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Old and new fossil birds from the Spanish Miocene

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Abstract

Now a long time ago, avian remains from the Vallès-Penedès Basin and from other Miocene localities inaugurated the study of the Tertiary birds from Spain. After so much time, it is suitable to review them. Fossils unknown so far of the same or close taxa from the rest of the Iberian Peninsula are also presented in this paper. The majority of species belong to Phasianidae. The present paper participates in a long discussion about the systematic validity of the various fossil species of *Tyto* described in the European Neogene. A considerable part of such discussion has as focal point *Tyto balearica*. Apparently, discrepancies have been raised around the size range of this species, although a conviction of the chronological and geographical distributions of this owl, in particular, if it were essentially an insular species, has likely had an unwanted influence on a debate that should be restricted to anatomical aspects.

Keywords Palaeornithology, avian systematics, avian paleontology, Neogene birds, paleo-subspecies.

Resumen

Hace mucho tiempo, los restos de aves de la cuenca del Vallés-Penedés y de otras localidades del Mioceno inauguraron el estudio de las aves del Terciario de España. Después de tanto tiempo, conviene su revisión. También se presentan en este artículo restos desconocidos hasta ahora de los mismos taxones, o próximos, procedentes del resto de la península ibérica. La mayor parte de las especies pertenecen a Phasianidae. Este artículo participa en una larga discusión acerca de la validez sistemática de varias especies fósiles de *Tyto* descritas en el Neógeno europeo. Una parte considerable de esta discusión tiene a *Tyto balearica* como punto focal. En apariencia, la discusión se ha planteado en torno al rango de talla de esta especie, si bien la convicción de las distribuciones cronológicas y geográficas de esta lechuza, en particular, si fue una especie esencialmente insular, probablemente ha tenido una influencia indeseada en un debate que debería estar restringido a aspectos anatómicos.

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32 **Palabras clave** Paleornitología, sistemática aviar, paleontología de aves, aves del Neógeno, paleo-
33 subespecies.

34

35 **Declarations**

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1 Introduction

In contrast to the abundant literature on Miocene mammals, proof of the interest in this animal group and its extensive fossil record, the fossil birds from the Iberian Miocene have attracted little attention from paleontologists. Most likely, this is due to the low number of fossil localities from this epoch yielding large collections of avian remains. Thus, with the exception of a few relatively rich deposits, Miocene avian remains from the Iberian Peninsula have come to light in small numbers and in a fragmentary state, which sheds uncertainties to subsequent taxonomic tasks. Available data on fossil finds and paleontological sites from the Iberian Miocene were summarized in three previous paleornithological catalogs (Sánchez Marco 1995a, 1995b, 1999) and in a subsequent compilation paper (Sánchez and Sastre 2001). One aim of the present paper is to report new avian remains from the Miocene of the Iberian Peninsula and critically revise previous studies on this topic.

Miocene avian remains from Iberian localities have been dealt with in a handful of works, beginning with some of the earliest Spanish papers in this field (Villalta and Crusafont Pairó 1950; Villalta 1963). After this time, there are only two publications of limited scope on this subject (Sánchez Marco 2001, 2006). A number of misidentifications arisen in early works had settled in the specialized literature, and such errors required a critical review.

The extinct owl *Tyto balearica* has been found in two new localities (this paper). This species has been misinterpreted in some recent publications and requires additional clarification concerning the understanding of what a taxon described on paleontological grounds means. Overall, this paper deals with a considerable part of the current Iberian record of Miocene galliforms, which shows how meagre it is so far.

2 Materials and Methods

For most of the mammal units and for the Neogene mammal ages, it has been followed de Bruijn et al. (1992), and Calvo et al. (1993) for the continental stages. The osteological nomenclature follows Baumel and Witmer (1993) and Livezey and Zusi (2006). Most of the measurements on phasianid coracoidea follow Göhlich and Mourer-Chauviré (2005). The fossil remains studied in this work are housed in the MNCN and the ICP.

Anatomical abbreviations: **Gl**, greatest length; **Pw**, proximal width; **Pd**, proximal depth; **Wd**, smallest width of the diaphysis; **Dw**, distal width (abbreviated as Wd in Göhlich and Mourer-Chauviré 2005); **Dd**, distal depth; **Lm**, medial length; **Wdf**, width of distal facies; **Lp**, proximal length from distal margin of facies articularis humeralis to the proximal end; **Wpa**, width of processus acrocoracoideus.

Institutional abbreviations: **IPS**, Museu del Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain); **MNCN**, Museo Nacional de Ciencias Naturales (Madrid, Spain).

Age of the localities: The ages for the localities of provenance of the studied material have been taken from the following published sources: Can Mas (el Papiol, Vallès-Penedès Basin; Agustí et al. 1985); Can Poncic (Sant Quirze, Vallès-Penedès Basin; Casanovas-Vilar et al. 2011a); El Fallol (Vallès-Penedès Basin; Casanovas-Vilar et al. 2011b); Hostalets de Pierola indeterminate (els Hostalets de Pierola, Vallès-Penedès Basin; Casanovas-Vilar et al. 2011a); Viladecavalls (Vallès-Penedès Basin; Alba et al. 2010). Batallones 1 and 3 (Cerro de los Batallones, Torrejón de Velasco, Madrid; Morales et al. 2008); La Artesilla (Villafeliche, Zaragoza; de Bruijn et al. 1992); Toril 3 (Daroca, Zaragoza; de Bruijn et al. 1992); Escobosa (Escobosa de Calatañazor village, Soria; de Bruijn et al. 1992); Valdecebro 5 (Valdecebro, Teruel Basin; Adrover et al. 1986; Sánchez Marco 1999); Los Mansuetos (Teruel, Teruel Basin; de Bruijn et al. 1992; Calvo et al. 1999); Los Valles de Fuentidueña (Segovia; de Bruijn et al. 1992).

3 Systematic palaeontology

Order Galliformes Linnaeus, 1758

Family Phasianidae Vigors, 1825

Miophasianus altus (Milne-Edwards, 1869)

(Figure 1a–f)

Phasianus altus Milne-Edwards, 1869, vol. 2, p. 239, pl. 131, fig. 27-36 (original description).

p. Miophasianus altus Milne-Edwards, 1869: Villalta and Crusafont 1950:147, fig. 1.

p. Miophasianus altus Milne-Edwards, 1869: Villalta 1963: 271, pl. 4-5.

Miophasianus altus Milne-Edwards, 1869: Ballmann 1969: 175, pl. 15.

Miophasianus altus Milne-Edwards, 1869: Cheneval 2000: 351, fig. 9-11.

p.? *Miophasianus altus* Milne-Edwards, 1869: Göhlich 2002: 178, fig. 1-4.

Localities. Can Mas (el Papiol, MN4, early Aragonian); Hostalets de Pierola indeterminate (els Hostalets de Pierola; MN7+8 to MN9, late Aragonian to early Vallesian).

Referred specimens. Can Mas: IPS12671 (Figure 1c), proximal end of left ulna; IPS12672 (Figure 1d), distal end of right ulna; IPS12670 (Figure 1e), proximal end of right femur; IPS12668 (Figure 1f), distal end of right tibiotarsus. Hostalets de Pierola indeterminate: IPS12649 (Figure 1b), distal end of left humerus; IPS12651 (Figure 1a), distal end of right humerus.

Description. The humerus show a smooth sulcus humerotricipitalis, as it is common within the family. However, this sulcus is deeper than in *Gallus* Brisson, 1766, and *Phasianus* Linnaeus, 1758. The condylus ventralis is more protruding distally regarding the condylus dorsalis than in *Gallus* and *Phasianus*. The cross-section of the diaphysis is elliptical. The fossa musculi brachialis is marked, but not deep. The processus flexorius is rounded and scarcely protruding. With regard to the ulna, as it is typical in Galliformes, the cotylae ventralis and dorsalis form a continuous shallow surface. The region of the olecranon is curved dorsally, and the olecranon is slightly protruding. The cross-section of the diaphysis is oval, cranially sharper. The proximal end has no distinctive characteristics. The condylus ventralis ulnae is poorly developed and protrudes distally. This condylus is more protruding than in *Gallus*, and as jutting as in *Phasianus*. In distal aspect, the ulna of *Phasianus* has a more flattened shape than in *Gallus* and *Miophasianus*. The tuberculum carpalis is small and rounded. The condylus dorsalis is large and round, which gives a triangular outline to the bone in distal view. The single available femur lacks its head, making it difficult to compare with other taxa. It has the typical wide and proximally protruding trochanter of galliforms. The fossa trochanteris is large and curved. The section of the bone is elliptical. In the tibiotarsus, both condyles are robust and well developed, being the lateral one the largest. In both condyles, the distal edges are more flattened than in *Gallus* and *Phasianus*. The incisura intercondylaris is wide and notably deeper than in the two mentioned genera.

Measurements. See Table 1.

Remarks. *Miophasianus altus* was originally described by Milne-Edwards (1869) based on fossil remains from Sansan (MN6, Astaracian, France) as *Phasianus altus*. Lambrecht (1933) erected the genus *Miophasianus* for the Miocene species previously allocated to *Phasianus*. Mlíkovský (2002) noticed that

the name *Miophasianus* was a nomen nudum because Lambrecht (1933) failed to indicate a type species (required for names after 1930). Nevertheless, the name *Miophasianus* was made available by Brodkorb (1952). At the mentioned work, Lambrecht (1933) erected the new genus *Miogallus*, with the type species *Miogallus longaevus* (Ammon, 1918), on material from the middle Miocene of Dechbetten (Germany), a taxon that was later synonymized by Mlíkovský (2002) with *Miophasianus altus*. However, Mlíkovský (2002) did not examined directly the skeletal elements of both taxa. Therefore, its synonymy has to be revised.

Villalta and Crusafont Pairó (1950) mentioned four species of galliforms from Hostalets de Pierola: *Miophasianus altus*, *M. medius*, *Palaeortyx miocaena* and *Palaeortyx edwardsi*. Later, Villalta (1963) incorporated *Palaeoperdix sansaniensis* to the record of this site. Likewise, Villalta (1963) reported the find of two galliforms in Can Mas: *Miophasianus altus* and *Palaeortyx edwardsi*. Part of this material was restudied by Sánchez Marco (2006), who agreed with most of the previous assignments by Villalta and Crusafont Pairó (1950). *Miophasianus altus* has been also identified in some other sites outside the Vallès-Penedès: La Grive-Saint-Alban (MN7+8; Déperet 1887; Lydekker 1893; Gaillard 1939; Ballmann 1969) in France; Attenfeld (MN7+8; Schlosser 1916), Dechbetten (MN5; Ammon 1918, as *Miophasianus augustus*), Oehningen (MN7+8; Lydekker 1891), Sandelzhausen (MN5; Göhlich 2002), and Steinheim (MN7+8; Heilmann and Hesse 1995) in Germany; Děvinská Nová Ves (MN6; Švec 1986) in Slovakia; Gratkorn (MN7+8; Göhlich and Gross 2014) in Austria; and Toril 3 (Sánchez Marco 2006) in central Spain. Moreover, Cheneval (2000) mentioned that the identification of *Miophasianus* sp. from the French locality of Vieux Collonges (MN5) by Ballmann (1972) might correspond to *Miophasianus altus*, and the same could be said about the fossil material from the Spanish locality of Córcoles (MN 4) (Alfárez et al. 1982).

[PLACE FIGURE 1 ABOUT HERE]

Miophasianus medius (Milne-Edwards, 1869)

(Figure 1g,h)

Phasianus medius Milne-Edwards, 1869, vol. 2, p. 242, pl. 131, fig. 24-26 (original description).

p. *Miophasianus altus* Milne-Edwards, 1869: Villalta and Crusafont 1950:147.

163 *Miophasianus medius* Milne-Edwards, 1869: Villalta and Crusafont 1950:149, fig. 2.
 164 *p. Miophasianus altus* Milne-Edwards, 1869: Villalta 1963:271.
 165 *Miophasianus medius* Milne-Edwards, 1869: Villalta 1963:272, pl. V, fig. 3, 3a.
 166 *Miophasianus medius* Milne-Edwards, 1868: Ballmann 1969:176, pl. 15.
 167 *Miophasianus medius* Milne-Edwards, 1869: Bocheński 1987:71, pl. XVII.
 168 *Palaeoperdix medius* Milne-Edwards, 1869: Cheneval 2000:349, fig. 8 (new combination).
 169 *Palaeoperdix medius* Milne-Edwards, 1869: Sánchez Marco 2006:253.
 170 “*Miogallus*” *medius* Milne-Edwards, 1869: Zelenkov 2017:74, fig. 3.

171
 172 Localities. Hostalets de Pierola (MN7+8-MN9), Batallones 3 (MN 10).

173 Referred specimens. Hostalets de Pierola indeterminate: IPS12648 (Figure 1g), proximal end of
 174 left humerus; without number, distal end of another –right- humerus, not seen for this study, although
 175 Villalta and Crusafont Pairó (1950, fig. 1) figured it and gave its distal width (17.3 mm). Batallones 3:
 176 2008-326 (Figure 1h), complete right radius.

177 Description. The head of the humerus is robust and rounded. The crista deltopectoralis is short
 178 and slightly developed. It is curved ventrally. The crista bicipitalis is relatively small and round. The
 179 fossa tricipitalis dorsalis is smooth. With regard to the radius, the cotyla humeralis is completely round.
 180 The tuberculum bicipitale radii is elongated and conspicuous. The shaft is straight and has a round section
 181 towards its cranial end, whereas it becomes flattened towards the distal end. The facies articularis
 182 radiocarpalis is smooth and curved. The tuberculum aponeurosis ventralis protrudes laterally. The
 183 humerus shows a deeper and narrower impressio coracobrachialis than in *Gallus* and *Phasianus*. In
 184 proximal view, the caput humeri is cranio-caudally wider and laterally shorter than in both mentioned
 185 species. *Miophasianus medius* does not seem to show distinctive morphological features with regard to
 186 *M. altus*. Both taxa are only distinguishable on their respective size-ranges.

187 Measurements. See Table 1.

188 Remarks. The genus *Palaeoperdix* was originally described from Sansan by Milne-Edwards
 189 (1869). This genus comprised *P. longipes* (type species by original designation), *P. prisca* and *P.*
 190 *sansaniensis*. Ballmann (1969) wrote down that *Palaeoperdix longipes* was synonymous with *Palaeortyx*
 191 *phasianoides* Milne-Edwards, 1869, which was also supported by Göhlich and Mourer-Chauviré (2005).
 192 As to the two other species originally placed within *Palaeoperdix*, Cheneval (2000) synonymized
 193 *Palaeoperdix sansaniensis* with *Palaeoperdix prisca* and transferred it to *Palaeortyx* Milne-Edwards,

1869. On the other hand, Cheneval (2000) transferred *Miophasianus medius* to *Palaeoperdix*. As a consequence, for this author two species remain in the genus *Palaeoperdix*: *P. longipes* and *P. medius*. However, I consider that *Miophasianus medius* must be placed within the same genus as *Miophasianus altus*. I agree with the original description in that the distinction between *medius* and *altus* is the smaller size of the former species (Milne-Edwards 1869-71). *M. medius* has been recorded in Olival da Susana (MN-5, Portugal; Mourer-Chauviré and Antunes 2003), Przeworno II (MN6-7+8, Poland; Bocheński 1987) and La Grive-Saint-Alban (MN7+8; Déperet 1887; Ennouchi 1930; Gaillard 1939; Ballmann 1969).

[PLACE TABLE 1 ABOUT HERE]

Palaeortyx joleaudi Ennouchi, 1930

(Figure 1i)

Localities. La Artesilla (MN4).

Referred specimens. MNCN 74035, proximal end of right humerus.

Description. The specimen is a bone fragment. It has a very deep and large fossa pneumotricipitalis dorsalis. The fossa pneumotricipitalis ventralis is well developed. It shows the characteristic indentation of *Palaeortyx* between de caput humeri and the tuberculum ventrale (Göhlich and Mourer-Chauviré 2005).

Measurements. See Table S1.

Remarks. The genus *Palaeortyx* was originally described by Milne-Edwards (1869-71) based on fossil material from Saint-Gérard-le-Puy (MN1-MN2, France). This author erected three new species for this genus: *Palaeortyx gallica*, *Palaeortyx brevipes* and *Palaeortyx phasianoides*. Later, the smallest-sized species within the genus known so far, *Palaeortyx joleaudi*, was described from La Grive-Saint-Alban (MN7+8) by Ennouchi (1930). Mlíkovský (2002) synonymized *Palaeortyx* with the extant genus of quails *Coturnix* Bonnatere, 1791, an opinion that has been revised and discussed by Göhlich and Mourer-Chauviré (2005). Regarding the few features that can be observed in the small fragment of bone from La Artesilla, the fossa pneumotricipitalis dorsalis is deeper and relatively larger in *Palaeortyx* than in *Coturnix*, whereas in *Coturnix* the fossa pneumotricipitalis ventralis is relatively wider than in

Palaeortyx. In *Megalocoturnix cordoni*, from the Ruscinian outcrop of Layna (Spain), the fossa pneumotricipitalis dorsalis is likewise fairly smoother than in *Palaeortyx* (Sánchez Marco 2009). This find in Artesilla constitutes the second record for this species, the first being that from La-Grive-Saint-Alban, on which basis this taxon was originally described.

Palaeortyx brevipes Milne-Edwards, 1869 / *Palaeortyx grivensis* Lydekker, 1893

(Figure 1j–p)

Coturnix (?) miocenica Villalta, 1963:271, pl. IV: fig. 1, 1a, 1b (original description).

p. *Coturnix gallica* Milne-Edwards, 1869: Mlíkovský 2002:154.

Localities. Toril 3 (MN7+8), Escobosa (MN 7+8), Can Poncic (MN9), Batallones 1 (MN10), Valdecebro 5 (MN12), Los Mansuetos (MN12).

Referred specimens. Toril 3: MNCN 74030, complete left coracoideum (Figure 1m); MNCN 74031, cranial end of right coracoideum; MNCN 74029, distal end of left tarsometatarsus (Figure 1k). Escobosa: MNCN 74032, cranial end of left coracoideum; MNCN 74033 (Figure 1l) and MNCN 74034, two proximal ends of left humerus (one of them, MNCN 74034, very damaged and not useful for taking measurements). Can Poncic: IPS87218, proximal end of left carpometacarpus (Figure 1j). Batallones 1: without number, cranial end of right scapula (Figure 1o), cranial end of right coracoideum, proximal end of right humerus (Figure 1n), distal end of left humerus, distal end of left ulna, and proximal end of left carpometacarpus. Valdecebro 5: MNCN 74036, distal end of right tarsometatarsus. Los Mansuetos: IPS12678 (Figure 1p), proximal end of right carpometacarpus (Figure 1p).

Description. In the scapula, the acromion is very large and crescent-shaped. The tuberculum coracoideum is patent. The facies articularis humeralis has a triangular shape. In the coracoideum of some phasianids the processus procoracoideus is very small, as in *Alectoris* Kaup, 1829, *Perdix* Brisson, 1760, or *Lagopus* Brisson, 1760. A characteristic feature of *Palaeortyx* is the extreme reduction of this processus (Cheneval and Adrover, 1993). Moreover, it forms a continuous surface with the facies articularis scapularis. In *Palaeocryptonyx* Depéret, 1892, there is a step between both anatomical elements. The facies articularis humeralis is large and fused with the cotyla scapularis. The extremitas omalis is not medially inclined. There is no foramen pneumaticum in the area of the impressio musculi

sternocoracoidei. The angulus medialis protrudes distally. The facies articularis sternalis is very short and more curved than in *Palaeocryptonyx*. With regard to the humerus, in *Palaeortyx* it is characterized by two deep (dorsal and ventral) fossae pneumotricipitalis, the former being larger. The impressio coracobrachialis is very deep and wide. The crista deltopectoralis is relatively more developed than in other phasianids. The fossa musculi brachialis is well marked. The region of the processus flexorius is very developed. In the ulna, the shaft is compressed laterally. The tuberculum carpale is small. The outline of the condylus dorsalis ulnae is round. Regarding the carpometacarpus, the available bone fragments show a typically galliform-shape. The dorsal edge of the trochlea carpalis is characteristically round. The processus extensorius is curved upwards and little developed. The processus alularis is scarcely developed, like the processus intermetacarpalis. The processus intermetacarpalis is not very developed (contra Cheneval and Adrover 1993). The three trochleae of the tarsometatarsus conform a semicircle. The trochlea for digit II protrudes distally less than the trochlea of digit IV and is likewise less developed.

Measurements. See Tables S1 and S2.

Remarks. The specimen from Los Mansuetos is the holotype and the only attributed specimen to *Coturnix miocenica* Villalta, 1963. This taxon was synonymized with *Coturnix gallica* Milne-Edwards, 1869, by Mlíkovský (2002), who in the same work also transferred some species of *Palaeortyx* to the extant genus *Coturnix*. As explained above, *Palaeortyx brevipes* was erected by Milne-Edwards (1869-71) based on some bones from Saint-Gérard-le-Puy (MN1-MN2, France). The author noted that this taxon was smaller than *Palaeortyx gallica*, another species also described by himself from the same locality. *Paleortyx brevipes* has been noticed from the Eocene and Oligocene of Quercy (France) by Gaillard (1908: *Palaeortyx cayluxensis*) and Mourer-Chauviré (1992) up to Aljezar B (Spain) (Cheneval and Adrover 1993: *Palaeortyx* cf. *brevipes*). The small-sized *Palaeortyx* (*P. gallica*, *P. brevipes*, *P. grivensis*, *P. joleaudi*) were synonymized by Mlíkovský (2002) and transferred to *Coturnix gallica*. *Palaeortyx grivensis*, was described by Lydeker (1893) on material from La Grive (MN7+8). From the same locality, Ennouchi (1930) described *Palaeortyx depereti* as being of intermediate in size between *Palaeortyx grivensis* and *Palaeortyx edwardsi* Depéret, 1887. However, Ballmann (1969) wondered whether the differences between *Palaeortyx grivensis* and *Palaeortyx depereti* were enough to justify the recognition of two distinct taxa. Subsequent reviewers (Mlíkovský 2002; Göhlich and Mourer-Chauviré 2005; Göhlich and Pavia 2011) have supported such an opinion. The remains from Gargano (Italy)

previously assigned to *Palaeortyx grivensis* by Ballmann (1973, 1976) have been subsequently considered to correspond to a new taxon, *Palaeortyx volans* Göhlich and Pavia, 2011. Ballmann (1973) synonymized *Palaeocryptonyx depereti* (Ennouchi, 1930) with *Palaeortyx brevipes*, of the same size range. The finds from the fossil localities studied in this paper have to be attributed to the genus *Palaeortyx*, within the size ranges of *Palaeortyx grivensis* and *Palaeortyx brevipes*. Zelenkov (2017) has transferred one coracoid from Rudabánya (MN9, Hungary) previously assigned to *Palaeortyx grivensis* by Jánossy (1993) and to *Palaeortyx brevipes* by Kessler (2009) to Rollulinae indet.

Palaeortyx phasianoides Milne-Edwards, 1869

(Figure 1q,r)

Localities. Can Mas (MN4), Toril 3 (MN7+8).

Referred specimens. Can Mas: IPS12647 (Figure 1q), distal end of left humerus. Toril 3: MNCN 74028 (Figure 1r), proximal end of right carpometacarpus.

Descriptions. In the humerus, the sulcus humerotricipitalis is relatively deep. The condylus ventralis protrudes distally. The condylus dorsalis is long in cranial view. The processus flexorius shows a pointed outline in ventral view. The cross section of the diaphysis near the end of the bone is ovate and flattened antero-posteriorly. In the carpometacarpus, the processus intermetacarpalis is well developed. The trochlea carpalis ends distally (towards the processus extensorius) abruptly. The ventral outline of the trochlea is very rounded. The processus extensorius is stout. The processus alularis is prominent.

Measurements. See Table S1.

Remarks. The specimen from Can Mas was attributed by Villalta (1963) to *Palaeortyx edwardsi*, which was originally described by Depéret (1887) based on some bones from La Grive-Saint-Alban. Ballmann (1969) pointed out the wrong attribution to the genus, and transferred it to *Palaeocryptonyx* Depéret, 1892, resulting in the new combination *Palaeocryptonyx edwardsi* (Depéret, 1887). In a later review, Mlíkovský (2002) synonymized the genus *Palaeocryptonyx* with *Alectoris*. Cheneval (2000) referred the humerus from Can Mas to *Palaeortyx prisca*. Göhlich and Mourer-Chauviré (2005) founded the distinction between *Palaeortyx phasianoides* and *Palaeortyx prisca* in their respective sizes, reaching *Palaeortyx phasianoides* the highest size range. The condylus ventralis is more prominent distally than in *Alectoris* and *Gallus*. In distal view, the processus flexorius juts from the bone more than in *Numida*

Linnaeus, 1766, *Alectoris*, *Lagopus*, *Gallus*, *Phasianus* and *Perdix*. This processus is little developed in *Numida* and *Coturnix*. The fossa musculi brachialis is wider in the humerus of *Palaeortyx phasianoides* than in *Palaeocryptonyx edwardsi*, giving to this part of the bone a more flattened appearance in *Palaeortyx phasianoides*. The proximal end of the carpometacarpus is the same size in *Palaeocryptonyx edwardsi* and *Palaeortyx phasianoides*. Here, the processus extensorius is curved and directed proximally, as in *Alectoris* and *Perdix*. In *Gallus*, *Phasianus*, *Lagopus*, *Coturnix* and *Palaeocryptonyx* this process is directed more laterally. This process is greatly reduced in *Numida*. In *Palaeortyx phasianoides*, the dorsal edge of the trochlea carpalis does not stand out from the ventral edge as in *Palaeocryptonyx edwardsi*.

Palaeortyx gallica Milne-Edwards, 1869

(Figure 1s–u)

Phalacrocorax ibericum Villalta, 1963:267, pl. II: fig. 4, 4a (original description).
Palaeoperdix sansaniensis Milne-Edwards, 1869: Villalta 1963:270, pl. IV: fig. 3, 3a, 3b.
p. Palaeortyx prisca (Milne-Edwards, 1869): Cheneval 2000:345 (new combination).
Phalacrocorax ibericus Villalta, 1963: Mlíkovský 2002:72 (ending corrected).

Localities. Toril 3 (MN7+8), Hostalets de Pierola indeterminate (MN7+8-MN9), Los Valles de Fuentidueña (MN9).

Referred specimens. Hostalets de Pierola indeterminate: IPS73336 (Figure 1s), distal end of right tibiotarsus. Toril 3: MNCN 74027 (Figure 1t), partial left tibiotarsus (missing its distal end). Los Valles de Fuentidueña: IPS12650 (Figure 1u), distal end of right humerus.

Description. The humerus is badly damaged: both condylus dorsalis and processus flexorius are partially lost. The fossa musculi brachialis is deep and well marked. The epicondylus dorsalis as well as the tuberculum supracondylaris ventrale are scarcely developed. This distal end of humerus is quite different from that of *Phalacrocorax* Brisson, 1760. A very small processus flexorius is a characteristic feature of the latter genus. The specimen from Los Valles de Fuentidueña has the overall shape of the Phasianidae. The two incomplete tibiotarsi have a characteristic overall galliform shape. The bone from Hostalets de Pierola has a wide pons supratendineus, and both condyles are round and similar in size. The

facies articularis lateralis of the bone from Toril 3 is relatively small. In proximal view, it has an elongated shape. The crista cnemialis is short.

Measurements. See Table S1.

Remarks. The distal tibiotarsus from Hostalets was identified by Villalta (1963) as *Palaeoperdix sansaniensis* Milne-Edwards, 1869. This species was described based on a distal end of tibiotarsus from Sansan, and considered by Milne-Edwards (1869) to be smaller than *Palaeoperdix prisca* Milne-Edwards, 1869, likewise described based on material from the same locality. However, owing to the fragmentary state of the holotype, Milne-Edwards (1869) had some doubts on the allocation of this species to genus *Palaeoperdix*, being originally spelled as “*Palaeoperdix* (?) *sansaniensis*”. As mentioned above, Cheneval (2000) synonymized *Palaeoperdix sansaniensis* with *Palaeoperdix prisca*, and subsequently transferred the latter species to genus *Palaeortyx*. The bones of *Palaeortyx prisca* reach larger sizes than *Palaeortyx gallica*, but there is some overlap in the measurements. However, the bones from Hostalets de Pierola and Toril 3 fit the tibiotarsus size ranges of *Palaeortyx gallica*, and are therefore attributed to this species. In turn, the specimen from Los Valles de Fuentidueña was designated as the holotype of *Phalacrocorax ibericum* Villalta, 1963. No other specimen has been subsequently assigned to this taxon. Mlíkovský (2002) corrected the ending of the specific epithet (i.e., *Phalacrocorax ibericus*) and indicated that the fragment was too eroded to allow for an exact identification.

Order Strigiformes (Wagler, 1830)

Family Tytonidae Ridgway, 1914

Tyto balearica Mourer-Chauviré et al., 1980

(Figure 1v,w)

Tyto campiterrae Jánossy, 1991:25-26, fig. 3, tab. 2 (original description)

p. *Tyto sanctialbani* Lydekker, 1893: Mlíkovský 1998:253.

p. *Tyto sanctialbani* Lydekker, 1893: Mlíkovský 2002:209.

Tyto campiterrae Jánossy, 1991: Pavia and Mourer-Chauviré 2001:1095, fig. 4.

Localities. Hostalets de Pierola indeterminate (MN7+8-MN9), Los Mansuetos (MN12).

Referred specimens. Hostalets de Pierola indeterminate: IPS12652 (Figure 1v), distal end of right humerus. Los Mansuetos: IPS12673 (Figure 1w), pedal phalanx 3 of digit III.

Description. Regarding the phalanx from Los Mansuetos, its proximal articular facet has a pyriform-rounded shape. The apophysis flexoris is large and fairly exceeds the apophysis extensoris, which is relatively small and pointed. Its plantar surface is slightly concave. With regard to the humerus, the distal humeral morphology of strigiforms is fairly distinguishable from that of accipitriforms. Among some of the most conspicuous features, the condylus dorsalis is more developed and distally protruding in the diurnal raptors. In Strigidae the epicondylus dorsalis is larger than in *Tyto* and is more protruding dorsally. The zone of the processus flexorius and the epicondylus ventralis is more robust in Strigidae. The fossa musculi brachialis is more marked in *Tyto* than in Strigidae. The humeral fragment from Hostalets is indistinguishable from *Tyto balearica*.

Measurements. For the humerus, see Table 2. There are few data on phalangeal measurements. The maximum length of the phalanx from Los Mansuetos is 16.4 mm, which is between the values for the extant *Tyto alba* (11.4–12.3 mm, N=17; Langer, 1980) and *Tyto balearica* from the Middle Pleistocene of Corsica and Sardinia (18.1 and 18.3 mm; Louchart 2002), but is very close to the measurements of *Tyto balearica* from the Pliocene of Sète (16.7 mm; Mourer-Chauviré and Sánchez Marco 1988).

[TABLE 2 ABOUT HERE]

Remarks. Villalta (1963) attributed with doubts the phalanx from Los Mansuetos to the strigiforms. Indeed, this phalanx belongs to *Tyto*. The articular facet is distinctively more elongated than in Strigidae. In this family, the processus flexorius does not exceed the extensorius process, or exceeds it slightly. However, in *Tyto* that happens in phalanges 3 III and 4 IV, as it can be seen in the fossil from Los Mansuetos. In diurnal raptors, this phalanx shows a subtriangular articular facet. There are no published data for this phalanx in *Tyto sanctialbani*, and hence it may not be excluded that the phalanx from Los Mansuetos might be attributable to such a taxon.

The humerus from Hostalets de Pierola, in turn, was first identified as *Aquila* cf. *minuta* Milne-Edwards, 1871 by Villalta (1963), and later assigned to *Hieraaetus edwardsi* (Sharpe, 1899) by Mlíkovský (2002). The distal width of this humerus is 16.9 mm, which exceeds the variation ranges of the extant barn owls *Tyto alba* (see Langer 1980) and *Tyto sanctialbani* (see Sánchez, 2001; Mlíkovský

1998; Pavia and Mourer-Chauviré 2011) , as well as the recently described *Miotyto montispetrosi* (Göhlich and Ballmann 2013) from Steinberg and Goldberg (MN6). *Tyto robusta* and *Tyto gigantea* from Gargano (Ballmann 1973, 1976) reach larger sizes. There are no published measurements of the distal end of this bone for *T. gigantea*, but its total length corresponds to a bone fairly larger than the humerus from Hostalets. *Tyto robusta* and *T. gigantea* were synonymized by Mlíkovský (1998), who considered *T. gigantea* as a larger-sized chronospecies of the earlier *T. robusta*, and consequently synonymized *Tyto robusta* Ballmann, 1973 with *Tyto gigantea* Ballmann, 1973. The size of the specimen from Hostalets fits into the corresponding range of values of *Tyto balearica* (Table 2).

Bones attributed to *Tyto sanctialbani* have been reported from Toril 3 (MN7+8) and La Grive-Saint-Alban (MN7+8) up to the upper Miocene (MN10) of Kohfidisch (Austria) (Mlíkovský 1998; Sánchez Marco 2001; Pavia and Mourer-Chauviré 2011). Mlíkovský (1998) synonymized *Tyto campiterrae* Jánossy, 1991 with *T. sanctialbani*. The former was described by Jánossy (1991) on the basis of bones from the Hungarian locality of Polgárdi (MN13), with the larger size *T. campiterrae* as the sole declared difference from *T. sanctialbani*. In a recent work on the remains of *T. sanctialbani* from La Grive-Saint-Alban, Pavia and Mourer-Chauviré (2011) supported the taxonomic validity of *T. campiterrae* as a valid species on the basis of a photograph, and against the view by Mlíkovský (1998) that these two nominal taxa are synonymous. However, Pavia and Mourer-Chauviré (2011) did not provide any measurements to support their view. The measurements of *T. campiterrae* provided by Jánossy (1991) fit into the size ranges of *T. balearica* (see Table 2). Pavia and Mourer-Chauviré (2011) further concluded that *T. balearica* is not recorded in the Miocene, as previously pointed out by Louchart (2002), but did not based their conclusion on the consideration of size and morphology. In fact, these authors did not deal throughout their paper with the Miocene fossil remains previously assigned to *Tyto balearica*, with the only exception of those attributed to *Tyto campiterrae*. Louchart (2002), in contrast, did discuss the bones allocated to *T. balearica* from Mio-Pliocene localities, and therefore deserves further discussion. On the remains from Aljezar B (MN12) assigned to *T. balearica* by Cheneval and Adrover (1993), Louchart (2002: 72) asserted (my translation from the French original): they “prove to be different from *T. balearica* (by the lower dimensions of certain bones, especially the posterior phalanges). This will not be detailed here, but separately (Louchart, in preparation). These data are therefore considered not related to *T. balearica*.” Louchart (2002) said nothing about the descriptions of the bones or the fact that the measurements given by Cheneval and Adrover (1993: table 4) fit the size ranges of *T.*

balearica from the localities where such a species was originally described. In that study, the reconsideration of the measurements of the fossils of *T. balearica* from other Miocene and Pliocene French and Spanish localities (Sète, Balaruc II, Layna, Valdecebro 5, Moreda; see Mourer-Chauviré and Sánchez Marco 1988; Sánchez Marco 2001) follows the same reasoning: some values fall above or below the original sample from the Balearic original localities plus the Pleistocene Corsican remains reported in that same work, apparently meaning that the samples from Balearic, Corsica and Sardinia islands encompass the whole size ranges of *Tyto balearica*. On this basis, it is difficult to understand why Louchart (2002) agreed the remains from the Spanish site of Almenara-Casablanca 1 (a distal end of tarsometatarsus and a pedal phalanx) were attributed to *T. balearica*, but not the bones from Sète (see Table 2), for instance. It is noteworthy that the osteometric data from the original localities are very scarce (the best represented measure being available only from three specimens), whereas data from Corsica and Sardinia are based on larger sample sizes (although even there only a few measures reach high numbers enough for statistical purposes). It is even more remarkable that some bones of the owl from Corsica and Sardinia reach values considerably different from those of the Balearic islands as well as from mainland localities. The *Tyto* described in Corsica and Sardinia is in general small-sized than the Balearic taxon. Only the femur, some measures of the tarsometatarsus and one of the humerus fit with *Tyto balearica*, which could be indicative of a singular process of insular differentiation, as in the cases of *Bubo insularis* Mourer-Chauviré and Weesie, 1986, and *Athene angelis* Mourer-Chauviré et al., 1997, on the same islands. After re-examining again the bones attributed to *T. balearica* from Iberian localities, and reviewing the corresponding descriptions and measurements (see Table 2) provided by Mourer-Chauviré and Sánchez Marco (1988), Cheneval and Adrover (1993) and Sánchez Marco (2001), it is concluded here that these bones are indistinguishable from the holotype and the associated material of *T. balearica* (Mourer-Chauviré et al. 1980). On the other hand, the diagnostic characters of the genus *Miotyto* Göhlich and Ballmann, 2013, are not present in the fossil material of *T. balearica*. Thus, in the tarsometatarsus of the latter species, there is no vestigial arcus extensorius (see dorsal views in Figure 4.2) and the tuberculum musculi fibularis brevis is not directed plantolaterally, unlike in *Miotyto*. *Tyto balearica* (see proximal views in Figure 4.2) shares both features with *T. alba*, which shows that the Neogene remains attributed to *T. balearica* cannot be alternatively assigned to a species of *Miotyto*.

[PLACE FIGURE 2 ABOUT HERE]

Order Accipitriformes Vieillot, 1816

Family Accipitridae Vieillot, 1816

(Figure 1x, y)

Localities. Hostalets de Pierola indeterminate (MN7+8-MN9), Los Valles de Fuentidueña (MN9), Viladecavalls (MN10).

Referred specimens. Hostalets de Pierola indeterminate: IPS12653, pedal (ungual) phalanx. Viladecavalls: IPS12674 (Figure 1x), pedal phalanx 1 of digit III; IPS12675, proximal end of pedal phalanx 1 of digit I. Los Valles de Fuentidueña: IPS12676 (Figure 1y), pedal (ungual) phalanx.

Description. The phalanx 1 digitis I from Viladecavalls lacks its distal end. Its articular cotyla is laterally elongated. The proximal end is compressed cranio-plantarly. A groove runs along the plantar side of the phalanx. The articular cotyla of the phalanx 1 digitis III from Viladecavalls adopts a rounded shape. Its plantar groove is deep at the proximal area of the bone. Fovea subtrochlearis absent, and foveae ligamenti collateralis marked.

Measurements. Viladecavalls—phalanx 1 digitis I: maximum length, 15.9 mm; maximum width of the proximal end, 5.7 mm. Viladecavalls—phalanx 1 digitis III: maximum width of the proximal end, 8.5 mm. Hostalets de Pierola indeterminate—pedal (ungual) phalanx: maximum length, ca. 26.2 mm; width of the proximal end, 4.8 mm. Los Valles de Fuentidueña—pedal (ungual) phalanx: maximum length, 21.0 mm; width of the proximal end, 5.0 mm.

Remarks. The two phalanges from Viladecavalls were attributed to *Aquila* sp. by Villalta (1963), and this assignment was retained by Mlíkovský (2002). Although lacking the distal end of the phalanx 1 digitis I, the bone did not stretch much more because the preserved remain retains the curve at the end of the bone. By its size and general shape, both phalanges from Viladecavalls are reminiscent of *Buteo* Lacépède, 1799, *Accipiter* Brisson 1760, and *Hieraaetus pennatus* Gmelin, 1788. A more detailed study of these phalanges is the subject of an ongoing separate work.

The two ungual phalanges from Hostalets de Pierola and Los Valles de Fuentidueña were attributed to *Aquila* cf. *minuta* Milne-Edwards, 1871 by Villalta (1963), although Lambrecht (1933) had previously established that this taxon was a junior synonym of *Aquila edwardsi* (Sharpe, 1899). Later, Mlíkovský (2002) proposed the new combination *Hieraaetus edwardsi*, in which the material from

Hostalets was included. The item from Los Valles de Fuentidueña was not mentioned in that work. However, due to the lack of diagnostic features, little can be said on the taxa to which these ungual phalanges belong, other than concluding that they belong to an accipitriform of intermediate size.

Order Charadriiformes (Huxley, 1867)

Family Recurvirostridae Bonaparte, 1831

Recurvirostra teruelensis (Villalta, 1963) new combination

(Figure 1z)

Totanus teruelensis Villalta, 1963:268, pl. II: fig. 5, 5a, 5b, pl. III: fig. 1, 1a, 1b (original description).

Tringa teruelensis (Villalta, 1963): Bocheński 1997:316 (new combination).

Larus teruelensis (Villalta, 1963): Mlíkovský 2002:137 (new combination).

Localities. Los Mansuetos (MN12).

Referred specimens. IPS12677, distal end of right humerus. The distal end of ulna reported by Villalta (1963) has not been found.

Description. This is the emended description of the fragment of humerus (holotype). The processus supracondylaris dorsalis is partially broken, but a wing-like surface in the dorsal edge of the distal end of the humerus (between the dorsal condyle and the dorsal epicondylar process), which is characteristic of several charadriiforms, is discernible. Its contour is sinuous. The sulcus humerotricipitalis is deep. The processus flexorius is relatively small and the epicondylus ventralis is round and very pronounced. The condylus dorsalis protrudes dorsally.

Measurements. Smallest width of the diaphysis, 3.4 mm; distal width, 7.6 mm; distal depth, 4.8 mm.

Remarks. Villalta (1963) erected the species *Totanus teruelensis* based on a distal end of humerus and a distal end of ulna. Both items were described and figured (Villalta 1963), but the ulnar fragment has not been found in the collection by the author of the present work. None of them was designated as the holotype. Although, whereas the humeral fragment was described first, this one should be considered the holotype. Olson (1985) indicated that this taxon had been based on the humeral

fragment, and noted down that the deep fossa musculi brachialis was more like to that seen in the humerus of gulls. Bocheński (1997) synonymized *Totanus* Bechstein, 1803 with *Tringa* Linnaeus, 1758. Finally, Mlíkovský (2002) considered Olson's (1985) opinion on the fossa musculi brachialis to be correct, and transferred the taxon to *Larus* Linnaeus, 1758. However, the fossa musculi brachialis is considerable deeper in *Larus*, *Sterna* Linnaeus, 1758 and *Gelochelidon* CL Brehm, 1830 than in the fossil from Los Mansuetos. The condylus dorsalis is prominent in the studied specimen, as in *Recurvirostra* and in *Gelochelidon*, but not as prominent in *Tringa*, *Limosa* Brisson, 1760, *Himantopus* Brisson, 1760, *Calidris* Pallas, 1764, *Arenaria* Brisson, 1760, *Actitis* Illiger, 1811, and *Lymnocyrtus* F. Boie, 1826. A sinuous contour of the dorsal edge of the bony wing is seen in *Recurvirostra*, whereas in *Tringa* Linnaeus, 1758, *Limosa* and *Himantopus* such an edge is smooth. The condylus ventralis protrudes more distally than the condylus dorsalis in the fossil. This feature is only seen in *Recurvirostra*, and *Haematopus* Bonaparte, 1838, and slightly in *Limosa*. The processus supracondylaris dorsalis is more developed in *Gelochelidon*, *Arenaria*, *Tringa*, *Sterna* and *Limosa*. The fossa musculi brachialis is less deep in: *Haematopus*, *Himantopus* and *Limosa*. The fossil specimen from Los Mansuetos is considerably smaller than the corresponding element in the extant *Recurvirostra avosetta* Linnaeus, 1758.

Charadriiformes indet.

(Figure 1a')

Localities. El Fallol (MN3).

Referred specimens. IPS56, distal end of left tarsometatarsus.

Description. This item is a very small bone fragment. The trochleae of digits II and IV are eroded and their corresponding plantar ends are absent. Both of them reach the same level distally. The trochlea of digit III is fairly larger and distally more protruding than the other two. In Cathartidae, the trochlea of digit IV reaches distally as far as the trochlea of digit III, or exceeds this one, which is not seen in the fossil from El Fallol. In distal view, the trochleae do not form a marked curvature. Its overall appearance points to the charadriiforms, but this small piece of bone lacks diagnostic traits to pinpoint its identification. *Sterna paradisaea* Pontoppidan, 1763 is the recent species to which the fossil bears a greater resemblance, although the former is smaller.

Measurements. Distal width, 6.6 mm; distal depth, ca. 4.2 mm.

Remarks. Based on this tiny distal end of tarsometatarsus, Villalta Comella and Crusafont Pairó (1955) erected the species ?*Plesiocathartes gaillardi*. This genus allocation was owed to the morphological similarities with the Eocene/Oligocene species *Plesiocathartes europaeus* Gaillard, 1908 from Quercy. However, according to Gaillard (1908), *Plesiocathartes europaeus* was in its turn even smaller than any other known Cathartidae. In the original description, *Plesiocathartes gaillardi* was considered to be even smaller than the type species of the genus (Crusafont and Villalta 1955). The taxonomic validity of the former taxon was maintained by Villalta (1963). However, Jollie (1977) dismissed any link between *Plesiocathartes europaeus* and the Cathartidae, and Mlíkovský (2002) placed both *Plesiocathartes europaeus* and *Plesiocathartes gaillardi* as Aves incertae sedis. *Plesiocathartes gaillardi* should be taken as *nomen dubium*.

Order Passeriformes (Linnaeus, 1758)

Parvorder Passerida Sibley et al., 1988

Localities. Los Mansuetos (MN12).

Referred specimens. IPS73335, distal end of left humerus.

Description. This bone shows a typical passeriform morphology. The processus flexorius is well developed and protrudes disto-ventrally. Brachial depression absent. The impression of the anterior articular ligament is deep and large. The fossa olecrani is deep.

Measurements. Smallest width of the diaphysis, 1.7 mm; distal width, 4.4 mm; distal depth, 2.2 mm.

Remarks. Villalta (1963) attributed this humeral fragment to *Fringilla* sp. However, several families of Passeriformes resemble the fossil in both size and shape, so that a more precise taxonomic attribution is not warranted. The bone size prevents it to be attributed to Corvidae.

4 Discussion and conclusions

A summary of the taxa discussed in this study provides is given in Table 3. Most of prior identifications gathered from the literature are wrong. The item from Can Mas assigned to *Palaeortyx edwardsi* is now attributed to *Palaeortyx phasianoides*. Three taxa have been found to be taxonomically

invalid: *Phalacrocorax ibericum* Villalta, 1963 is a junior subjective synonym of *Palaeortyx gallica*; *Coturnix miocenica* Villalta, 1963 is a junior subjective synonym of *Palaeortyx brevipes*/P. *grivensis* , and ?*Plesiocathartes gaillardi* Crusafont et al., 1955 is a *nomen dubium*, being attributed to an indeterminate charadriiform. The species *Totanus teruelensis* Villalta, 1963, later transferred to *Larus teruelensis* by Mlíkovský (2002), is now transferred to *Recurvirostra teruelensis* (Villalta, 1963) comb. nov. The fragment of humerus from Los Mansuetos assigned to *Fringilla* sp. shares features with several families of Passerida and should be thus considered an indeterminate representative of this taxon. There is no evidence of *Aquila minuta* Milne-Edwards, 1871—transferred to *Aquila edwardsi* by Lambrecht (1933) and to *Hieraetus edwardsi* by Mlíkovský (2002)— in the Iberian record. The distal end of humerus from Hostalets de Pierola formerly attributed to *Aquila* cf. *minuta* is now attributed to *Tyto balearica*, whereas the two ungual phalanges from Hostalets and Los Valles de Fuentidueña are assigned to Accipitridae indet. Two pedal phalanges from Viladecavalls, previously assigned by Villalta (1963) to *Aquila* sp., are now attributed to Accipitridae indet.

A large phasianid, *Miophasianus altus*, is recorded from the Early to the Late Miocene of the Iberian Peninsula (Sánchez Marco 2006; and the present study). Another large-sized taxon of this group, *Miophasianus medius*, was already known from the Middle to Late Miocene of Hostalets de Pierola (Sánchez Marco 2006), and now it is also reported from the Late Miocene of Batallones. Also, a number of skeletal remains belonging to smaller-sized forms have been found along the Miocene. The smallest is *Palaeortyx joleaudi*, from the MN 4 of La Artesilla. Other small-sized skeletal elements from the Middle to the Late Miocene could be assigned to either *Palaeortyx brevipes* or *Palaeortyx grivensis*. Some bones slightly larger, from the Middle and Late Miocene, belong to *Palaeortyx gallica*. Finally, *Palaeortyx phasianoides* has been found from the Early and Middle Miocene.

[TABLE 3 ABOUT HERE]

Villalta and Crusafont (1950) attributed a distal end of humerus from Hostalets de Pierola to *Palaeortyx miocaena*. That work yielded a poor-quality drawing of it. The same taxonomic assignment was kept by Villalta (1963), in which all the studied bones were figured with photographs, with the exception of this humeral fragment. That is why it is likely that the bone was already lost in 1963.

In the Neogene of Europe, there are owl skeletal remains referable to the family Tytonidae. Apart from *Miotyto montispetrosi*, these remains are morphologically indistinguishable from the extant species *Tyto alba*, or discernible only by minor details. *Tyto sanctialbani* has a similar size to *Tyto alba* and *Miotyto montispetrosi*, and has been recorded from the late Aragonian to the Vallesian. Larger bones than those of the extant barn owl, and of similar size than those of *Tyto balearica* from its original localities, have been reported likewise from the Middle Miocene to the Middle Pleistocene. The bones attributed to *Tyto campiterrae* can not be distinguished from those of *Tyto balearica*, the former thus being a junior subjective synonym of the latter. In contrast, *Tyto robusta* and *Tyto gigantea*, from the Mio-Pliocene of Gargano island, are remarkably larger than their congeneric species.

Louchart (2002) found abundant material of a species of *Tyto* in the Middle Pleistocene of Sardinia and Corsica. These bones are larger than those of the extant *Tyto alba*, and some of its measurements are similar to those of *Tyto balearica*, but most of them correspond to a smaller-sized form of barn owl. Rather than describing a new species, Louchart (2002) attributed this material to a new subspecies, *Tyto balearica cyrneichnusae*. The subspecies notion is useful when it refers to populations bearing few different features, but capable of interbreeding with other populations with the result of fertile offspring. A fossil or paleontological species designates a collection of morphological features observed on fossil items. Predictably, many species described on fossils correspond to extinct biological species, but such an assumption is not free of uncertainty in each particular case. A subspecies within a paleontological species raises a controversial issue because the theoretical criterion of required interbreeding among individuals of different subspecies cannot be tested. Two sets of morphological characters that differ in a few of them have to be designated with different specific names because it cannot be assumed that they formed in the past a single breeding community. The fossil material in itself must be the only base for describing new taxa. Geographical and temporal distributions of the findings should be viewed as extrinsic features, not valid for the decision of erecting a new taxa. Methodologically, it is incorrect to take the size ranges of the bones of Corsica and Sardinia as those of *Tyto balearica*, and then discard the entire peninsular record with the exception of Almenara-Casablanca 1, a site from the last Pliocene and located on the Iberian Mediterranean coast. Indeed, the measurements on the mainland remains of *Tyto balearica* overlap with those from Sardinia and Corsica.

The rejection of the continental record of *Tyto balearica* is based on the interpretation consisting in an owl, larger than the extant *Tyto alba*, spread over the west of the Mediterranean, appearing in the

Plio-Pleistocene boundary and becoming extinct in Corsica around the middle to late Pleistocene. Implicit in this reasoning is to take *Tyto balearica* as a biological species. An alternative explanation, knowing that *Tyto alba* was widely extended over the continent from the early Pleistocene onwards (see Tyrberg 1998), would be that the fossil remains from Sardinia and Corsica might represent a process of insular differentiation from populations of *Tyto alba*, which avoids the chronological and geographical gaps between the localities in the Balearic Islands as well as in Sardinia and Corsica.

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803 **Figures and tables captions**

- 804 Figure 1. Avian fossil remains from several Miocene Iberian localities. **(a–f)** *Miophasianus altus*:
805 IPS12651, right humerus in cranial aspect (a); IPS12649, left humerus in cranial view (b); IPS12671, left
806 ulna in ventral view (c); IPS12672, right ulna in ventral view (d); IPS12670, right femur in cranial aspect
807 (e); IPS12668, right tibiotarsus in cranial view (f). **(g, h)** *Miophasianus medius*: IPS12648, left humerus
808 in caudal view (g); without number (Batallones 3), right radius in dorsal view (h). **(i)** *Palaeortyx joleaudi*:
809 MNCN 74035, right humerus in caudal view. **(j–p)** *Palaeortyx brevipes* / *Palaeortyx grivensis*:
810 IPS87218, left carpometacarpus in ventral view (j); MNCN 74029, left tarsometatarsus in dorsal view (k);
811 MNCN 74033, left humerus in caudal view (l); MNCN 74030, left coracoideum in dorsal aspect (m);
812 without number (Batallones 1), left humerus in caudal view (n); without number (Batallones 1), right
813 scapula in lateral view (o); IPS12678, right carpometacarpus in ventral view (p). **(q, r)** *Palaeortyx*
814 *phasianoides*: IPS12647, left humerus in caudal view (q); MNCN 74028, right carpometacarpus in
815 ventral view (r). **(s–u)** *Palaeortyx gallica*: IPS73336, right tibiotarsus in cranial view (s); MNCN 74027,
816 left tibiotarsus in caudal view (t); IPS12650, right humerus in cranial view (u). **(v, w)** *Tyto balearica*:
817 IPS12652, right humerus in cranial aspect (v); IPS12673, pedal phalanx in lateral view (w). **(x)**
818 Accipitridae indet.: IPS12674, pedal phalanx in plantar view. **(y)** Accipitridae indet.: IPS12676, pedal

(ungual) phalanx in lateral view. (z) *Recurvirostra teruelensis*: IPS12677, right humerus in cranial view.

(a') Charadriiformes indet.: IPS56, left tarsometatarsus in dorsal aspect. Scale bar equals 1 cm.[planned for page width]

Figure 2. Tarsometatarsi of *Tyto balearica* from Valdecebro 5 (a–f) and Layna (g–j), in dorsal (a, c, e, g, i) and proximal (b, d, f, h, j) views. Scale bar equals 1 cm. [planned for column]

Table 1. Measurements (in mm) of forelimbs of large-sized European Miocene galliforms. References are indicated as superscripts: 1, Göhlich (2002); 2, Bocheński (1987); 3, Sánchez Marco (2006); 4, this study. Notes: *, *Miophasianus altus* for Göhlich (2002); **, *Miophasianus altus* for Villalta and Crusafont Pairó (1950). Number of specimens in brackets.

Table 2. Measurements (in mm) of strigiforms. References are indicated as superscripts: 1, Langer (1980); 2, Louchart (2002); 3, Mourer-Chauviré et al. (1980); 4, Mourer-Chauviré and Sánchez Marco (1988); 5, Sánchez Marco (2001); 6, Ballmann (1973); 7, Jánossy (1991); 8, Mlíkovský (1998); 9, Pavia and Mourer-Chauviré (2011); 10, Göhlich and Ballmann (2013); 11, this study. Number of specimens in brackets.

Table 3. Some taxa found in Miocene Iberian localities. Localities: 1, Fallol; 2, Can Mas; 3, La Artesilla; 4, Hostalets de Pierola indeterminate; 5, Toril 3; 6, Escobosa; 7, Los Valles de Fuentidueña; 8, Can Poncic; 9, Viladecavalls; 10, Batallones 1 and 3; 11, Valdecebro 5; 12, Los Mansuetos.

Table S1. Measurements (in mm) of scapulae and humeri of medium and small-sized European Miocene galliforms. References are indicated as superscripts: 1, this study; 2, Göhlich (2002); 3, Göhlich and Mourer-Chauviré (2005); 4, Cheneval (2000); 5, Göhlich and Pavia (2008); 6, Ballmann (1969); 7, Cheneval and Adrover (1993). Number of specimens in brackets.

Table S2. Measurements (in mm) of coracoidea of medium and small-sized European Miocene galliforms. References are indicated as superscripts: 1, Göhlich and Mourer-Chauviré (2005); 2,

848 Ballmann (1969, as *Palaeortyx depereti*); 3, Cheneval and Adrover (1993); 4, Göhlich and Pavia (2008);
849 5, this study. Number of specimens in brackets.
850

Table 3. Some taxa found in Miocene Iberian localities. Localities: 1, Fallol; 2, Can Mas; 3, La Artesilla; 4, Hostalets de Pierola indeterminate; 5, Toril 3; 6, Escobosa; 7, Los Valles de Fuentidueña; 8, Can Poncic; 9, Viladecavalls; 10, Batallones 1 and 3; 11, Valdecebro 5; 12, Los Mansuetos.

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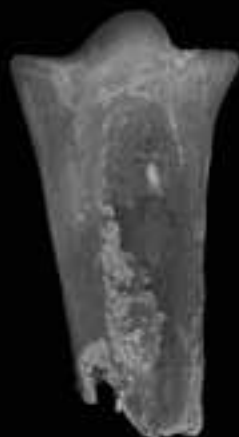




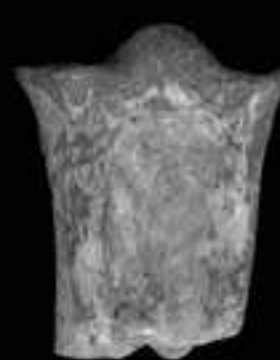
a



c



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g



i



b



d



f



h



j



Number of specimens in brackets.

Humerus	Age	Gl	Pw	Pd	Wd	Dw	Dd
<i>M. altus</i> (La Grive) ¹	MN7+8	103.2	24.3–26.1 (4)	—	9.9	20.7–21.1 (2)	—
<i>M. altus</i> (Steinheim) ¹	MN7+8	100.5	ca. 25.9–27.0 (2)	—	9.6–10.0 (2)	19.7–21.0 (2)	—
<i>M. medius</i> * (Sandelzhausen) ¹	MN5	—	ca. 18.0	—	—	ca. 17.5	—
<i>M. medius</i> (La Grive) ¹	MN7+8	—	17.9	7.4–7.6 (2)	—	—	—
<i>M. medius</i> (Przeworno II) ²	MN6-	—	>15.5–16.4 (2)	6.9 (2)	—	—	—
	MN7+8	—	—	—	—	—	—
<i>M. medius</i> (Toril 3) ³	MN7+8	—	—	—	—	17.2	8.7
<i>M. altus</i> (Hostalets de Pierola, IPS12649, IPS12651) ⁴	MN7+8-	—	—	—	—	19.0–19.5 (2)	—
	MN9	—	—	—	—	—	—
<i>M. medius</i> (Hostalets de Pierola, IPS 12648) ⁴	MN7+8-	—	17.6	—	—	—	—
	MN9	—	—	—	—	—	—
<i>M. medius</i> ** (Hostalets de Pierola, IPS 12649) ⁴	MN7+8-	—	—	—	—	17.3	—
	MN9	—	—	—	—	—	—

<i>M. altus</i> (Sandelzhausen) ¹	MN 5	—	13.7	—	—	—	—
<i>M. altus</i> (Can Mas, IPS 12671) ⁴	MN7+8-	—	13.6	—	—	—	—
	MN9						
<i>M. altus</i> (Can Mas, IPS 12672) ⁴	MN7+8-	—	—	—	—	12.2	—
	MN9						
Radius							
<i>M. medius</i> (Batallones 3)	MN10	62.5	5.7	5.6	2.8	7.5	3.5
Femur							
<i>M. altus</i> (Steinheim) ¹	MN7+8	101	21	—	—	19	—
<i>M. altus</i> (Dechbetten) ¹	MN5	100	20	—	—	20	—
<i>M. altus</i> (Sandelzhausen) ¹	MN5	116	24.0	14.3	9.5	21.7	17.5
<i>M. altus</i> (Toril 3) ³	MN7+8	87.3	20.0	11.9	8.2	17.4	—
<i>M. altus</i> (Can Mas, IPS12670) ⁴	MN7+8-	—	—	13.7	8.7	—	—
	MN9						
Tibiotarsus							
<i>M. altus</i> (Sansan) ¹	MN6	—	—	—	7.8	ca. 16	15.1
<i>M. altus</i> (La Grive) ¹	MN7+8	—	—	—	8.3	13.3–15.8 (2)	12.2–15.8 (3)
<i>M. altus</i> (Steinheim) ¹	MN7+8	—	—	—	—	15–16 (3)	15–16 (3)

<i>M. altus</i> (Sandelzhausen) ¹	MN5	ca.188	—	—	8.8	12.9–17.5 (3)	ca.12.6– <i>ca.</i> 16.3
							(4)
<i>M. altus</i> (Toril 3) ³	MN7+8	147.5	17.9	16.2	8.7	11.8–14.9 (3)	11.6–15.0 (3)
<i>M. medius</i> (La Grive) ¹	MN7+8	—	—	—	—	ca.10	ca.10.1–10.3
<i>M. medius</i> (Przeworno II) ²	MN6-	—	—	—	—	10.7	ca.10.5
	MN7+8	—	—	—	—		
<i>M. altus</i> (Can Mas, IPS 12668) ⁴	MN4	—	—	—	—	16.0	15.0

Table 2. Measurements (in mm) of strigiforms. References are indicated as superscripts: 1, Langer (1980); 2, Louchart (2002); 3, Mourer-Chauviré et al. (1980); 4, Mourer-Chauviré and Sánchez Marco (1988); 5, Sánchez Marco (2001); 6, Ballmann (1973); 7, Jánosy (1991); 8, Mlíkovský (1998); 9, Pavia and Mourer-Chauviré (2011); 10, Göhlich and Ballmann (2013); 11, this study. Number of specimens in brackets.

	Biozone	Humerus		Ulna		Tibiotarsus	Tarsometatarsus		
		max. length	distal width	prox. width	distal width	distal width	max. length	prox. width	distal width
<i>Tyto alba</i> ¹	—	73.7–85.3 (28)	11.6–13.5 (28)	8.1–9.4 (26)	6.3–7.1 (26)	8.5–10.0 (29)	55.4–64.6 (29)	8.4–9.9 (29)	9.5–11.2 (28)
<i>Tyto balearica</i> (Corsica and Sardinia) ²	Middle Pleistocene	110.6	15.2–16.6 (4)	11.1	8.3–9.2 (8)	10.5–12.7 (12)	72.5	11.8	13.4
<i>Tyto balearica</i> (Canet and S'Ònix) ³	MN17	102.0	16.4–16.9 (2)	—	—	—	—	—	14.4
<i>Tyto balearica</i> (Almenara-Casablanca 1) ⁴	MN17	—	—	—	—	—	—	—	13.1
<i>Tyto balearica</i> (Balaruc II) ⁴	MN16	—	—	>10.4	—	—	—	—	—
<i>Tyto balearica</i> (Moreda) ⁵	MN16	—	—	—	—	10.5	—	—	11.6

<i>Tyto balearica</i> (Sète) ⁴	MN15	—	—	>9.7	>7.2	—	—	—	12.9
<i>Tyto balearica</i> (Layna) ^{5,11}	MN15	—	15.2–16.9 (4)	10.1	—	—	—	10.6–12.1 (4)	11.5–13.0 (2)
<i>Tyto robusta</i> (Gargano) ⁶	MN14– MN15	—	ca. 24.0	—	ca. 11.0	ca. 15.0	—	ca. 15.0	—
<i>Tyto balearica</i> (=T. <i>campiterrae</i> Jánossy, 1991) (Polgárdi) ⁷	MN13	—	14.0–14.5 (3)	—	—	—	64.5–65.7 (2)	10.2–12.5 (11)	11.2–11.4 (3)
<i>Tyto balearica</i> (Valdecebro 5) ⁵	MN12	—	—	—	7.9	11.6	—	10.6–11.6 (3)	—
<i>Tyto sanctialbani</i> (Kohfidisch) ⁸	MN10	—	—	—	—	—	—	10.1	—

<i>Tyto sanctialbani</i> (La Grive) ⁸	MN7+8	—	—	—	—	ca. 8.8	—	ca. 9	10.8–10.9 (2)
<i>Tyto sanctialbani</i> (La Grive) ⁹	MN7+8	—	11.7–14.8 (12)	—	6.8–7.9 (3)	ca. 8.6–10.3 (13)	58.1–60.0 (2)	9.4–ca. 10.5 (7)	10.4–11.9 (18)
<i>Tyto sanctialbani</i> (Toril 3) ⁵	MN7+8	86.9	13.0	—	—	—	—	—	—
<i>Miotyto montispetrosi</i> (Steinberg) ¹⁰	MN6	—	14.4	ca. 9.5–9.7 (2)	—	10.9–11.0 (2)	55.1–55.1 (2)	10.4–10.5 (2)	11.8–11.8 (2)
<i>Tyto balearica</i> (Hostalets de Pierola, IPS12652)	MN7+8– MN9	—	16.9	—	—	—	—	—	—