.1	
phalanx III 2 sin.	888	12.9		4.6			3.2	3.8	4.2	
phalanx III 3 or IV 4 dext.?	889						3.6	3.7	3.7	
phalanx IV 1 dext.	890	4.8		6.7	5.0					
phalanx IV 2 dext.	891	5.0		5.3	4.1			4.0		
phalanx IV 3 dext.	892	6.8		4.7	4.5			4.0	4.0	
phalanx III 3 or IV 4 dext.?	893	14.4		4.3	4.6		3.5	3.8	3.8	
phalanx terminalis (claw)	894	(13.7)		3.8	5.0					
phalanx terminalis (claw)	895	13.9		3.3	5.1					
phalanx terminalis (claw)	896			3.0	4.9					
phalanx terminalis (claw)	897	13.8		3.8	4.9					
Goldberg	BSPG 1966 XXXIV									
coracoid sin.	3276									
femur dext.	3277	55	53.8*	11.1	(6.3)		4.6	10.5		
tibiotarsus sin. (subadult)	3279						4.7	9.5	9.5	
tarsometatarsus dext. (juvenile)	3278	(50)		(11.3)			4.3	(10.1)		

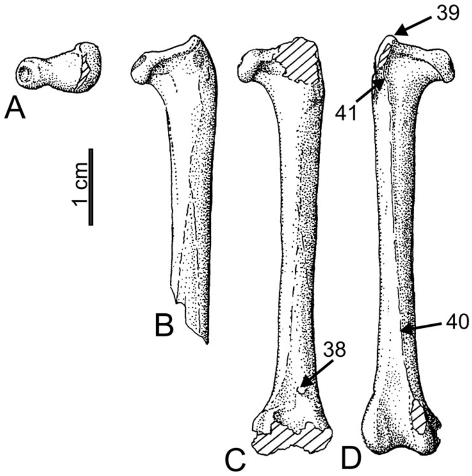

FIGURE 7. Femur dext. of *M. montispetrosi* nov. spec. from Steinberg (BSPG 1970 XVIII 865) (**A, B**) and from Goldberg (BSPG 1966 XXXIV 3277) (**C, D**). **A**) proximal, **B**) caudal, **C**) caudal, **D**) cranial.

comes from the Goldberg locality. For description see holotype.

Pedal phalanges (Figs 9A-J): 18 phalanges, including four claws, are preserved.

The three proximal phalanges of the reversible fourth toe are extremely short. Phalanx I 1 in proximal view notched on the plantar side (55); apophysis extensoris of phalanx II 2 less developed than apophysis flexoris (56); length of phalanx II 1 almost three quarters the length of phalanx II 2 (57); phalanx III 1 slightly more than half the length of phalanx III 2 (58); phalanx II 1 less than double the length of phalanx III 1 (59). (for indices see Tab. 3).

Four claws (Fig. 9J): are preserved, but cannot been assigned with certainty to the corresponding digits.

Taxonomic evaluation of the described characters

The most diagnostic characters of the described skeletal elements are listed in Tab. 2. Together they allow reference of the type material to the Strigiformes, more precisely to the Tytonidae.

A few characters listed in the text are not mentioned on Table 2 as they are purely descriptive and some others have received no numerical value because they describe to the general shape or proportions of a skeletal element. None of the features listed on Tab. 2 is a really unique one, which would, on its own, permit to place the fossil owl in question into a given taxon. But in combination they allow to allocate it accurately. The features listed as strigiform are characteristic of the order but are by no means exhaustive. Nonetheless, the postcranial skeleton of the Tytonidae is fairly well characterized by the features listed.

TABLE 2. Synopsis of diagnostic osteological features for *Miotyto montispetrosi* nov. spec. (numbers correspond to character numbering in description of material). * Ratios for the relative length of tarsometatarsus and coracoid are given on Tabs 4 and 5.

skeletal element	**osteological features**		
	strigiform	agree with Tytonidae	more specific characters
tarsometatarsus	12, 16	1,2,6,9,10,13,14	short and robust* 3,4, 5,7,8,15
coracoid	short and stout, 20, 22	17, 18, 19, 23,	short and stout*
scapula		24	25
humerus	shaft sigmoidal	27, 28, 30	
ulna	32, 33, 34		
phalanx prox. dig maj		36	37
femur	shaft straight, 39	40	41
tibiotarsus	42, 43, 45	46, 48, 50, 51, 52, 53	42, 47, 49
pedal phalanges	basal phalanges extremely short in reversible toe IV	55, 56, 57	59

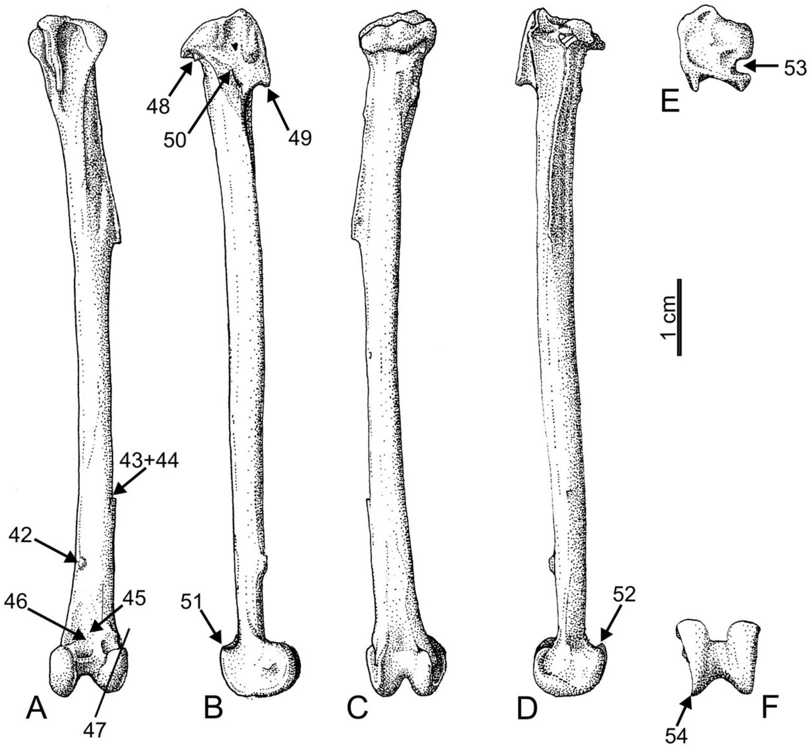

FIGURE 8. Tibiotarsus sin. (1970 XVIII 866) of *M. montispetrosi* nov. spec. from Steinberg. **A**) cranial, **B**) medial, **C**) caudal, **D**) lateral, **E**) proximal, **F**) distal.

Comparisons

Comparison with *Tyto (alba)*

The following features of *Miotyto montispetrosi* nov. spec. are of specific nature within the Tytonidae and some of them appear to have an intermediate character between recent *Tyto alba* and strigid owls. For a separate comparison with *Phodilus* see below and Fig. 11.

The tarsometatarsus of *M. montispetrosi* nov. spec. differs from *Tyto* by being shorter and stouter (see Fig. 10 and Tab. 4), a condition also found in most Strigidae and in Paleogene Tytonidae. The arcus extensorius (1) is not lacking completely as in *Tyto*, but vestigial if compared to Strigidae. The tuberositas m. tibialis cranialis is positioned lower on the shaft than in *Tyto* (3), a feature typical for Strigidae. The sulcus extensorius (4) is longer than in *Tyto*. Also the sulcus of trochlea III (5) is extending further proximally. The proximal part of the sulcus flexorius (7) is more deeply excavated than in *Tyto*, but less so than in Strigidae. The tuberculum m. fibularis brevis (15) is not merely directed plantarly as in *Tyto*, but is not drawn strongly in lateral direction as in strigids. The coracoid is shorter and stouter than in *Tyto.* The cranial face of the phalanx proximalis digiti majoris is flat unlike *Tyto* where it is concave (37). Cranially on the proximal end of the femur, the linea intermuscularis merges in a curve with the crista trochanteris , unlike *Tyto* where it is straight and reaches up to the facies articularis antitrochanterica (41). The lateral condyle of the tibiotarsus is more slanted proximo-laterally than in *Tyto*; the apophysis of the crista cnemialis cranialis projects distally (49) unlike *Tyto*; however this latter feature is potentially age-related and might identify the Steinberg owl as an aged individual.

In his description of the osteology of pedal phalanges of extant owls, Ford (1967) points out that, in *Tyto*, the two basal phalanges of the second toe, i.e. II 1 and II 2, are nearly equal in length, while in Strigidae phalanx II 1 is only about one half the length of phalanx II 2. This finding is supported by the index II 1/ II 2 in Tab. 3 which for *Tyto alba* is 0.8 while in recent Strigidae it is 0.5–0.6. Ford (1967) furthermore points out that, in the third toe of *Tyto* phalanx 1 is one half the length of phalanx 2 while in Strigidae

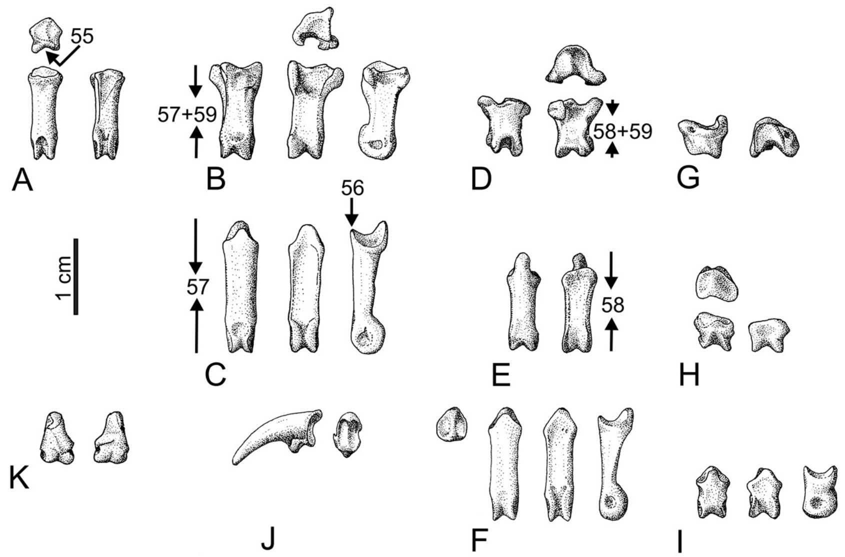

FIGURE 9. Pedal phalanges of the right foot and metatarsal I of the left foot of *M. montispetrosi* nov. spec. from Steinberg (BSPG 1970 XVIII…). **A**) phalanx I 1 dext. (881), **B**) phalanx II 1 dext. (882), **C**) phalanx II 2 dext. (884), **D**) phalanx III 1 dext. (885), **E**) phalanx III 2 dext. (887), **F**) phalanx III 3 or IV 4 dext? (889), **G**) phalanx IV 1 dext. (890), **H**) phalanx IV 2 dext. (891), **I**) phalanx IV 3 dext. (892), **J**) claw of uncertain toe affiliation (897), **K**) os metatarsale I sin. (879). **A**, **D**, and **H** in dorsal, plantar, and proximal view; **B** and **F** in dorsal, plantar, medial and proximal view; **C** and **I** in dorsal, plantar, and medial view; **K** and **E** in dorsal and plantar view; **G** in dorsal and proximal view; **J** in mediolateral and proximal view.

TABLE 3. Length and indices of selected pedal phalanges of extant and fossil Tytonidae and extant Strigidae. Measurements of extant species taken by the authors; measurements of *T. robusta* and *T. gigantea* from Ballmann (1973, 1976).

Length of pedal phalanges	mm **Ph II 1**	mm **Ph II 2**	mm **Ph III 1**	mm **Ph III 2**	Index **II 1 / II 2**	Index **II 1 / III 1**
extant Tytonidae						
Tyto alba (average, n=5)	12.5	15.5 (n=2)	6.3	12.7	0.8	2.0
fossil Tytonidae						
Tyto robusta (different individuals)	20.6 (n=3)	28.0 (n=1)	10.0 (n=1)	21.8 (n=2)	0.7	2.1
Tyto gigantea (different individuals)	26.0 (n=2)	40.0 (n=1)	13.5 (n=2)	28.8 (n=2)	0.7	1.9
M. montispetrosi nov. spec.	13.0	17.5	7.6	12.9	0.7	1.7
extant Strigidae						
Bubo bubo (average, n=2)	15.7	29.5	12.2	17.7	0.5	1.3
Bubo scandiacus (n=1)	12.3	23.3	9.5	14.9	0.5	1.3
Strix aluco (average, n=2)	10.4	17.6	7.3	11.9	0.6	1.4
Asio flammeus (n=1)	9.3	15.3	8.0	10.0	0.6	1.2
Asio otus (average, n=2)	9.1	15.6	6.8	10.0	0.6	1.3
Ninox novaeseelandiae (n=1)	9.0	–	8.0	10.0	–	1.1
Athene noctua (average, n=2)	6.8	10.9	5.2	7.4	0.6	1.3
Athene cunicularia (n=1)	6.2	10.0	5	7.1	0.6	1.2
Otus scops (n=1)	5.4	9.8	3.9	5.7	0.6	1.4
Glaucidium passerinum (n=1)	4.1	7.7	3.6	4.4	0.5	1.1

phalanges III 1 and III 2 are approximately the same length. Again, this is supported by the index III 1/ III 2 in Tab. 3 which is 0.5 for *Tyto* as compared to 0.6 – 0.8 for Strigidae. Consequently for the distinction of *Tyto* from Strigidae the index II 1/ III 1 might usefully be applied. It shows in fact (Tab. 3) a higher index value for *Tyto* (2.0) as compared to strigids (1.1–1.4).

The indices for the fossil species of *Tyto* on Tab. 3 fit well into the general picture if we consider that the measurements do not come from the same individuals.

In the first index (phalanx II 1/ II 2, feature 57) *M. montispetrosi* nov. spec. agrees with the other barn owls. In the other index (phalanx III 1/phalanx III 2, i.e. feature 58) *M. montispetrosi* nov. spec. is intermediate between *Tyto* and the strigids considered.

TABLE 4. Comparison of averaged metrical data and robustness-indices of tarsometatarsus (TMT) of Tertiary European Tytonidae. For comparison the recent European *Tyto alba* has been included. Measurements for *Necrobyas edwardsi, N. harpax, N. rossignoli, N. arvernensis, Sophiornis quercynus,* and *Palaeobyas cracrafti* from Mourer-Chauviré (1987, tab. 5), for *Prosybris antiqua* from Milne-Edwards (1867–1871), for *T. sanctialbani* from La Grive-Saint-Alban from Pavia & Mourer-Chauviré (2011), for *T. campiterrae* from Jánossy (1991) for *T. gigantea* from Ballmann (1973, 1976), and for recent European *Tyto alba* from Langer (1980).

			Tarsometatarsus						
species	**type locality**	**age**	**mean L**	**mean Wp**	**mean Wd**	**mean Ws**	**Wp/L**	**Wd/L**	**Ws/L**
P. cracrafti	Phosphorites du Quercy (F)	Eocene – Oligocene	~53.6 (n=1)	~16.5 (n=1)	~17.9 (n=1)	13.0 (n=1)	0.31	0.33	0.24
N. rossignoli	Phosphorites du Quercy (F)	Late Eocene	33.6 (n=8)	8.4 (n=7)	9.2 (n=8)	4.9 (n=7)	0.25	0.27	0.15
N. harpax	Phosphorites du Quercy (F)	Early Oligocene	37.1 (n=10)	9.1 (n=9)	10 (n=9)	4.9 (n=10)	0.25	0.27	0.13
N. edwardsi	Phosphorites du Quercy (F)	Late Oligocene	41.2 (n=6)	9.8 (n=5)	11 (n=5)	5.4 (n=9)	0.24	0.27	0.13
S. quercynus	Phosphorites du Quercy (F)	Late Oligocene	74.0 (n=1)	19.9 (n=1)	23.7 (n=1)	12.1 (n=1)	0.27	0.32	0.16
N. arvernensis	Staint-Gérand-le-Puy (F)	Early Miocene	43.8 (n=2)	9.8 (n=2)	11.6 (n=1)	4.1 (n=2)	0.22	0.27	0.09
P. antiqua	Saint-Gérand-le-Puy (F)	Early Miocene	34 (n=1)	6 (n=1)	6.5 (n=1)	3.0 (n=1)	0.18	0.19	0.09
M. montispetrosi nov. spec.	Steinberg (D)	Middle Miocene	55.1 (n=2)	10.5 (n=2)	11.8 (n=2)	5.5 (n=2)	0.19	0.21	0.10
T. sanctialbani	La Grive (F)	Middle Miocene	59.1 (n=2)	9.7 (n=6)	11.1 (n=17)	4.7 (n=16)	0.16	0.19	0.08
T. sp* (formerly *T. sanctialbani*)	Gargano, San Giovannino (I)	Late Miocene	77 (n=1)	12 (n=1)	–	–	0.16	–	–
T. campiterrae	Polgárdi (H)	Late Miocene	65.1 (n=2)	10.8 (n=9)	11.3 (n=5)	4.4 (n=3)	0.17	0.17	0.07
T. gigantea	Gargano, San Giovannino (I)	Late Miocene – Early Pliocene	129 (n=1)	21.6 (n=3)	25.6 (n=3)	–	0.17	0.20	–
T. alba, (males)	Europe	Recent	62.3 (n =11)	8.9 (n =11)	10.1 (n =11)	3.7 (n=11)	0.14	0.16	0.06
T. alba, (females)	Europe	Recent	58.7 (n=14)	9.0 (n = 14)	10.1 (n = 14)	3.9 (n=14)	0.15	0.17	0.07

* Formerly described as *T. sanctialbani* from Gargano, Italy (Ballmann 1973, 1976) is synonymized by Mlíkovský (1998, 2002) with *T. balearica,* whereas Louchart (2002: 73) suggests that it probably is a different (new) species (see also Pavia & Mourer-Chauviré 2011). However, it should be considered that the barn owls of Gargano were island inhabiting and show a remarkable increase in size. It is therefore the owl of the lowest stratigraphic level, *i.e.*, Biancone, which must be compared to *T. sanctialbani* from La Grive-Saint-Alban. The age of the Gargano faunas according to Masini *et al.* (2013) span from the Late Miocene to the Early Pliocene.

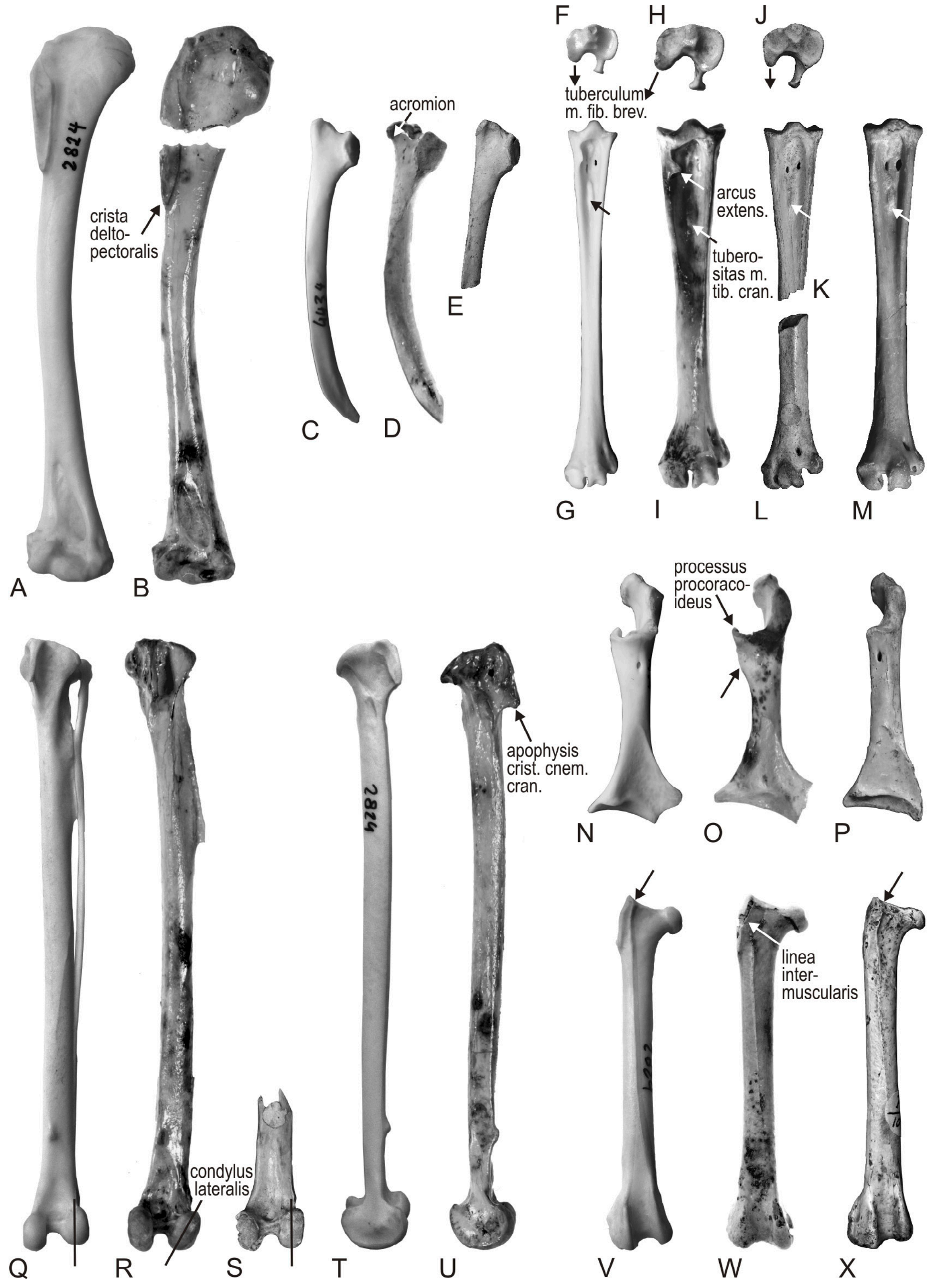

FIGURE 10. Selected distinguishing characters between *M. montispetrosi* nov. spec. (**B**, **D**, **H**, **I**, **O**, **R**, **U**, **W**), the extant *Tyto alba* (**A**, **C**, **F**, **G**, **N**, **Q**, **T**, **V**), and *Tyto sanctialbani* from La Grive-Saint-Alban (**E** invers, **J**, **K**, **L**, **M** invers, **P** invers, **S**, **X**). **A** and **B**) humerus dext. cranial view; **C-E**) scapula dext. lateral view; F-M) tarsometatarsus sin. proximal view (**F**, **H**, **J**), dorsal view (**G**, **I**, **K**, **L**, M); **N–P**) coracoid dext. dors. view; **Q-U**) tibiotarsus sin. cran. view (**Q–S**), medial view (**T**, **U**); **V–X**) femur dext. cran. view. Not to scale. Specimens of *T. alba* (**A**, **Q**, **T**, **V**: NHMW 2824 and **C**, **F**, **G**, **N**: NHMW 4434). Specimens of *T. sanctialbani* (**E**: NHMUK A345, **J**, **K**: NHMUK A305 lectotype, **L**: NHMUK A303 paralectotype, **M**: FSL 91627, **P**: NHMUK A324, **S**: NHMUK A304 paralectotype, **X**: NHMUK A1058; images of *T. sanctialbani* provided by M. Pavia (University Torino).

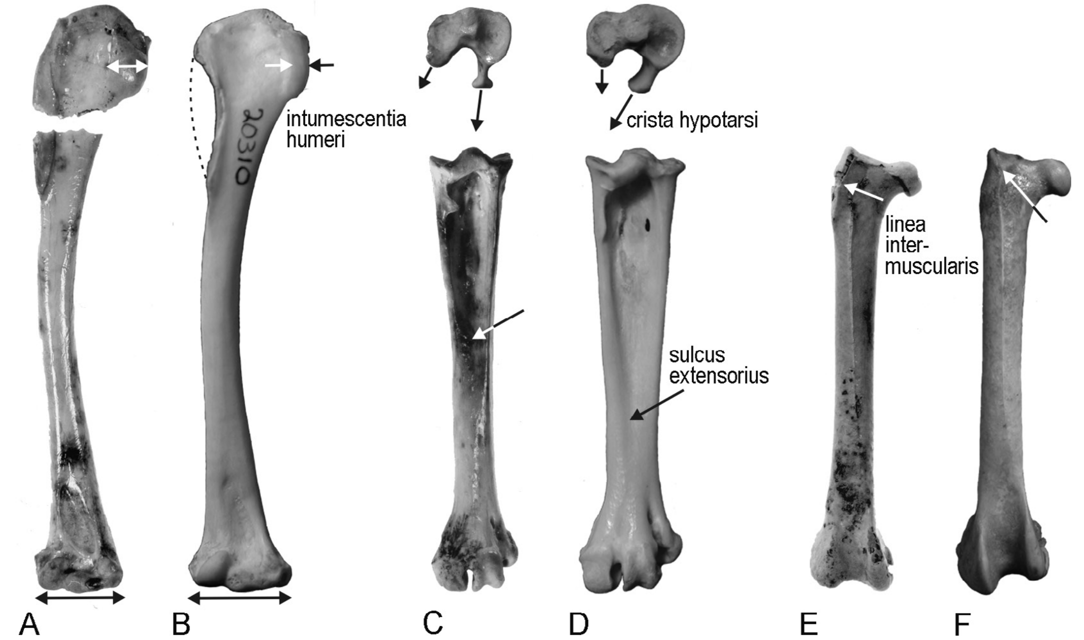

FIGURE 11. Selected distinguishing characters between *M. montispetrosi* nov. spec. (**A**, **C**, **E**) and *Phodilus badius* (USNM 20310) (**B**, **D** invers, **F** invers). **A** and **B**) humerus dext. cranial view, **C** and **D**) tmt sin. in dorsal and proximal view, **E** and **F**) femur dext. cranial view. Not to scale.

Comparison with *Phodilus* (Fig. 11)

The length of the tarsometatarsus of the measured specimen of *Phodilus badius* (USNM 20310) is 40.5 mm, the length of its femur is 46.0 mm. The index of tmt/femur of 0.8 compared to 1 for *M. montispetrosi* nov. spec. (see Tab. 5) shows that the tmt of *Phodilus* is markedly shorter in proportion. Furthermore, in *Phodilus* the sulcus extensorius on the tmt is longer than half the shaft and the crista hypotarsi more deflected in lateral direction (proximal view). On the slightly stouter femur the cranial linea intermuscularis does not merge proximally with the crista trochanteris but reaches up to the facies articularis antitrochanterica. The intumescentia humeri is clearly narrower in *Phodilus* than in *M. montispetrosi* nov. spec. and the distal end of the humerus is more extended to both sides. In *Phodilus* the relative sizes of the phalanges are much the same as in *Tyto* (Ford 1967), whereas *M. montispetrosi* nov. spec. occupies an intermediate position to the strigids in this respect (Tab. 3). Ford (1967) mentions that in *Phodilus* the pedal phalanges IV 1 and IV 2 are fused, which is not the case in *M. montispetrosi* nov. spec.. Unfortunately, pedal phalanges were not available for the investigated specimen USNM 20310.

Comparison with Palaeogene and Neogene Tytonidae

In Tab. 4 the pertaining species are listed including their type localities and measurements of their tmt.

The tmt of Paleogene owls, where it is known (*Sophiornis quercynus, Palaeobyas cracrafti)* is characteristically stout. The distal extremity of the humerus is broad, where documented (*Nocturnavis incerta*). The species of *Necrobyas* are smaller than *Miotyto montispetrosi* nov. spec. and their tmt again is stouter, especially its distal extremity is broader (Tab. 4). Starting with *Prosybris antiqua* in the Early Miocene the proportions of the tmt become more comparable to extant *Tyto*. *Prosybris antiqua* is very similar to *M. montispetrosi* nov. spec. by its tmt proportion, but is distinctly smaller; furthermore, its tuberculum m. fibularis brevis is shorter and directed plantarly. Of the Neogene barn owls of the genus *Tyto, T. campiterrae* is larger. The skeletal elements of *T. balearica* from the type locality Cova de Canet (Mallorca), of which the length is known (humerus: 102mm; coracoid: 45mm; phalanx II 2: 20.7 mm) are longer than the corresponding bones in *M. montispetrosi* nov. spec. Also its tmt, as far as preserved, is more slender than in *M. montispetrosi* nov. spec. The subspecies *T. balearica cyrneichnusae* from Corsica and Sardinia is also clearly of greater size and its tarsometatarsus is more slender.

Nearest in size and shape to *M. montispetrosi* nov. spec. is *T. sanctialbani* from the type locality La Grive-Saint-Alban (France) such as described by Lydekker (1893) and more recently by Pavia & Mourer-Chauviré (2011). There are, however, some morphological differences (see also Fig. 10). The tarsometatarsus of *M. montispetrosi* nov. spec. is shorter and stouter (Tab. 4). The ratio of length of tarsometatarsus and coracoid to the femur, respectively, shows that the proportions of the leg and shoulder girdle of *M. montispetrosi* nov. spec. were different (Tab. 5). On the tarsometatarsus the arcus extensorius (1) of *M. montispetrosi* nov. spec. is vestigial, whereas completely missing in *T. sanctialbani.* The sulcus extensorius (4) is shorter in *M. montispetrosi* nov. spec., reaching further distal in *T. sanctialbani*. The tuberositas m. tibialis cranialis (3) in *M. montispetrosi* nov. spec. is positioned slightly more distally on the shaft than in *Tyto sanctialbani.* The tuberculum m. fibularis brevis is directed plantolaterally in *M. montispetrosi* nov. spec. (15), while in *T. sanctialbani* it points in a purely plantar direction. In *M. montispetrosi* nov. spec. the trochlea III bulges less dorsally and its sulcus extends further proximally (5) than in *T. sanctialbani*. On the femur of *M. montispetrosi* nov. spec., the linea intermuscularis cranialis merges with the crista trochanteris (41) while in *T. sanctialbani* it reaches up to the facies articularis. The condylus lateralis on the tibiotarsus of *M. montispetrosi* nov. spec. is slanted proximolaterally (47) unlike in *T. sanctialbani.* The proportions of the pedal phalanges (57 and 59) in *M. montispetrosi* nov. spec. are diagnostic features, but cannot be compared to *T. sanctialbani* where the material is not complete enough.

Discussion and conclusions

The barn owl described here from the Middle Miocene (MN6) of the Nördlinger Ries represents a fossil genus near but not identical to *Tyto*. In a number of special characters (Tab. 2) it is distinct from *Tyto* and in some even resembles the Strigidae. *Prosybris antiqua* documented in the Early Miocene of Saint-Gérand-le-Puy (France), but possibly already present in the Oligocene of the Phosphorites of the Quercy

TABLE 5. Metrical comparison of *Miotyto montispetrosi* nov. spec. with *Tyto sanctialbani* from La Grive-Saint-Alban (measurements of the latter from Pavia & Mourer-Chauviré (2011)). Estimated measurements of slightly damaged bones are given in parenthesis.

	M. montispetrosi nov. spec from Steinberg and Goldberg			*T. sanctialbani* from La Grive-Saint-Alban		
	GL	**Wp**	**Wd**	**GL**	**Wp**	**Wd**
coracoid	(35)	–	(13)	37.8	–	–
humerus	*c.* 90	17.0	14.4	–	–	11.7–14.8 mean (n = 12) = 13.07
femur	55	10.8–11.1 (n = 2)	10.5	51.5–55.8 (n = 2)	9.5–11.4 mean (n = 3) = 10.13	8.9–11.8 mean (n = 13) = 10.08
tibiotarsus	90.5	–	10.9–11.0	–	–	9.0–10.3 mean (n = 10) 9.78
tarsometatarsus	55.1 (n = 2)	10.4–10.5 (n = 2)	11.8 (n = 2)	58.1–60.0 (n = 2)	9.3–10.0 mean (n = 6) = 9.6	10.4–11.9 mean (n = 17) = 11.06
phalanx I 1	12.5–12.7 (n = 2)	4.5–4.6 (n = 2)	3.4–3.5 (n = 2)	12.1	4.0	3.0
phalanx II 1	13.0–13.1 (n = 2)	7.0 (n = 2)	4.3–4.5 (n = 2)	13.1	6.6	4.2
index coracoid/femur	0.64			0.70		
index tmt/femur	1.00			1.08		

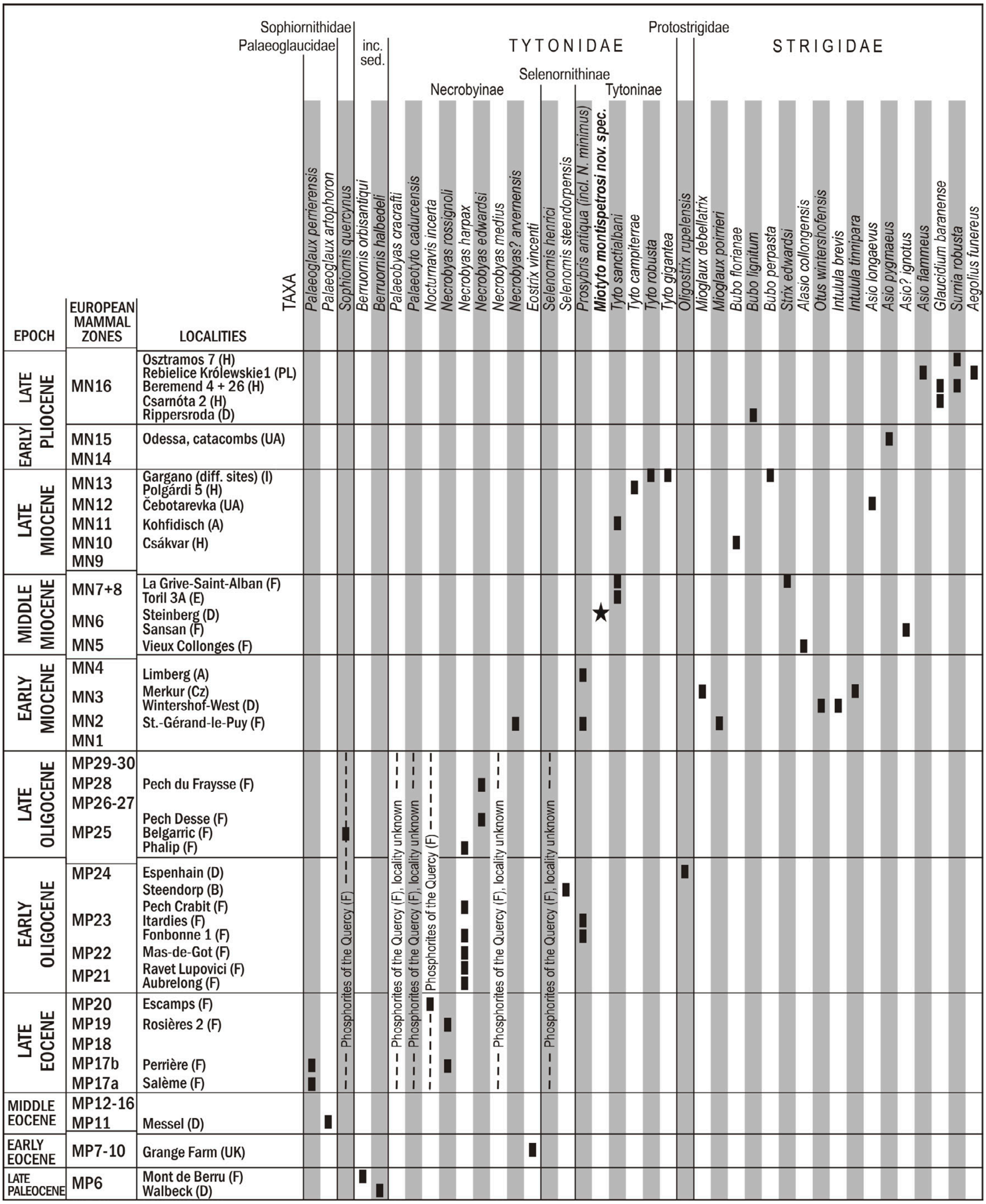

FIGURE 12. Fossil record of Paleogene and Neogene Strigiformes (taxa adjusted) in Europe. Stratigraphy of the Paleogene and Neogene and correlation between epochs and the European mammal zones follow Hilgen *et al.* (2012) and Vandenberghe *et al.* (2012), respectively. Epochs and mammal zones not to scale. Note: Following the Neogene Stratigraphy (Vandenberghe *et al.* 2012) of the International Stratigraphic Chart 2012, the Mammal Neogene unit MN17 is not part of the Pliocene anymore; therefore *T. balearica*, which can only be confirmed from MN17 on (Louchart 2002), is not considered in this figure.

(France) might be at the base of the Tytoninae. The Early Miocene Strigidae from Saint-Gérand-le-Puy (France), Wintershof-West (Germany), and Merkur (Czechia) can be considered to be the earliest typical owls known in Europe. We do not know when exactly the branching of the two families took place, but the Strigidae are younger. The extant genus *Phodilus* is credited with intermediate characters between the barn owls and the typical owls (Brodkorb, 1970). The comparison of *M. montispetrosi* nov. spec. with *Phodilus,* however, shows no special resemblance beyond the short tarsometatarsus without an ossified extensor loop (arcus extensorius). We may assume that *Phodilus* is a relict and that in the Middle Miocene and earlier a greater number of Strigiformes of intermediate systematic position existed.

Although distinguishable by several osteological details, as shown above, *M. montispetrosi* nov. spec. resembles most *T. sanctialbani* among European Miocene tytonids, especially in size and proportions; unfortunately, the proportions of the pedal phalanges (features 57 and 59) which are diagnostic for *M. montispetrosi* nov. spec., cannot be verified for *T. sanctialbani* as they are unknown to date.

M. montispetrosi nov. spec. is the only owl documented from the Middle Miocene deposits of the Nördlinger Ries and certainly most of the small-sized bird and small mammal remains (Heizmann & Fahlbusch 1983, Heizmann & Hesse 1995) originate from its regurgitated pellets. Probably the owl nested or had roosting places in crevices of the hills and spring mounds that emerged from the Ries crater lake.

At least one juvenile owl is documented by a tarsometatarsus and a tibiotarsus from the Goldberg 9 site. The presence of bones from a juvenile individual of *M. montispetrosi* nov. spec. indicates that the species was breeding at the Middle Miocene Ries Lake. A resident barn owl adds another species to the fossil bird fauna for the Nördlinger Ries indicative of warm climatic conditions.

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