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A palaeornithological assemblage from the early Pliocene of the Mediterranean island of Mallorca: Raptorial birds as bioaccumulators at Na Burguesa-1



Un assemblage paléornithologique du début du Pliocène de l'île méditerranéenne de Majorque : oiseaux rapaces comme bioaccumulateurs à Na Burguesa-1

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ABSTRACT

A palaeornithological assemblage from the early Pliocene of Mallorca (Balearic Islands) is documented on 583 fossil bones from Na Burguesa-1 site. Ten different taxa have been identified: two Tytonidae, one small-sized Strigidae, one Phasianidae, one Charadriiform, and at least five Passeriformes. The specimens included in the Tytonidae correspond to a giant Barn Owl, *Tyto* sp. 1, with size similar to *Tyto robusta*, and a second Barn Owl, *Tyto* sp. 2, similar in size to *Tyto sanctialbani*. The small-sized Strigidae is attributed to *Otus* sp., although some of the pedal phalanges obtained are included only tentatively in this genus. The presence of these nocturnal raptorial birds combined with the prevalence of small vertebrates (mainly ranging from ca. 8 g to almost 1 kg) with practically unaltered bones suggests that this deposit was originated by the accumulation of prey remains of these owls.

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RÉSUMÉ

Un assemblage paléo-ornithologique du début du Pliocène de Majorque (îles Baléares) est documenté à partir de 583 os fossiles obtenus dans le gisement de Na Burguesa-1. Dix taxons différents ont été identifiés dans cet assemblage : deux Tytonidae, un Strigidae de petite taille, un Phasianidae, un Charadriiforme et au moins cinq Passeriformes. Les fossiles inclus dans les Tytonidae correspondent à une chouette effraie géante, *Tyto* sp. 1, de taille similaire à *Tyto robusta*, et à une deuxième chouette effraie, *Tyto* sp. 2, de taille similaire à celle de *Tyto sanctialbani*. Les Strigidae de petite taille sont attribuées à *Otus* sp., bien que certaines

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des phalanges pédales obtenues ne soient attribuées à ce genre que de manière provisoire. La présence de ces rapaces nocturnes et celle, prédominante, de restes de petits vertébrés (dont la taille varie entre environ ca. 8 g et presque 1 kg), avec leurs ossements pratiquement inaltérés, permet d'interpréter l'origine du gisement comme une accumulation dérivée de la prédation par ces strigiformes.

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1. Introduction

The Balearic Islands form the most isolated archipelago in the Mediterranean Sea. They consist of two groups of islands: the Gymnesic Islands (Mallorca, Menorca and surrounding islets) and the Pityusic Islands (Eivissa, Formentera and surrounding islets). Before the arrival of the first humans in these islands, about 4300 years ago (Bover et al., 2016), the fauna and ecosystems present on both groups of islands were highly peculiar (Palmer et al., 1999). At that time, the community of terrestrial vertebrates in the Pityusics did not have terrestrial mammals and consisted only of birds, bats, the endemic Pityusic lizard *Podarcis pityusensis*, and an extinct endemic snake recently discovered (Torres-Roig et al., in press). In contrast, on the Gymnesics lived an endemic terrestrial vertebrate fauna consisting of three non-flying endemic mammals (a dwarf and highly modified bovid, *Myotragus balearicus*; a large-sized dormouse, *Hypnomys morpheus*, and a shrew, *Nesiotites hidalgo*), the endemic Balearic lizard *Podarcis lilfordi*, the endemic Mallorcan midwife toad *Alytes muletensis*, plus birds and bats (Bover, 2011). All these faunas were the result of a complex palaeogeographic and evolutionary history that started 5.3 million years ago (Mya), at the end of the Messinian Salinity Crisis (MSC), when the Balearic Islands arose as separated entities isolated from their neighbouring continental landmasses.

Bover et al. (2008) established that three different faunistic assemblages lived in Mallorca, Menorca, and Eivissa during the Pliocene. While the foregoing *Myotragus* fauna lived in Mallorca, Menorca was inhabited by a peculiar fauna characterized by the presence of the giant leporid *Nuralagus rex*, the giant glirid *Muscardinus cyclopeus* and a giant tortoise, aff. *Titanochelon gymnesica* (Bate, 1914; Luján et al., 2017; Quintana et al., 2011). In Eivissa, the early Pliocene was characterised by the presence of a giant and not yet formally described gerbillid, *Debruijnimys* sp. (Moyà-Solà et al., 1984, 1999). On Menorca, the *Nuralagus* fauna was later replaced by the *Myotragus* fauna of Mallorca, since both islands merged for the first time during the first glaciation event, roughly 2.58 Mya ago (Bover et al., 2008). The geographic isolation between the Pityusics and the Gymnesics has remained unchanged and as it currently stands since 5.3 Mya until the present.

The recent discovery of two early Pliocene paleontological sites in Mallorca has enabled one to shed light on the oldest faunistic assemblage present on the Balearics. First, the discovery of the Caló den Rafelino deposit, which yielded the ancestors of the classic triad of mammals of the *Myotragus* fauna together with the giant and highly modified cricetid *Tragomys macpheeii*, the leporid *Hypolagus balearicus*, and several reptiles (a large-sized tortoise, a

giant viper, a large-sized lizard, and others; see Bover et al., 2014, for a review of this deposit). Later on, the fossiliferous karstic deposit of Na Burguesa-1 (hereafter, NB-1) was discovered and it has become a key site to understand the origin of the endemic *Myotragus* fauna from Mallorca (e.g., Bover et al., 2014; Mas et al., 2017; Torres-Roig et al., 2017, 2019a, and in press). The aim of the present paper is to describe the bird assemblage recovered at NB-1 and analyse the key role that nocturnal birds of prey have played in the formation of this vertebrate deposit. This sample represents the best available window to know the peculiar vertebrate faunal assemblage that lived in Mallorca ca. 5 million years ago.

2. The NB-1 deposit

The NB-1 deposit is located in the Na Burguesa mountains, on the southwestern part of the Serra de Tramuntana range of Mallorca (Balearic Islands, western Mediterranean; Fig. 1). It consists of a fossil-rich breccia infilling a palaeocave or fissure excavated in lower Lias grey limestone, situated at 160 m asl, close to the road from Génova to Mirador de Na Burguesa (Palma). Nowadays, this ancient cavity is completely eroded and only the infilling sediments are preserved as isolated blocks. The breccia consists of sharp pebbles of limestone embedded in a matrix of red-brown silts strongly cemented by calcite. The recovered blocks contain layers with abundant remains of small vertebrates (Bover et al., 2014).

3. Material and methods

The palaeornithological material obtained at NB-1 consists of 583 fossil bird bones curated at the “Institut Mediterrani d'Estudis Avançats” (acronym: IMEDEA; see Supplementary Table 1) of which ca. 90% are pedal phalanges of low taxonomic value. Furthermore, the fragmentary condition of an important part of the rest of the material recovered precludes its taxonomic identification beyond the genus level. Up to 321 bones have been diagnosed below the class level, of which 200 have been identified at order level and 121 at the genus level.

The fossils were recovered using a chemical treatment to dissolve the breccia blocks. The preparation task, which lasted up to two years, consisted of cyclic immersions of these blocks in acetic acid (10–15%) for 48 h, then in water for 48 h, air-drying, and consolidation of bones with a thermoplastic acrylic resin (Paraloid B-72). Once extracted, the bones were manually cleaned to eliminate the remains of the adhesive matrix.

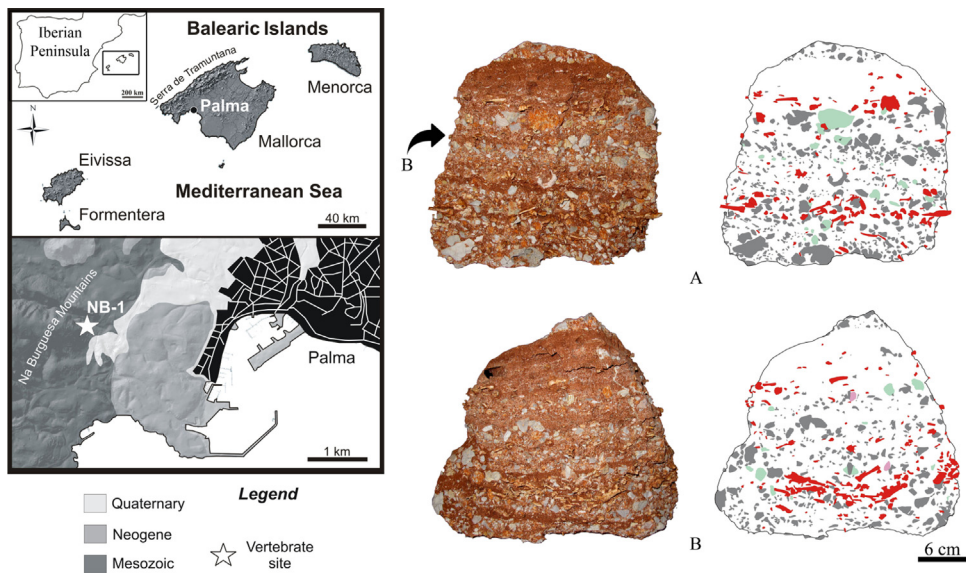


Fig. 1. Geological and geographical location of the early Pliocene palaeontological site of Na Burguesa-1 (NB-1) with details and schematic illustration of a fossiliferous breccia block from the deposit here studied from two different views (A and B). The different bone elements are highlighted in red, clasts of limestone in grey, clasts of sterile breccia resedimented in green, and speleothem clasts in pink.

Fig. 1. Localisation géologique et géographique du site paléontologique du Pliocène inférieur de Na Burguesa-1 (NB-1) avec le détail et l'illustration schématique d'un bloc de brèche fossilifère en provenance du dépôt ici étudié, selon deux vues différentes (A et B). Les différents éléments osseux figurent en rouge, les clastes de calcaire en gris, les clastes de brèche stérile resédimentés en vert et les clastes de spéléothème en rose.

The NB-1 bird bones were identified by direct comparison with material curated at the osteological bird collection of the “Institut Mediterrani d’Estudis Avançats” (Esporles, Mallorca; acronym of the collection: IMEDEA; see Supplementary Table 2), and using the available bibliography for each identified taxon (e.g., Bock and McEvey, 1969; Dyke et al., 2003; Fitzgerald, 1969; Ford, 1967; Holman, 1964; Langer, 1980; Louchart, 2002; Lydekker, 1893; Milne-Edwards, 1869–1871; Olson, 1976).

Measurements of bird long bones were taken when possible following the criteria of von den Driesch (1976) or Mourer-Chauviré (1975). Body mass for the different bird taxa, when possible, was estimated using two approaches: (a) the equation for the femur $Y = -0.069X^{2.414}$, where Y = body mass and X = perimeter of the femur diaphysis (Campbell & Marcus, 1992), estimating the diameter as the average of the depth and width of the diaphysis, and (b) $Y = 0.56X^{0.342}$ (Olmos et al., 1996), where Y = femur length and X = body mass. We estimated the body mass of the potential prey of the recorded raptorial birds (i.e. small mammal bones from NB-1) using the allometric equations to predicting body mass (Y) of Moncunill-Solé et al., 2014; Moncunill-Solé et al., 2015; Moncunill-Solé et al. (2014, 2015, 2016): $Y = 0.323X^{0.960}$, where X = distal humeral antero-posterior diameter, for murids and glirids; $Y = 0.009X^{0.935}$, where X = distal femoral transverse diameter, for the cricetid and for one adult glirid; $Y = 0.498X^{2.217}$, where X = proximal transversal diameter, for a femur of an adult leporid; $Y = 1.13X^{2.553}$, where X = distal antero-posterior diameter, for a humerus of an adult leporid; and $Y = 0.219X^{2.577}$, where X = proximal tibia transversal diameter, for young leporids (see Supplementary Table 3).

The micro-specimens were examined under a Leica S8 APO stereomicroscope and images were obtained with a digital camera Leica DFC420 digital camera. Macro-specimens images were obtained with a Cannon EOS 1200D. The nomenclature used in the description follows Livezey and Zusi (2006). The specific identity of all specimens remains unsolved, and for this reason we applied to them an open nomenclature following Bengtson (1988).

4. Systematic palaeontology

4.1. Order Strigiformes (Wagler 1830)

Extant species used for comparison: Tytonidae: *Tyto alba*. Strigidae: *Strix aluco*, *S. uralensis*, *S. nebulosa*, *Asio otus*, *A. flammeus*, *Athene noctua*, *Aegolius funereus*, *Bubo*, *Otus scops*, *Glaucidium passerinum*, *Surnia ulula*. Extinct species used for comparison: Tytonidae: *Tyto balearica* (type series), *Tyto ostologa*. Strigidae: *Athene cretensis*, *Athene vallgornerensis*, *Otus fruticosi* (See Supplementary Table 2).

The members of this order present a skeleton with numerous diagnostic features (e.g., Milne-Edwards, 1869–1871). The most characteristic osteological trait is the presence of an ossified arch in the radius, the arcus origo musculi extensor longus digiti majoris (Bock and McEvey, 1969). The osteological differences between Tytonidae and Strigidae have been described by many authors (e.g., Arredondo and Olson, 1994; Ballmann, 1973, 1976; Ford, 1967; Louchart, 2002; Lydekker, 1893; Mourer-Chauviré, 1987; Pavia, 2004; Steadman and Hilgartner, 1999; Suárez and Olson, 2015, among others). Unlike the Strigidae, in Tytonidae the first and second toes present the same

Table 1Measurements (mm) of *Tyto* sp. 1, *Tyto* sp. 2 from Na Burguesa-1 and different extinct and extant *Tyto* species.**Tableau 1**Mesures (en mm) de *Tyto* sp. 1 et *Tyto* sp. 2 de Na Burguesa-1 et de différentes espèces de *Tyto* éteintes et actuelles.

		<i>Tyto</i> sp. 1	<i>Tyto</i> sp. 2	<i>Tyto balearica</i>	<i>Tyto balearica cyrneichnusae</i>	<i>Tyto robusta</i>	<i>Tyto mourerchauvirae</i>	<i>Tyto sanctialbani</i>	<i>Tyto alba</i>
Radius	Bp	6.1		5.7 ^b	5.25–5.45 ^b n = 3	–	–	–	3.68–4.28 ^g n = 11
	SC	3.4	2.5	3.5 ^b	2.75–3.05 ^b	–	–	–	1.8–2.2e n = 26
	Bd		7.2		7.1–7.9 ^b n = 4	–	–	–	5.5–6.6e n = 25
Coracoid	Lm	43.5		42.1 ^b	38.0–40.5 ^b n = 5	–	–	34.9–35.7 ^a n = 3	30.4–37.0 ^c n = 26
	SC	6.4		5.4–5.9 ^b n = 3	4.7–5.6 ^b n = 10	–	–	4.1–4.8 ^b n = 4	3.4–4.6 ^c n = 26
Scapula	Dic	11.8		–	–	–	–	–	3.3–4.3e n = 33
	LAF	8.3		–	–	–	–	5.2 ^a	7.7–9.5e n = 32
	WAF	4.8		–	–	–	–	3.7 ^a	4.74–5.97 n = 11
Femur	GL	68.8		–	62.9–67.2 ^b n = 4	–	74.3–85.5 ^f n = 4	51.5–55.8 ^a n = 2	46.4–53.7e n = 34
	Lm	65.9		–	59.8–65.1 ^b n = 5	–	–	–	44–51.2e n = 34
	Bp	15.2		–	12.0–13.1 ^b n = 16	16 ^d	15.2–17.5 ^f n = 6	9.5–11.4 ^a n = 3	8.5–10.1e n = 34
	SC	6.5		6–(5.6) ^b n = 2	5.3–6.3 ^b n = 25	–	6.4–7.7 ^f n = 6	4.3–5.0 ^a n = 12	3.8–4.4e n = 34
	Bd	15.3		12.6–12.7 ^b n = 2	11.9–13.5 ^b n = 11	15 ^d	16.0–18.9 ^f n = 5	8.9–11.8 ^a n = 13	8.9–10.5e n = 34

Bd: breadth of the distal end; Bp: breadth of the proximal end; Dic: greatest cranial diagonal diameter; GL: greatest length; LAF: length of the articular facet; Lm: medial length; SC: smallest breadth of the corpus; WAF: width of the articular facet. ^e*Tyto alba/guttata*, in Louchart, 2002.

^a Pavia and Mourer-Chauviré (2011).

^b Louchart (2002).

^c Pavia et al. (2015).

^d Ballmann (1973).

^f Pavia, 2004. Measurements of *Tyto* spp. bones, in mm.

^g See Supplementary Table 4.

Table 2Measurements (mm) of *Otus* sp. from Na Burguesa-1, *Otus scops* and *Athene noctua*.**Tableau 2**Mesures (mm) d'*Otus* sp. de Na Burguesa-1, *Otus scops* et *Athene noctua*.

		<i>Otus</i> sp.	<i>Otus scops</i>	<i>Athene noctua</i>
Ulna	Bp	5.0	4.7–5.1 n = 11	4.9–6 n = 9
	SC	2.4	1.9–2.3 n = 11	2.3–2.7 n = 9
Femur	Bp	6.1	5.4–6.1 n = 11	5.9–7.3 n = 9
	Bd	6.5	5.1–5.9 n = 11	6.4–7.4 n = 9
	SC	2.8	2.3–2.5 n = 11	2.9–3.3 n = 9
Tibiotarsus	Bd	6.2	4.9–5.5 n = 11	6.5–7.2 n = 9
	SC	2.6	2.1–2.4 n = 11	2.6–3.2 n = 9

Bd: breadth of the distal end; Bp: breadth of the proximal end; SC: smallest breadth of the corpus.

length. Both basal phalanges of the second toe in Tytonidae are very similar, while in Strigidae the first phalanx of the second toe is only half as long as the second phalanx; Ford, 1967. The tarsometatarsus of the Tytonidae lacks a retinaculum extensorium osseum or arcus extensorius (bony loop), whereas the premaxilla is more elongated than in the Strigidae.

4.2. Family Tytonidae Ridgway 1914

The material included herein is referred to Tytonidae and differs from the Strigidae from the western Palaearctic by the following combination of osteological features: coracoid with scapular end less voluminous and not pneumatized; facies articularis scapularis, facies articularis

sternalis and foramen nervi supratoracoides proportionally smaller; facies articularis humeralis proportionally larger; procoracoideus process wide and shorter. Femur with a trochanterian edge more vertical; medial and lateral condyles more forwardly oriented; medial condyle larger in internal view, with a cranial margin that joins the diaphysis stepwise; a wide lateral epicondyle in lateral view; tubercle for the M. gastrocnemialis lateralis located distally. The scapula has the lateral region of the acromion less laterally projected than in the Strigidae, while the costal side of the acromion is more developed; the articularis humeralis facet is more elongated (oval) than in the Strigidae; the acromion is not pneumatized, contrary to the usual condition in the Strigidae (except *Otus*). In Tytonidae, the radius presents a cotyla humeralis more rounded than in the Strigidae, where it is narrower dorso-ventrally; finally, the distal end of the radius presents a concavity better marked in its medial tubercle in the Tytonidae.

The genus *Tyto* is known at least from the Middle Miocene (MN7 to MN10), with *Tyto sanctialbani* (Ballmann, 1969; Lydekker, 1893; Pavia and Mourer-Chauviré, 2011). The taxonomy of the Miocene and Pliocene species of *Tyto* is controversial. In the Late Miocene of eastern Europe is known *Tyto campiterra*, which is larger and slender than *Tyto sanctialbani* (Jánosy, 1991). However, there are other Miocene taxa without resolved identity (Pavia & Mourer-Chauviré, 2011). Two Mediterranean giant insular barn owls, *Tyto robusta* and *Tyto gigantea*, both described from Gargano, lived during the Late Miocene/Early Pliocene, while during the Early/Middle Pleistocene appears *Tyto balearica* in the fossil record, also a giant species, but smaller than the Gargano taxa. The description of *Tyto balearica* was based on bones from the Gymnesic Islands (Mallorca and Menorca; Mourer-Chauviré et al., 1980), and the species was later identified in many localities on the mainland (e.g., Mourer-Chauviré & Sánchez-Marco, 1988), although the attribution of all this continental material should be re-evaluated (e.g., Louchart, 2002). Remains from Pleistocene sites in Corsica and Sardinia were described as a subspecies, *Tyto balearica cyrneichnusae*, which could be potentially raised to species status (Pavia et al., 2012). *Tyto mourerchauvirae* was described from the Middle Pleistocene of Sicily, displaying a size similar to *Tyto robusta*. Some other large continental Barn Owls probably represent species pending description (Louchart, 2002).

4.3. Genus *Tyto* Billberg 1828

4.3.1. *Tyto* sp. 1 (size similar to *Tyto robusta* Ballmann, 1973)

Material: IMEDEA 106330, near complete left femur. IMEDEA 106331, near complete right coracoid. IMEDEA 106332, proximal fragment of right radius. IMEDEA 106333, humeral fragment of right scapula (Fig. 2A–D).

The material included under *Tyto* sp. 1 has a size very similar to *Tyto robusta* from Gargano. The minimum number of individuals (MNI) in the deposit is one. Some of their measurements (see Table 1) fall also within the range of measurements of *Tyto mourerchauvirae* from Sicily, while others are slightly smaller (see Table 1). Some morphological traits (e.g., femoral characters 3 and 9 of Ballmann,

1973) are not in full agreement with the description of *Tyto robusta*, although the actual range of variability of *Tyto robusta* and *Tyto* sp. 1 remains unknown. Additionally, *Tyto* sp. 1 shares some diagnostic characters of *Tyto mourerchauvirae*, but much less developed than in this species (such as a very small tubercular prominence in the tubercular part of the linea intermuscularis cranialis and a relatively wide distal epiphysis of the femur). The body mass of *Tyto* sp.1 has been estimated at ca. 1200 g on the basis to its femoral diaphysis diameter (Campbell and Marcus, 1992) and, although the trochanter of IMEDEA 106330 is slightly damaged, a body mass about 1360 g has been estimated on the basis of its femoral length (Olmos et al., 1996).

4.3.2. *Tyto* sp. 2 (size similar to *Tyto sanctialbani* [Lydekker, 1893])

Material: IMEDEA 107594, distal fragment of right radius (Fig. 2E).

This distal fragment of radius is slightly larger than in *Tyto alba*, and considerably smaller than in *Tyto robusta*. (see Table 1). It corresponds to a Barn Owl of similar size to *Tyto sanctialbani* (Lydekker, 1893), but no radii of this species have ever been found. Differences in size have been eventually interpreted as a result of sexual dimorphism (e.g., Pavia, 2004), but the lack of such sexual dimorphism in bones of extant *Tyto alba* do not show such sexual dimorphism in bones (see measurements in Langer, 1980) leads us to consider that fossil Barn Owls of different sizes actually represent different species. As the differences in size between the radii IMEDEA 106332 from *Tyto* sp. 1 (see above) and IMEDEA 107594 are considerable (diaphysis diameter 26.5% larger in the former), and as on various islands (e.g., Cuba, Gargano), two different species of *Tyto* coexisted, we can suggest that the radius IMEDEA 107594 actually belongs to a species different to *Tyto* sp. 1.

4.4. Family Strigidae (Vigors 1825)

4.4.1. Genus *Otus* Pennant 1769

4.4.1.1. *Otus* sp.. Material: IMEDEA 106998, distal fragment of right tibiotarsus (Figs. 3–5

). IMEDEA 106999, left pedal phalanx I of toe 3. IMEDEA 107000, proximal fragment of right ulna. IMEDEA 107620, pedal phalanx. IMEDEA 107625, pedal phalanx. IMEDEA 107626, pedal phalanx. IMEDEA 107627, pedal phalanx. IMEDEA 107628, pedal phalanx. IMEDEA 107629, pedal phalanx. IMEDEA 107630, pedal phalanx. IMEDEA 107631, pedal phalanx. IMEDEA 107632, pedal phalanx. IMEDEA 107633, pedal phalanx. IMEDEA 107634, right pedal phalanx III of toe 4. IMEDEA 107635, left pedal phalanx IV of toe 3. IMEDEA 107636, left pedal phalanx I of toe 1. IMEDEA 107637, left pedal phalanx III of toe 3. IMEDEA 107638, left pedal phalanx IV of toe 4. IMEDEA 107639, left pedal phalanx II of toe 2. IMEDEA 107640, pedal phalanx. IMEDEA 107641, pedal phalanx. IMEDEA 107642, pedal phalanx. IMEDEA 107643, sternum fragment. IMEDEA 107644, right pedal phalanx I of toe 2. IMEDEA 107645, proximal fragment of left femur. IMEDEA 107646, distal fragment of right femur. IMEDEA 107647, proximal fragment of right femur. IMEDEA 107648, pedal phalanx.



Fig. 2. Comparison of *Tyto* sp. 1 (specimens A–D) and *Tyto* sp. 2 (specimen E) from NB-1, with *Tyto alba* (specimens F–I) and *Tyto balearica* (specimens J–L). Specimen A (IMEDEA 1063316), right coracoid in dorsal (left) and ventral (right) views; specimen B (IMEDEA 106333), proximal fragment of right scapula in costal (left) and lateral (right) views; specimen C (IMEDEA 106332), proximal fragment of right radius in dorsal, medial and ventral views (from left to right); specimen D (IMEDEA 106330), left femur in cranial, caudal and medial views (from left to right); specimen E (IMEDEA 107594), distal fragments of right radius in dorsal (top), lateral (bottom left) and ventral (bottom right) views; specimen F (IMEDEA 106870), right coracoid in dorsal (left) and ventral (right) views; specimen G (IMEDEA 21884), right scapula in costal (left) and lateral (right) views; specimen H (IMEDEA 21884), right radius in dorsal, lateral and ventral views (from left to right); specimen I (IMEDEA 106870), left femur in cranial, caudal and medial views (from left to right); specimen J (IMEDEA 473), left coracoid in dorsal (left) and ventral (right) views; specimen K (IMEDEA 481), proximal fragment of right scapula in costal (left) and lateral (right) views; specimen L (IMEDEA 477), distal fragment of right femur in cranial, caudal and medial views (from left to right).

Fig. 2. Comparaison de *Tyto* sp. 1 (spécimens A–D) et *Tyto* Sp. 2 (spécimen E), en provenance de NB-1, avec *Tyto alba* (spécimens F–I) et *Tyto balearica* (spécimen J–L). Spécimen A (IMEDEA 1063316), coracoïde droit en vues dorsale (gauche) et ventrale (droite) ; spécimen B (IMEDEA 106333), fragment proximal de scapula droite en vues costale (gauche) et latérale (droite) ; spécimen C (IMEDEA 106332), fragment proximal de radius droit en vues dorsale, médiale et ventrale (de gauche à droite) ; spécimen D (IMEDEA 106330), fémur gauche, en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen E (IMEDEA 107594), fragments distaux de radius droit en vues dorsale (en haut), latérale (en bas à gauche) et ventrale (en bas à droite) ; spécimen F (IMEDEA 106870), coracoïde droit en vues dorsale (gauche) et ventrale (droite) ; spécimen G (IMEDEA 21884), scapula droite en vues costale (gauche) et latérale (droite) ; spécimen H (IMEDEA 21884), radius droit en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen I (IMEDEA 106870), fémur gauche en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen J (IMEDEA 473), coracoïde gauche en vues dorsale (gauche) et ventrale (droite) ; spécimen K (IMEDEA 481), fragment proximal de scapula droite en vues costale (gauche) et latérale (droite) ; spécimen L (IMEDEA 477), fragment distal de fémur droit en vues crânienne, caudale et médiale (de gauche à droite).

The material listed above belongs to a small Strigidae that falls in the size range of *Otus scops* and *Athene noctua* (see Table 2 and Supplementary Tables 4 and 5). The obtained fossils are slender than those of *Aegolius*, *Glaucidium* and *Surnia*. Thus *Otus* and *Athene* are the best candidates, amongst European owls, to explore the taxonomical affinities of the fossil strigid present at NB-1. The osteological discrimination between *Athene* and *Otus* was initially approached by Olson and Hilgartner (1983). Ulna: the cotyla dorsalis, in proximal view, is not internally pointed and its facies articularis radialis is deeper and better defined in *Athene* than in *Otus*. Femur: the trochanterian edge is more developed in *Athene* than in *Otus*. Tibiotarsus: the tendon concavity is deeper in *Athene* than in *Otus*; in cranial view, the condyles are practically parallel in *Athene*,

while in *Otus* the medial condyle is medially inclined to its distal end. In addition to these characteristics, we used *Otus scops* and *Athene noctua* as representatives of both genera to establish new discrimination criteria. Sternum: the labrum externum sterni is more projected in *Athene* than in *Otus*, whereas *Athene* usually displays a small concavity in the ascendant part from the side of the ridge closest to the labrum, while it is absent in *Otus*. The long bones and sternum of the NB-1 strigid fit better to *Otus* than to *Athene*. Regarding pedal phalanges, phalanx I 1: the tuberculum flexorum is poorly developed as in *Otus*, whereas it is larger in *Athene*; the ventral margin of the phalanx has a continuous profile between the caput phalangis and the tuberculum flexorum as in *Otus*, while in *Athene* it is interrupted by a pointed prominence. Phalanx I 2: it lacks a small

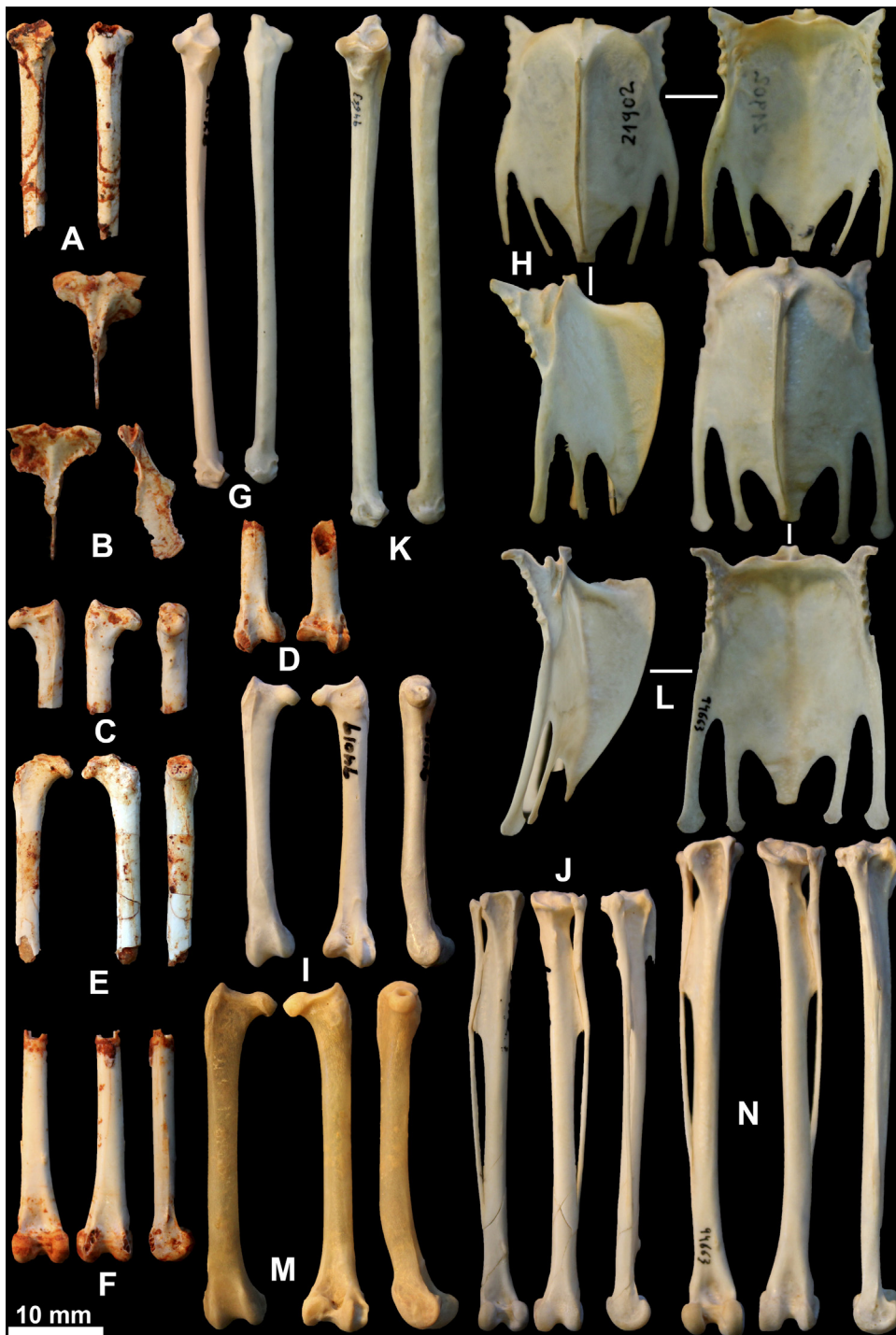


Fig. 3. Comparison of *Otus* sp. (specimens A–F) from NB-1 with *O. scops* (specimens G–J) and *Athene noctua* (specimens K–N). Specimen A (IMEDEA 107000), proximal fragment of right ulna in palmar (left) and anconal (right) views; specimen B (IMEDEA 107643), sternum fragment in ventral (top), dorsal (bottom left) and lateral (bottom right) views; specimen C (IMEDEA 107645), proximal fragment of left femur in cranial, caudal and medial views (from left to right); specimen D (IMEDEA 107646), distal fragment of right femur in cranial, caudal and medial views (from left to right); specimen E (IMEDEA 107647), proximal fragment of right femur in cranial (left) and caudal (right) views; specimen F (IMEDEA 106998), distal fragment of right tibiotarsus in cranial, caudal, and lateral views (from left to right); specimen G (IMEDEA 94019), right ulna in palmar (left) and anconal (right) views; specimen H (IMEDEA 21902), sternum in ventral (top left), dorsal (top right) and lateral (bottom) views; specimen I (IMEDEA 94019), right femur in cranial, caudal and medial views (from left to right); specimen J (IMEDEA 94019), right tibiotarsus in cranial, caudal, and lateral views (from left to right); specimen K (IMEDEA 94663), right ulna in palmar (left) and anconal (right) views; specimen L (IMEDEA 94663), sternum in ventral (top), dorsal (bottom right) and lateral (bottom left) views; specimen M (IMEDEA 21717), right femur in cranial, caudal and medial views (from left to right); specimen N (IMEDEA 94663), right tibiotarsus in cranial, caudal, and lateral views (from left to right).

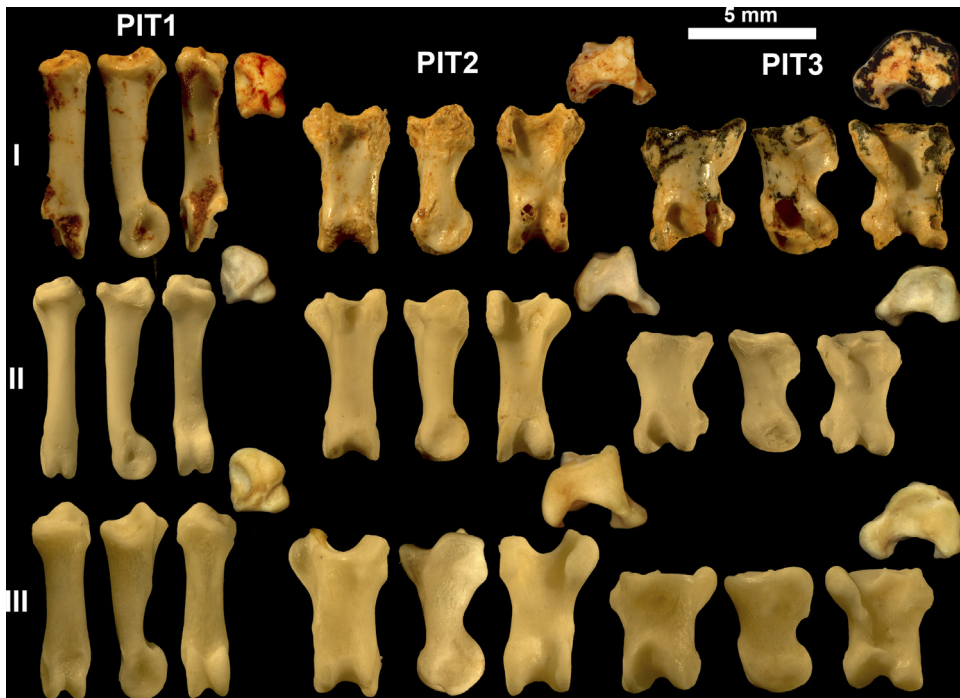


Fig. 4. Comparison of proximal pedal phalanges. PIT1, phalanx I toe 1; PIT2, phalanx I toe 2; PIT3, phalanx I toe 3. Row I: *Otus* sp. from NB-1 (left PIT1 IMEDEA 107636, right PIT2 IMEDEA 107644 and left PIT3 IMEDEA 106999). Row II: *O. scops* (IMEDEA 94019). Row III: *Athene noctua* (IMEDEA 21717). Views in dorsal, lateral, ventral, and proximal (from left to right).

Fig. 4. Comparaison des phalanges à pédales proximales. PIT1, phalange 1 doigt 1 ; PIT2, phalange 1, doigt 2 ; PIT3, phalange 1, doigt 3. Rangée I : *Otus* sp. de NB-1 (PIT 1 gauche IMEDEA 107636, right IMEDEA 107644 et PIT3 IMEDEA 106999). Rangée II : *O. scops* (IMEDEA 94019). Rangée III : *A. noctua* (IMEDEA 21717). Vues dorsale, latérale, ventrale et proximale (de gauche à droite).

medial tuberculum extensorium as in *Athene*, while in *Otus* it is present. Phalanx I 3: it has a well-developed tuberculum in the lateral site of the caput phalangis, as in *Otus*, whereas it is very reduced or absent in *Athene*. Phalanx II 2: it is slightly arched, as in *Otus*, while in *Athene* is more recitilinear. In contrast, the orientation of the caput phalangis of the fossil specimen is more similar to *Athene*. Phalanx III 3 and phalanx IV 4: both display a well delimited caput phalangis with respect to the dorsal wall as in *Athene*, while in *Otus* it is practically not interrupted. The terminal phalanx IV 3 (and all other terminal phalanges of unidentified): present tuberculum extensorium dorso-caudally oriented as in *Otus*, while in *Athene* it is oriented caudally. Finally, with regard to phalanx III 4, the main differences between these two genera rely on size and proportions. The fossil

specimen is robust as in *Athene*, while in *Otus* is more gracile.

These remains could represent a single individual. Based on the characters listed above, we consider that the small-sized Strigidæ fossils of NB-1 should be included in the genus *Otus*. However, the pedal phalanges obtained at NB-1 display characters similar to those observed in *Otus*, in *Athene*, or even display an intermediate morphology between the latter two genera. The size and proportions of the proximal and medial phalanges are more similar to those encountered in *Athene*, in which they are generally more robust than those of *Otus*. The morphology of the distal phalanges studied herein is better fitted to *Otus*.

So far, the whole known record of the genus *Otus* is mainly limited to the Quaternary (Kessler, 2017; Tyrberg,

Fig. 3. Comparaison d'*Otus* sp. (spécimens A–F) en provenance de NB-1 avec *O. scops* (spécimens G–J) et *Athene noctua* (spécimens K–L). Spécimen A (IMEDEA 107000), fragment proximal d'ulna droite en vues palmaire (gauche) et anconale (droite) ; spécimen B (IMEDEA 107643), fragment de sternum en vues ventrale (en haut), dorsale (en bas à gauche) et latérale (en bas à droite) ; spécimen C (IMEDEA 107645), fragment proximal de fémur gauche en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen D (IMEDEA 107646), fragment proximal de fémur droit, en vues crânienne (gauche) et caudale (droite) ; spécimen E (IMEDEA 107647), fragment proximal de fémur droit en vues crânienne (gauche) et caudale (droite) ; spécimen F (IMEDEA 106998), fragment distal de tibiotarse droit, en vues crânienne, caudale et latérale (de gauche à droite) ; spécimen G (IMEDEA 94019), ulna droite en vue palmaire (gauche) et anconale (droite) ; spécimen H (IMEDEA 21092), sternum en vues ventrale (en haut à gauche), dorsale (en haut à droite) et latérale (en bas) ; spécimen I (IMEDEA 94019), fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen J (IMEDEA 94019), tibiotarsus droit en vues crânienne, caudale et latérale (de gauche à droite) ; spécimen K (IMEDEA 94663), ulna droite en vues palmaire (gauche) et anconale (droite) ; spécimen L (IMEDEA 94663), sternum en vues ventrale (en haut), dorsale (en bas à droite) et latérale (en bas à gauche) ; spécimen M (IMEDEA 21717) fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen N (IMEDEA 94663), tibiotarsus droit en vues crânienne, caudale et latérale (de gauche à droite).

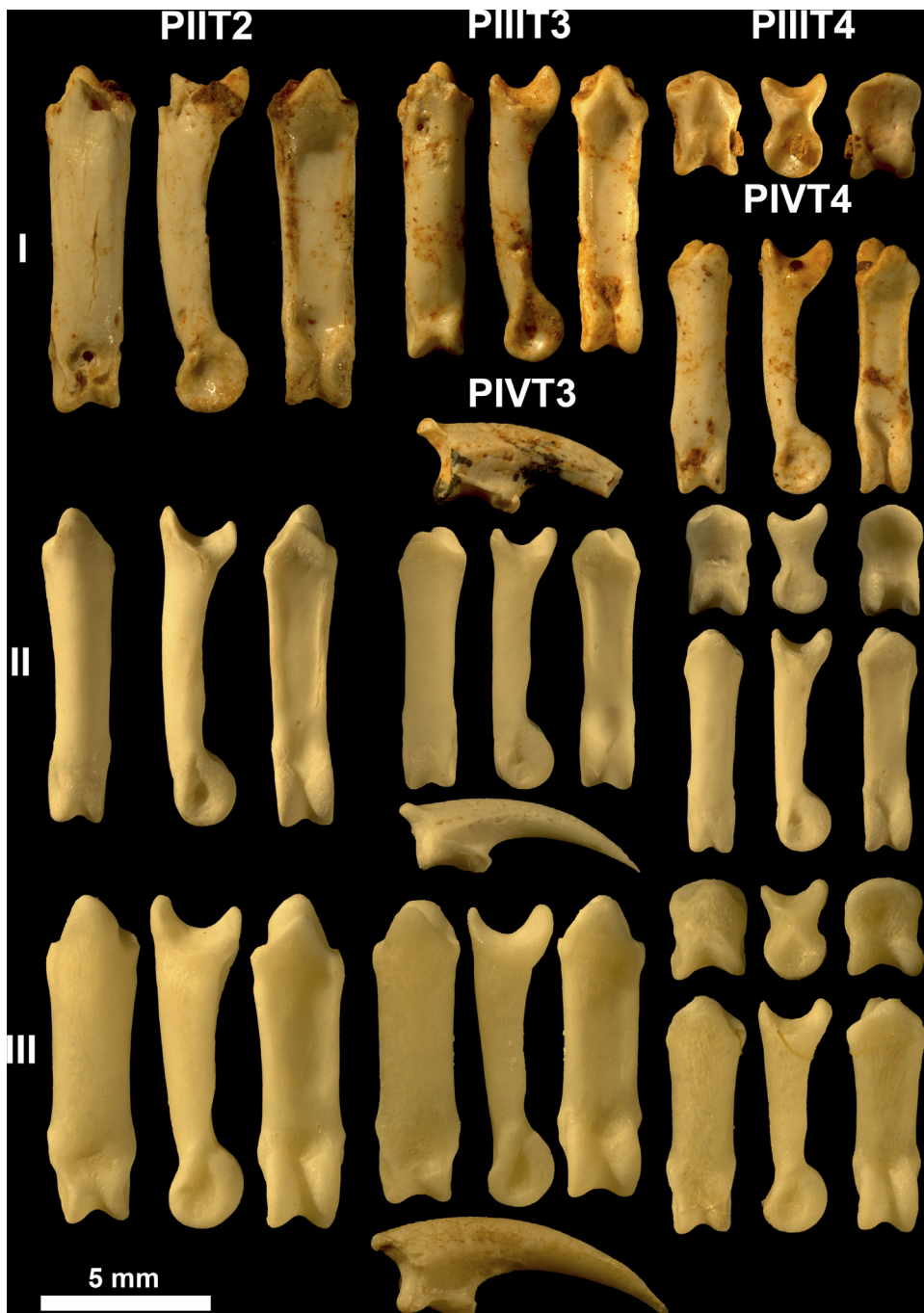


Fig. 5. Comparison of medial and terminal pedal phalanges. PIIT2, phalanx II toe 2; PIIT3, phalanx III toe 3; PIVT3, phalanx IV toe 3; PIIT4, phalanx III toe 4; PIVT4, phalanx IV toe 4. Row I: *Otus* sp. from NB-1 [left PIIT2 IMEDEA 107639 in dorsal, medial, and ventral views (from left to right), left PIIT3 IMEDEA 107637 in dorsal, lateral, and ventral views (from left to right), left PIVT3 IMEDEA 107635 in medial view, right PIIT4 IMEDEA 107634 in dorsal, medial and ventral views (from left to right), and left PIVT4 IMEDEA 107638 in dorsal, lateral and ventral views (from left to right)]. Row II: *O. scops* (IMEDEA 94019). Row III: *Athene noctua* (IMEDEA 21717).

Fig. 5. Comparaison des phalanges à pédale médiales et terminales. PIIT2, phalange II doigt 2 ; PIIT3, phalange III doigt 3 ; PIVT3, phalange IV doigt 3 ; PIIT4, phalange III doigt 4 ; PIVT4, phalange IV doigt 4. Rangée I : *Otus* sp. de NB-1 [PIIT2 gauche IMEDEA 107639, en vues dorsale, médiale et ventrale (de gauche à droite), PIIT3 gauche IMEDEA 107637 en vues dorsale, latérale et ventrale (de gauche à droite), PIVT3 gauche IMEDEA 107635 en vue médiale, PIIT4 droite IMEDEA 107634, en vues dorsale, médiale et ventrale (de gauche à droite) et PIVT4 IMEDEA gauche 107638 en vues dorsale, latérale et ventrale (de gauche à droite)]. Rangée II : *O. scops* (IMEDEA 94019). Rangée III : *Athene noctua* (IMEDEA 21717).

1998), with the exception of a distal fragment of humerus from the early Miocene of Songor (Kenya), tentatively attributed to *Otus* (Walker and Dyke, 2006), and some Burdigalian bones described as *Otus wintershofensis* from Bavaria (Germany; Ballmann, 1969). The bones of *Otus* obtained at NB-1 document the presence of the genus between the Burdigalian and the Quaternary.

4.5. Order Galliformes Temminck 1820

4.5.1. Family Phasianidae Horsfield 1821

4.5.1.1. cf. *Coturnix* Garsault 1764. Material: IMEDEA 107595, near complete right femur. IMEDEA 107596, proximal fragment of left humerus. IMEDEA 107597, proximal fragment of left femur (Fig. 6). IMEDEA 107598, sternum fragment. IMEDEA 107610, distal fragment of right tarsometatarsus. IMEDEA 107611, proximal fragment of right tarsometatarsus. IMEDEA 107612, apical fragment of premaxilla. IMEDEA 107621, pelvis fragment. IMEDEA 107622, pelvis fragment. IMEDEA 107623, pelvis fragment.

Extant species used to establish comparisons: *Coturnix*, *Alectoris rufa* (see Supplementary Table 2).

A few remains belonging to at least two individuals of a small-sized species of galliform have been obtained at NB-1. These remains have been attributed to cf. *Coturnix* because they are consistent with the size and osteological features presented by Holman (1964), Olson (1976), Fitzgerald (1969), and Dyke et al. (2003), although their fragmentary condition and the lack of a general review of the Mio-Pliocene quails preclude any further analysis. The premaxilla is characteristically short and slightly curved. The proximal end of the humerus displays a well-developed secondary fossa pneumotricipitalis. The femur is elongated and characteristically curved. The shaft diameter of the femur is 2.77 mm, and falls in the range of *Coturnix* (2.18–2.87 mm, $n=9$).

4.6. Order Charadriiformes Huxley 1867

4.6.1. Undetermined family, genus and species

Material: IMEDEA 107650, proximal fragment of right carpometacarpus.

The general morphology of this single proximal fragment of right carpometacarpus allows us to record the presence of a species of Charadriiformes similar in size to *Philomachus pugnax*, but its preservation state precludes further analysis.

4.7. Order Passeriformes Linnaeus 1758

4.7.1. Indetermined family, genus and species

Material: IMEDEA 107601, distal end of tarsometatarsus. IMEDEA 107602, distal end of tarsometatarsus. IMEDEA 107603, distal fragment of left tarsometatarsus. IMEDEA 107604, near complete right ulna. IMEDEA 107605, right carpometacarpus. IMEDEA 107606, proximal fragment of right carpometacarpus. IMEDEA 107607, proximal fragment of right humerus. IMEDEA 107608, distal fragment of right humerus. IMEDEA 107609, distal fragment of right humerus. IMEDEA 107613, distal end of tibiotarsus. IMEDEA 107614, distal fragment of left

Table 3

Vertebrate bones recovered at Na Burguesa-1. The minimum number of individuals (MNI) is indicated for mammals.

Tableau 3

Vertèbres récupérées à Na Burguesa-1. Le nombre minimum d'individus (MNI) est indiqué pour les mammifères.

Taxa	Number of bones	MNI
Soricinae	368	23
<i>BdApocricetus darderi</i>	2174	55
<i>Paraethomys balearicus</i>	161	11
Gliridae	2748	50
Leporidae	470	16
Bovidae	8	2
Anura	47	–
Squamata	968	–

tibiotarsus. IMEDEA 107615, proximal fragment of right carpometacarpus. IMEDEA 107624, 14 terminal pedal phalanges. IMEDEA 107649, 173 pedal phalanges.

The presence of Passeriformes at NB-1 is documented by 26 bones. The fragmentary state of most of this material impedes identification beyond the order level, whereas the more complete bones (e.g., phalanges) do not display enough diagnostic features to allow their identification with species. The bones of Passeriformes from NB-1 belong to at least to 5 different species.

5. Discussion

NB-1 yielded ca. 7000 bones, of which most were mammals, including Eulipotyphla (Soricinae), Rodentia (*Apocricetus*, *Paraethomys*, Gliridae), Lagomorpha (Leporidae), and Cetartiodactyla (Bovidae). In addition, four anurans, twelve reptiles, and several birds and bats were recovered as well (Bover et al., 2014). A preliminary study of this material already suggested close ties with the taxa present at the Early Pliocene deposit of Caló den Rafelino (Bover et al., 2014). The lower degree of insular evolution displayed by the NB-1 taxa suggested an Early Pliocene (Zanclean) age for this deposit. Moreover, the rodent species described from NB-1 [*Apocricetus darderi* (closely related to the mainland *A. alberti*; Torres-Roig et al., 2019a), and the first murine ever recorded in the fossil record of the Balearics, *Paraethomys balearicus* (closely related to the mainland *P. meini*)] allow us to establish for the first time a close, direct relationship of some taxa of the *Myotragus* fauna with their continental ancestors, a paleontological evidence that links the origin of the *Myotragus* fauna with the MSC (Mas et al., 2018; Torres-Roig et al., 2019b in press).

In the fossil bird assemblage of NB-1, the presence of three Strigiformes contributes to explain the origin of the site. Numerous authors have highlighted the role of nocturnal raptor birds as accumulators of remains of small vertebrates. Strigiformes (1) normally swallow their entire prey, and (2) the regurgitated bones show little damage and traces of digestion (e.g., Andrews, 1990). Andrews (1990) points out that Barn Owls (*Tyto*) are among the birds that produce the fewest modifications to the bones of consumed prey. The presence of a giant Barn Owl at NB-1, morphologically close to *Tyto robusta*, suggests that at least a part of this deposit should have derived from the accumulation

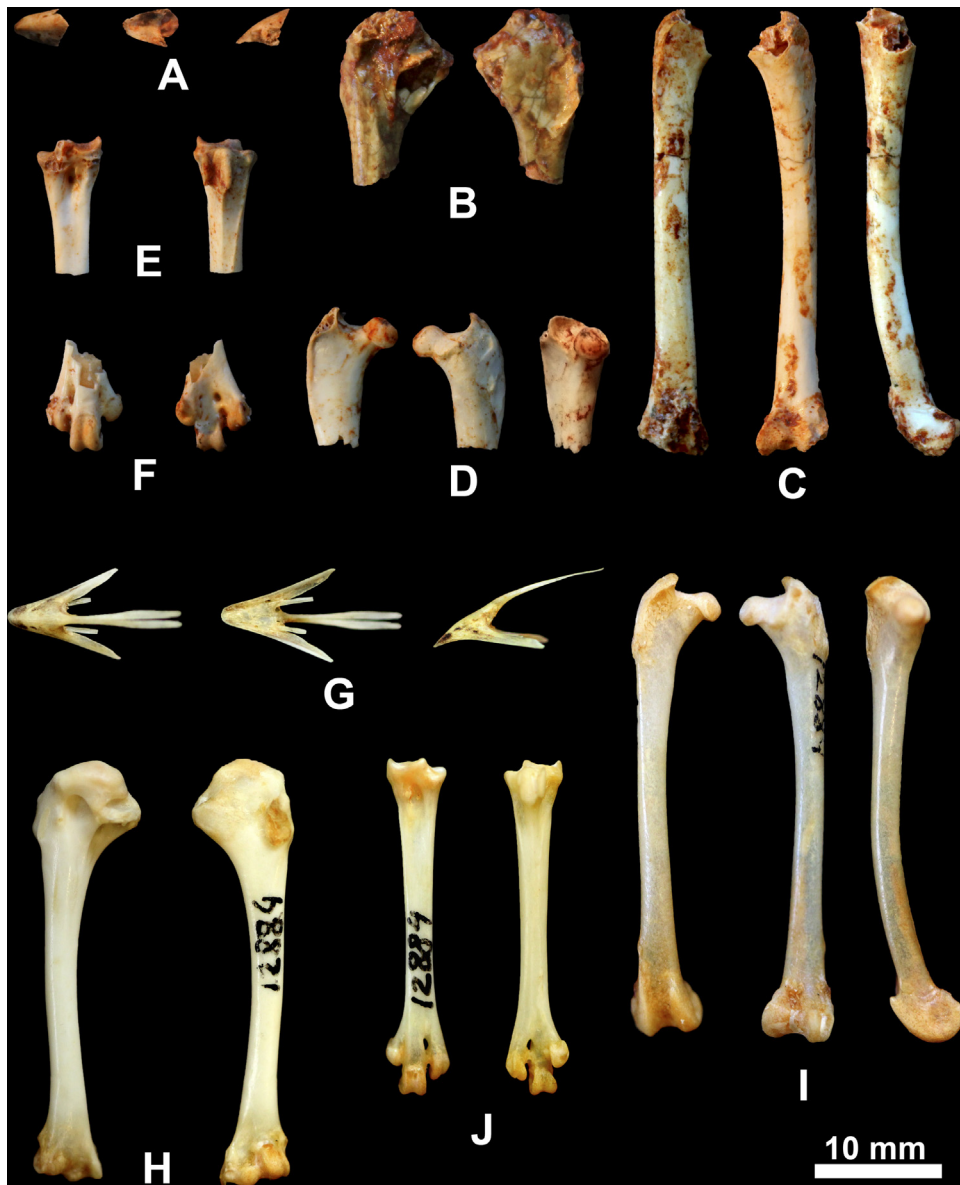


Fig. 6. Comparison of cf. *Coturnix* sp. (specimens A–F) from NB-1 with *C. coturnix* (specimens G–J). Specimen A (IMEDEA 107612), fragment of premaxilla in dorsal, lateral, and ventral views (from left to right); specimen B (IMEDEA 107596), proximal fragment of left humerus in caudal (left) and cranial (right) views; specimen C (IMEDEA 107595), right incomplete femur in cranial, caudal, and medial views (from left to right); specimen D (IMEDEA 107595), proximal fragment of right femur in cranial, caudal, and medial views (from left to right); specimen E (IMEDEA 107611), proximal fragment of right tarsometatarsus in cranial (left) and caudal (right) views; specimen F (IMEDEA 107610), distal fragment of right tarsometatarsus in cranial (left) and caudal (right) views; specimen G (IMEDEA 12884), premaxilla in dorsal, lateral, and ventral views (from left to right); specimen H (IMEDEA 12884), left humerus in caudal (left) and cranial (right) views; specimen I (IMEDEA 12884), right femur in cranial, caudal, and medial views (from left to right); specimen J (IMEDEA 12884), left tarsometatarsus in cranial (left) and caudal (right) views.

Fig. 6. Comparaison de cf. *Coturnix* sp. (spécimens A–F) de NB-1 avec *C. coturnix* (spécimens G–J). Spécimen A (IMEDEA 107612), fragment de prémaxillaire en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen B (IMEDEA 107596), fragment proximal d'humérus gauche en vues caudale (gauche) et crânienne (droite) ; spécimen C (IMEDEA 107595), fémur droit incomplet en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen D (IMEDEA 107595), fragment proximal de fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen E (IMEDEA 107611), fragment proximal de tarsométatarse droit en vues crânienne (gauche) et caudale (droite) ; spécimen F (IMEDEA 107610), fragment distal de tarsométatarse droit en vues crânienne (gauche) et caudale (droite) ; spécimen G (IMEDEA 12884), prémaxillaire en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen H (IMEDEA 12884), humérus gauche en vues caudale (gauche) et crânienne (droite) ; spécimen I (IMEDEA 12884), fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen J (IMEDEA 12884), tarsométatarse gauche en vue crânienne (gauche) et caudale (droite).

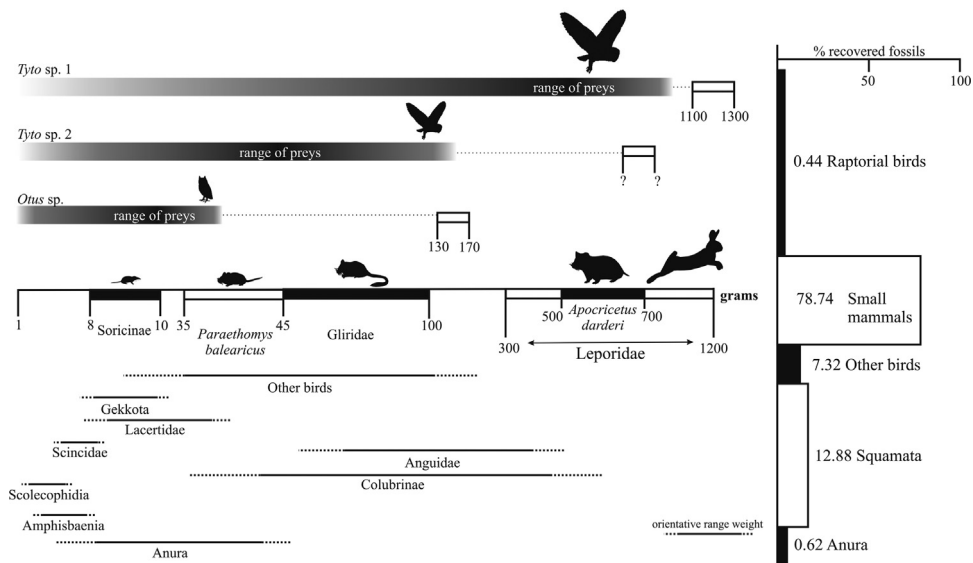


Fig. 7. Schematic diagram showing the potential prey of the Strigiformes based on their body mass estimation (on the left) and the percentages in the composition of the different small vertebrates recovered at site NB-1 (on the right).

Fig. 7. Diagramme schématique montrant les proie potentielles des Strigiformes, sur la base de l'estimation de leur masse corporelle (à gauche) et les pourcentages de composition des différentes petites vertèbres trouvées sur le site NB-1 (à droite).

of its pellets. NB-1 yielded thousands of small vertebrate bones (see Table 3). The microscopic analyses of the surface of the teeth and bones reveal that most of them display no (or negligible) alterations due to ingestion or digestion. Associated material belonging to a same individual has been repeatedly obtained (e.g., associated rodent jaws, associated gecko skeleton, associated vertebrae), despite the difficulties inherent to the extraction of bones with acid. In addition, the preservation of the considerable amount of micromammal bones is remarkably good, including complete or near complete bones (skulls, jaws and long bones), which is a noticeable finding in a hardly cemented karstic fossil site about 5 My old. Although *Tyto* sp. 1 displayed a large body size – an usual trait among insular owls (e.g., Louchart, 2005) – it is not possible to establish if its giantism was the result of its evolution on an island or if it shared its large size with its mainland ancestor.

It is well established that prey size is related to predator size (e.g., Comay and Dayan, 2018; Herrera and Hiraldo, 1976). The size of the giant cricetid *Apocricetus darderi* (estimated body mass in adult stage, 560–730 g), the juvenile specimens of the leporid (estimated body mass, 320–840 g), and the undescribed glirid (estimated body mass at adult stage, 60–100 g) recovered at NB-1 agrees with the prey size expected for *Tyto* sp. 1, a Barn Owl with an estimated body mass of 1190–1360 g (see Supplementary Table 3 and Fig. 7). This size range of prey items (60–840 g) and the large amount of bones from these taxa combined with the unaltered condition of the bones suggest that *Tyto* sp. 1 was a key species in the formation of the fossiliferous deposit. The role of *Tyto* sp. 2 at NB-1 remains unknown, as it could have been acted also as a bioaccumulation agent or have been introduced as a prey by *Tyto* sp. 1. Large-sized owls are known to prey on a wider size range of species than the small-sized owls (e.g., Comay and Dayan, 2018), and

thus the large *Tyto* sp. 1 could potentially include smaller prey items, such as the murid (estimated body mass in adult stage, 42 g), some birds, reptiles and amphibians in its diet. However, some of the taxa retrieved from NB-1 suggest that other bioaccumulators could have potentially contributed to the formation of the deposit. Remains of very small-sized taxa (such as a scoleophidian and an amphisbaenid), or large-sized taxa such as adult/subadult hares (four bones), the bovid *Myotragus*, four bones, a large tortoise, one phalanx and a large viper – several bones – are outside of the presumed size range of prey expected for *Tyto* sp. 1 (Fig. 7).

Although some cases of predation by Barn Owls or true owls on small-sized owls (*Otus*) have been recorded (e.g., García et al., 2008), these are rare occurrences (e.g., Mikkola, 1976). Actually, it cannot be ruled out that *Otus* sp. from NB-1 was incorporated into the deposit as a prey by *Tyto* sp. 1 (or even by the smaller *Tyto* sp. 2). Nevertheless, the role of *Otus* sp. as potential bioaccumulator of small vertebrates in NB-1 should be considered. Small mammals like the shrew (with an estimated body mass of 8–10 g) and the murid, small passerines, or small reptiles (geckos, lizards, scoleophidians, small culebrines, amphisbaenids) and amphibians, all them present in the deposit, fall within the prey range of a small-sized owl. The abundance of vertebrates smaller than the estimated size range of *Tyto* spp.'s preferred prey suggests a link with the presence of the small-sized *Otus*. The material available suggests that the hindlimb long bones of *Otus* sp. are slightly larger than those of *Otus scops*, while the measurements of wing bones fall within the range of variability of *Otus scops*. The larger and stouter phalanges of *Otus* sp. compared to those of *Otus scops* are in agreement with its long hindlimb bones. All these features suggest a high terrestriality of *Otus* sp. from NB-1, which could be linked to a preferred predation on small terrestrial vertebrates (like the scoleophidian, the

amphisbaenid, etc). A high terrestriality is a widespread trend among insular owls living on islands lacking mammalian predators (e.g., Louchart, 2005).

In summary, at least two of the Strigiformes (*Tyto* sp. 1 and *Otus* sp.) present in the deposit should be considered as bioaccumulation agents of the small vertebrate bones found at NB-1. The third one (*Tyto* sp. 2) could be considered either as a prey of *Tyto* sp. 1 or as another bioaccumulation agent. The differences in size between *Tyto* sp. 1 and *Otus* sp. are great enough that we assume that their prey size ranges differed or showed only a negligible overlap. The predatory role of both genera of strigiforms could have generated an owl pellet deposit showing a prey range wider than expected if it was produced by a single bioaccumulation agent. Thus, according with the available size range of prey, the sample obtained at NB-1 could be considered highly representative of the terrestrial small vertebrate fauna present in the Early Pliocene of Mallorca.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2019.08.003>.

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