A new species of Palaeortyx (Aves: Galliformes: Phasianidae) from the Neogene of Gargano, Italy.

A new species of *Palaeortyx* (Aves: Galliformes: Phasianidae) from the Neogene of Gargano, Italy

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ABSTRACT - A new species, *Palaeortyx volans* n. sp., of Phasianidae (Aves: Galliformes) is described from the Neogene vertebrate assemblage of the Gargano (Italy). The Gargano fossil vertebrate association has been well known since 1971, and it is considered to be an island fauna because of the high degree of endemism shown by different taxa. The original description of the fossil avifauna of Gargano referred all the phasianid specimens to *Palaeortyx grivensis*, a fossil species described form the Miocene (MN7+8) of La Grive-Saint-Alban (France). The present study reveals the differences between *Palaeortyx volans* n. sp. and the other species of *Palaeortyx* described until now. The new species described herein represents the smallest species of the genus known, except for *P. joleaudi* from La Grive-Saint-Alban. The systematic position of *P. grivensis* from La Grive-Saint-Alban is supported. Morphometric analysis of the fossil remains of *P. volans* n. sp. suggests good flying capabilities and an ecology similar to that of the recent *Coturnix coturnix*. These features allowed *P. volans* n. sp. to colonize isolated islands such as Gargano, which are normally not inhabited by short-distance flyers like the phasianids.

Keywords: *Palaeortyx, Phasianidae, Galliformes, Gargano, Italy, Neogene,*

Une nouvelle espèce de *Palaeortyx* (Aves, Galliformes, Phasianidae) du Néogène du Gargano - Les gisements de Vertébrés néogènes de la presqu'île du Gargano (Italie) ont livré une nouvelle espèce de Phasianidae (Aves, Galliformes), décrite ici sous le nom de *Palaeortyx volans* n. sp.. Les faunes de ces gisements, signalées pour la première fois en 1971, sont des faunes insulaires dont les taxons présentent un fort degré d'endémisme. L'avifaune a été étudiée par Peter Ballmann en 1973 et 1976. Dans ces deux publications tous les restes de Phasianidae ont été attribués à *Palaeortyx grivensis*, une espèce éteinte décrite dans le Miocène (MN 7 + 8) de La Grive-Saint-Alban (France). Notre étude montre que la forme du Gargano est différente de toutes les autres espèces du genre *Palaeortyx*. La nouvelle espèce est la plus petite connue jusqu'à présent dans ce genre, à l'exception de *P. joleaudi* de La Grive-Saint-Alban. Notre étude confirme également la validité de l'espèce *P. grivensis*. L'analyse morphométrique des différents éléments de *P. volans* montre que cette espèce avait une bonne capacité de vol et suggère une autoécologie semblable à celle de l'actuelle *Coturnix coturnix*. Cette capacité lui a permis de coloniser des îles assez lointaines, comme celles de l'archipel du Gargano, qui normalement ne sont pas atteintes par les autres Phasianidae, qui volent seulement sur de faibles distances.

Mots clés: *Palaeortyx, Phasianidae, Galliformes, Gargano, Italie, Néogène*

INTRODUCTION

The fossil vertebrates of the Mio-Pliocene fissure fillings of Gargano, Italy, are known since the 1970s (Freudenthal, 1971). The avifauna was first described by Ballmann (1973, 1976); in these studies, all the galliform remains were referred to *Palaeortyx grivensis* Lydekker, 1893. Several studies on the mammal fauna [see Abbazzi et al. (1996) for list of references] have been published that reveal that the mammals represent an island fauna, based on the high degree of endemism shown by some taxa. This fact can also be observed in the avifauna (Ballmann, 1973, 1976; Pavia

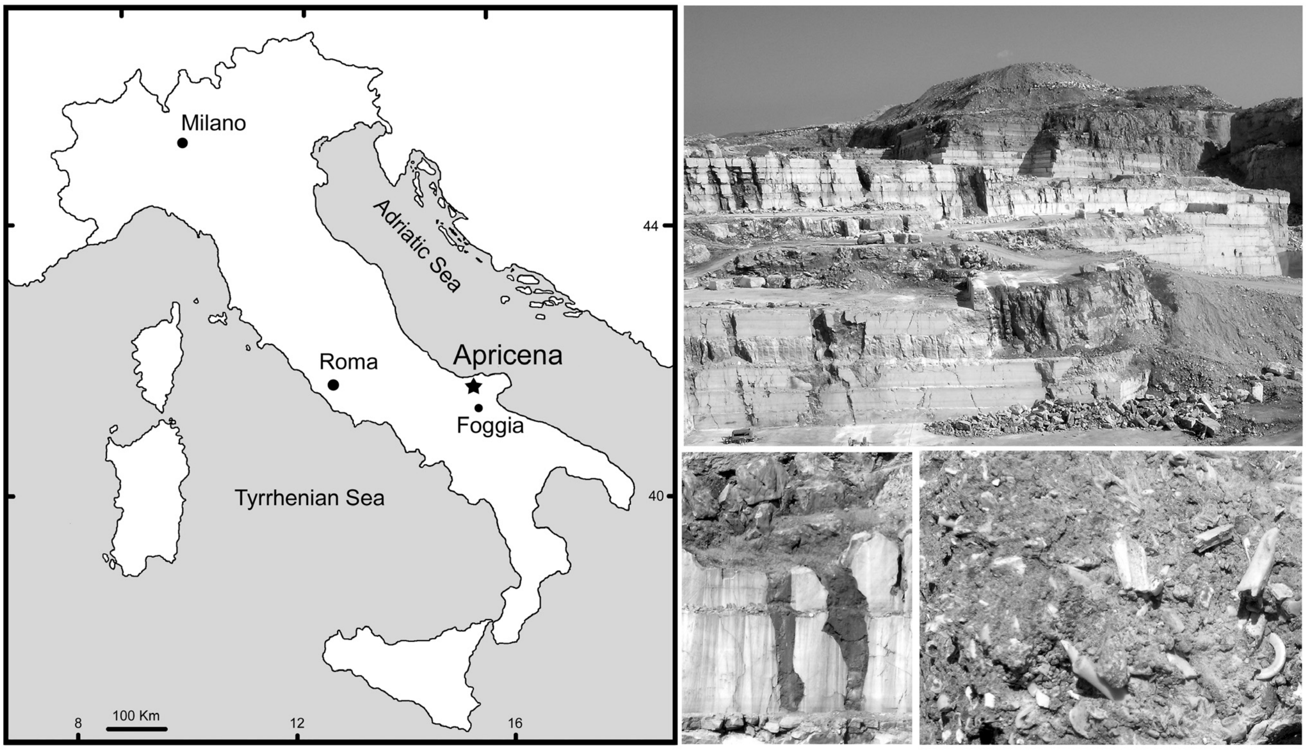

Figure 1 – Location map of the Apricena quarries area (left) and view of the Dell'Erba quarry (right top) and details on the extensive fossiliferous karst network developed in the Mesozoic limestone (right bottom).

& Göhlich, 2004). The whole vertebrate association is very rich, and it comprises several mammalian, avian, reptilian, and amphibian taxa. It is known as the "*Microtia* fauna" after the endemic murid rodent *Microtia* (Freudenthal, 1971). It is assumed that the fissure fillings comprise a notable time span. Whereas Freudenthal (1971, 1976) proposed a Middle Miocene age for the deposits, after more recent analyses, Abbazzi et al. (1996) came to the conclusion that the fossils represent a Late Miocene to Early Pliocene fauna. The "*Microtia* fauna" is assumed to be the remnant of an endemic fauna that inhabited a much larger bioprovince during the Miocene, an interpretation that is also supported by the discoveries at the Tortonian locality of Scontrone, Central Italy, where similar taxa have been found (Mazza & Rustioni, 1996).

The fossiliferous localities of Gargano are located in the area of Apricena (Foggia, Apulia, southern Italy) on the north-western slope of the Gargano promontory. After the first report on the occurrence of fossil vertebrates in this area (Freudenthal, 1971), systematic field research has been carried out by the Nationaal Natuurhistorisch Museum of Leiden (The Netherland) and the University of Firenze (Italy). These field efforts established extensive and varied collections of Neogene and Pleistocene vertebrate remains (Freudenthal, 1976; De Giuli & Torre, 1984; Abbazzi et al., 1996). The Pleistocene fossil assemblage consists of several mammalian, avian, reptilian, and amphibian taxa, which were described in several papers (Abbazzi et al., 1996, Delfino & Bailon, 2000; Rook et al., 2004; Bedetti, 2003).

The Neogene fossil localities consist of a karst network filled by residual clays ("terre rosse") that are locally very rich in continental vertebrate remains. These deposits represent the "*Microtia* fauna". The residual clays accumulated over a wide area during a long period of emergence of the Gargano region, probably from the Late Oligocene to the Early Pliocene. Locally, these clays filled fissures opened in the Mesozoic limestone following long-term sub-aerial exposure of the carbonate platform (Abbazzi et al., 1996). The fissure fillings, exposed in the walls of various quarries in the area, are indicated by the name of the quarry or its owner, followed by a number. As in other karst networks, one fissure filling might be different in age from adjacent fissures, thus the different fissures are treated as separate localities, as listed in Ballmann (1973, 1976) and in the other systematic papers on the Neogene Gargano fossil vertebrates (see Abbazzi et al., 1996, for complete references).

MATERIAL AND METHODS

The material from Gargano described by Ballmann (1973, 1976) is housed in the Naturalis – Nationaal Natuurhistorisch Museum, Leiden (The Netherlands), formerly Rijksmuseum van Geologie en Mineralogie (RGM). This paper concerns new material also housed at RGM, and also several specimens in the collections of the Museo di Geologia e Paleontologia, University of Torino, Italy (PU), Dipartimento di Scienze della Terra, University of Firenze (IGF), and the Naturmuseum Augsburg, Germany (NMA).

For this study, the specimens of *Palaeortyx* from Gargano were compared with the type and additional material of *Palaeortyx brevipes*, *P. gallica*, *P. grivensis*, *P. joleaudi*, and *Palaeocryptonyx depereti* from the following localities: Saint-Gérand-le-Puy (Early Miocene, MN2, France), La Grive-Saint-Alban (Middle Miocene, MN7+8, France), and Quercy (Oligocene, MP25-28, France). This material is in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN), the Muséum d'Histoire Naturelle, Lyon (ML), the Faculté des Sciences de Lyon (FSL) [= Université Claude Bernard, Lyon 1 (UCBL)], and the Natural History Museum, London (NHM). We also used for comparison material of extant *Coturnix coturnix* and *Coturnix coromandelica* from the collections of the Staatssammlung für Anthropologie und Paläoanatomie München (SAPM) and UCBL.

Osteological terminology used in this publication principally follows Baumel et al. (1993) and occasionally Ballmann (1969*a*, *b*); measurements were taken after von den Driesch (1976). Anatomical abbreviations—cmc: carpometacarpus; mc: metacarpale; tt: tibiotarsus; tmt: tarsometatarsus; dist.: distal; prox.: proximal.

Systematic Palaeontology

Class Aves Linnaeus, 1758
Order Galliformes Temminck, 1820
Family Phasianidae Vigors, 1825
Sub-family Phasianinae Vigors, 1825

Genus *Palaeortyx* Milne-Edwards, 1869

Synonymy—see Göhlich and Mourer-Chauviré (2005).

The systematics of the species and the validity of the genus *Palaeortyx* follow Göhlich & Mourer-Chauviré (2005) and differ from those proposed by Mlíkovský (2000, 2002), which included a synonymy of *Palaeortyx* and *Coturnix* (Mlíkovský, 2002: 152f).

Type species—*Palaeortyx gallica* Milne-Edwards, 1869 (designated by Milne-Edwards 1867-71: 230).

Diagnosis—A detailed generic diagnosis was given by Ballmann (1969*b*: 30f), which he emended in 1973 (p. 24f). Cheneval (2000: 344) translated the original diagnosis into French. Göhlich & Mourer-Chauviré (2005) presented an English translation of Ballmann's (1969b, 1973) original and emended diagnoses, and further emended the diagnosis of *Palaeortyx*.

Remarks—The phasianid represented in Gargano is a very small sized species of *Palaeortyx*. Other small sized Neogene phasianids, originally described as *Palaeortyx* are *P. brevipes* Milne-Edwards, 1869, *P. grivensis* Lydekker, 1893, *P. depereti* Ennouchi, 1930, and *P. joleaudi* Ennouchi, 1930. *Palaeortyx brevipes* is recorded from its type locality of Saint-Gérand-le-Puy (Lower Miocene, MN2) and several other Late Oligocene and Early and Middle Miocene localities in Europe (see Göhlich & Mourer-Chauviré, 2005); both *P. grivensis* and *P. depereti* have been described from the Middle Miocene of La Grive-Saint-Alban. Ballmann (1973, 1976) considered *P. depereti* as a junior synonym of *P. grivensis*. However, the lectotype humerus of *P. depereti*, selected recently by Mlíkovský (2002: 154), shows a shallow dorsal fossa pneumotricipitalis and a pneumatic ventral fossa pneumotricipitalis, with a distal bony crest bordering the fossa. Therefore Göhlich & Mourer-Chauviré (2005) referred it to *Palaeocryptonyx* Depéret 1892 [which is not to be confused with *Palaeocryptonyx depereti* Gaillard (1908) from Quercy, which was moved to *Quercymegapodius* by Mourer-Chauviré 1992: 81]. *Palaeortyx grivensis* from La Grive-Saint-Alban was described by Lydekker in 1893 on the basis of one humerus (NHM A319, fig. 2, A). Later, Ennouchi (1930: 72) referred three more humeri (ML LGr 52-54) from the same locality to *P. grivensis*. We agree with Ballmann (1969a, 1973, 1976), that most of the material in the collections at ML and the FSL from La Grive locality labelled as *P. depereti* cannot be distinguished in size and morphology from *P. grivensis*. However, because Mlíkovský (2002) later chose a specimen of *P. depereti* as lectotype, which Göhlich & Mourer-Chauviré (2005) found to belong to the genus *Palaeocryptonyx*, the species *P. depereti* and *P. grivensis* cannot be synonymized as per Ballmann (1969a). Furthermore, *P. grivensis* was synonymized with *Coturnix gallica* by Mlíkovský (2002: 154) [actually *P. gallica* following Göhlich & Mourer-Chauviré (2005)], a decision with which we do not agree because *P. grivensis* is clearly smaller than *P. gallica*, as comparison with the type material demonstrates. However, *P. grivensis* from La Grive-Saint-Alban was later synonymized with *P. brevipes* from Saint-Gérand-le-Puy by Göhlich & Mourer-Chauviré (2005). *P. joleaudi*, known only by one humerus, is distinctly smaller than the species from Gargano and all other named species and can therefore be excluded from further comparisons.

Palaeortyx volans n. sp.
fig. 2, B-O

Synonymy:
Palaeortyx grivensis Lydekker – Ballmann 1973, p. 25, pl. 4, fig. 13-14
Palaeortyx grivensis Lydekker – Ballmann 1976, p. 8, pl. 3, fig. 1-9
Coturnix coturnix (Linnaeus) – Mlíkovský 2002, p.155

Holotype – A complete left humerus RGM 178899, from Chirò 27 (Ballmann, 1976) (fig. 2, B). The humerus is chosen as the holotype because of the various species of *Palaeortyx* are defined by their humeri (Göhlich & Mourer-Chauviré, 2005).


A
B
C
D
E
F
G
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K
L
M
N
O

Type locality – Chirò 27, Chirò quarry, Apricena, (Foggia) Gargano area, Southern Italy (fig. 1). The Chirò 27 fissure excavaded by Freudenthal in the Chirò quarry no longer exists because of the quarry activities; the Chirò quarry is still active at the present time.

Paratypes – Right scapula RGM 425529, proximal half; left coracoid RGM 425513, almost complete; left ulna RGM 425493, complete; left radaius RGM 425969, complete; right carpometacarpus RGM 425504, lacking os mc minus; left femur RGM 425490, complete; left tibiotarsus RGM 425501, distal half; right tarsometatarsus RGM 425514, lacking trochlea IV, all from the Chirò 27 fissure filling.

Stratigraphic and geographic distribution – *Palaeortyx volans* n. sp. is reported from several fissure fillings of the Gargano area, from the older (Biancone) to the younger (San Giovannino) in the most recent interpretation of the "*Microtia* fauna" evolution (Freudenthal, 1976).

Referred specimens – Material (see Annex).

Measurements – See table 1, 2 and 3.

Differential diagnosis – small sized *Palaeortyx*, smaller than *P. brevipes*, but larger than *P. joleaudi. Palaeortyx volans* n. sp. differs from all other species of *Palaeortyx* by its wing and leg proportions, with a proportionally longer carpometacarpus and a proportionally shorter tibiotarsus. *Palaeortyx volans* n. sp. differs from *Coturnix coturnix* and *Palaeocryptonyx depereti* (Ennouchi, 1930) by a humerus with a deeper dorsal fossa pneumotricipitalis and non-pneumatic ventral fossa pneumotricipitalis. *Palaeortyx volans* n. sp. differs from *Coturnix* by a straighter humerus, a carpometacarpus with craniocaudally longer ventral trochlea carpalis and distally longer facies articularis digitalis minus, a tibiotarsus with more strongly developed crista cnemialis lateralis and cranialis, a scapula with a broader and more angled acromion, a femur with a less developed crista trochanteris, and a stouter tarsometatarsus.

Description and comparison – *Palaeortyx volans* n. sp. from Gargano was compared with five specimens of extant *Coturnix coturnix* (SAPM No. 3, female; SAPM No. 9, male, UCBL 130.1, 130.2, 130.4) and two specimens of *Coturnix coromandelica* (UBCL 1980.1, 1980.2). This analysis was to detect any possible differences between these forms and to verify the proposed synonymy of the Gargano specimens with *Coturnix coturnix* as proposed by Mlíkovský (2002: p. 155).

The scapula of *Palaeortyx volans* n. sp. differs from that of *Coturnix* by having an acromion slightly broader which in proximal view forms an angle of distinctly more than 90° (about 110°) with the axis of the proximal end, whereas it is a slightly thinner and forms an angle of about 90° in *Coturnix*. In the proximal part of the humerus, the dorsal fossa pneumotricipitalis of *Coturnix* is more shallow than in *P. volans* n. sp.; and the ventral fossa pneumotricipitalis is pneumatic in *Coturnix*, but not in *P. volans* n. sp.. The humerus shaft of *Coturnix* is straighter and not curved as in *P. volans* n. sp. (in caudal/cranial view). The proximal outline of the proximal end in *P. volans* n. sp. is characterized by an indentation between the caput humeri and the tuberculum ventrale (in caudal/cranial view), as in *Perdix* whereas this indentation is very weak or lacking in *Coturnix*.

The carpometacarpus of *P. volans* n. sp. differs from that of *Coturnix* by having the ventral side of the trochlea carpalis more lengthened caudally and the distal facies articularis digitalis minus more lengthened distally, whereas in *Coturnix* the facies articulares digitales major and minor have about the same length and are about the same level.

The crista trochanteris of the femur of *Coturnix* extends farther distally than in *P. volans* n. sp. Therefore, and in contrast to *Coturnix*, the proximal end of the femur of *P. volans* shows in lateral view a concavity of the cranial edge distally to the crista trochanteris. In addition, the crista trochanteris is proximally more protruding in *P. volans*, as can be seen best in cranial view. *Palaeortyx volans* n. sp. shows two foveae on the caput femoris, whereas there is only one in *Coturnix*.

The proximal tibiotarsus of *Palaeortyx volans* n. sp. differs from that of *Coturnix* by a stronger developed cristae cnemialis lateralis and cranialis.

The tarsometatarsus of *Palaeortyx volans* n. sp. is stouter than that of *Coturnix*.

As shown in fig. 3 the relationships of the limb bone length in *Palaeortyx volans* n. sp. are different from that of *Coturnix coturnix*. The humerus and femur of *Palaeortyx volans* n. sp. are shorter relative to that in *C. coturnix*, whereas

Figure 2 (opposite) – Long bones of *Palaeortyx volans* n. sp. from various locality of the Gargano area compared with the holotype of *P. grivensis* from La Grive-Saint-Alban. A: *Palaeortyx grivensis*, holotype right humerus NHM A 319, caudal view, from La Grive-Saint-Alban; B: *Palaeortyx volans* n. sp., holotype left humerus RGM 178899, caudal view, from Chirò quarry (Chirò 27); C: *Palaeortyx volans* n. sp., distal left humerus RGM 425541, cranial view, from Chirò quarry (Chirò 14a); D: *Palaeortyx volans* n. sp., proximal left humerus RGM 425519, caudal view, from Chirò quarry (Chirò 27); E *Palaeortyx volans* n. sp., paratype incomplete right scapula RGM 425529, lateral view, from Chirò quarry (Chirò 27); F: *Palaeortyx volans* n. sp., paratype left ulna RGM 425493, ventral view, from Chirò quarry (Chirò 27); G: *Palaeortyx volans* n. sp., left carpometacarpus PU 102029, ventral view, from Pirro quarry; H: same bone, dorsal view; I: *Palaeortyx volans* n. sp., left coracoid RGM 425967, dorsal view, from Chirò quarry (Chirò 27); J: *Palaeortyx volans* n. sp., paratype left femur RGM 425490, cranial view, from Chirò quarry (Chirò 27); K: same bone, caudal view; L: *Palaeortyx volans* n. sp., proximal right tibiotarsus PU 102047, caudal view, from Dell'Erba quarry; M: *Palaeortyx volans* n. sp., paratype distal left tibiotarsus RGM 425501, cranial view, from Chirò quarry (Chirò 27); N: *Palaeortyx volans* n. sp., left tarsometatarsus RGM 425553, dorsal view, from Chirò quarry (Chirò 30c); O: same bone, plantar view. The scale bars represent 0,5 cm.

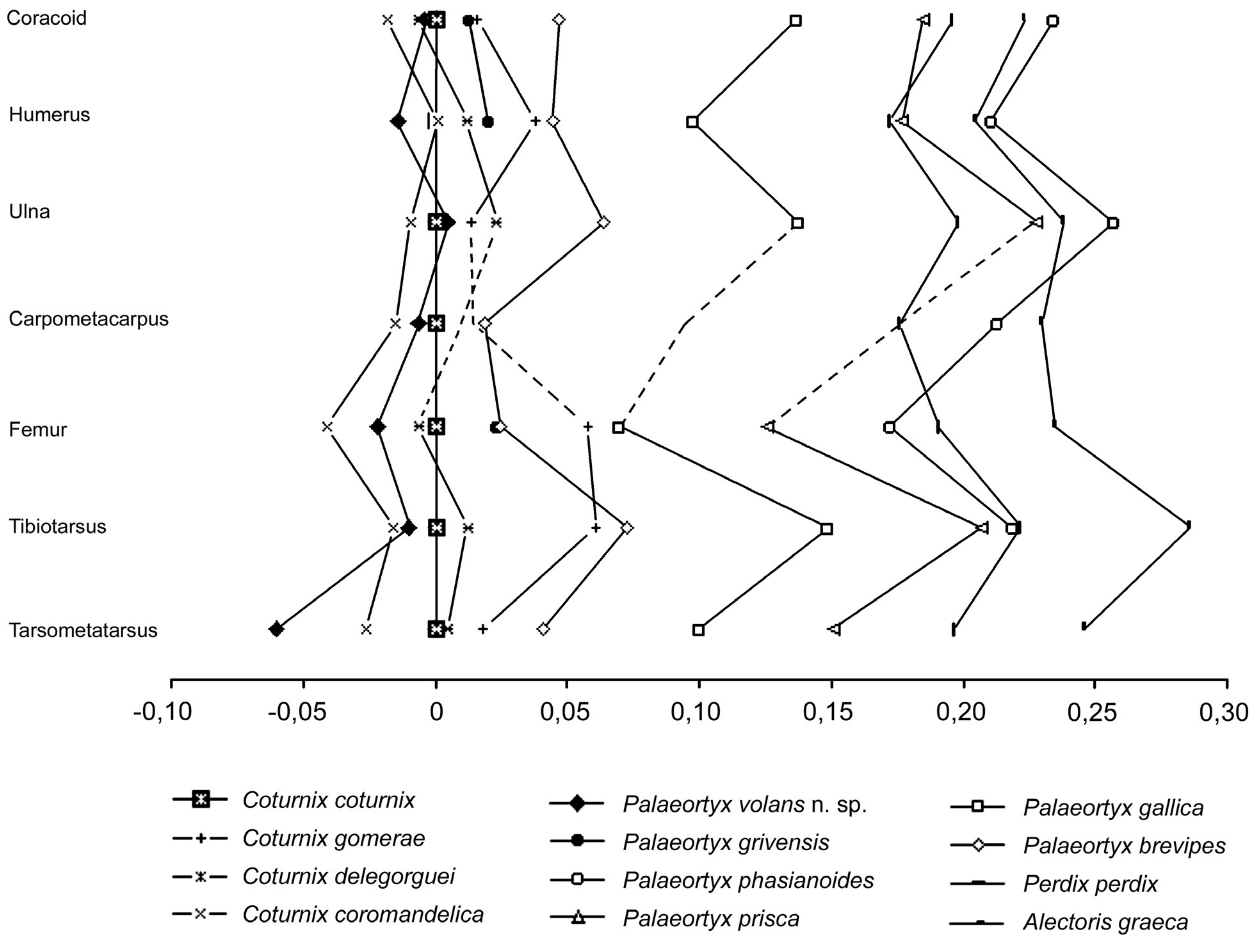

Figure 3 – Ratio diagram of the log differences of the mean dimensions of the long bones of *Palaeortyx volans* n. sp. compared with those of *Coturnix coturnix* (selected as standard), *C. gomerae*, *C. delegorguei*, *C. coromandelica*, *Palaeortyx grivensis*, *P. phasianoides*, *P. prisca*, *P. gallica*, *P. brevipes*, *Perdix perdix* and *Alectoris graeca* (data from Kraft, 1974; Jaume et al., 1993; Göhlich & Mourer-Chauviré, 2005)

the ulna is longer, even if the structure of *Palaeortyx volans* n. sp. is more similar to that of *Coturnix coturnix* than to that of other known species of *Palaeortyx*. The morphological and metrical characteristics of *Palaeortyx volans* n. sp. indicate that this species clearly belongs to the genus *Palaeortyx*, as also shown by the shortness of the tarsometatarsus, which is typical of the various species of this genus (fig. 3); it does not belong to the modern genus *Coturnix*, particularly to *C. coturnix*, as stated by Mlíkovský (2002).

DISCUSSION

In his papers on the Gargano fossil bird assemblages, Ballmann (1973, 1976) referred all the galliform material to *Palaeortyx grivensis*. This species was described by Lydekker (1893) on the basis of a single humerus (NHM A 319) from La Grive-Saint-Alban, France. Later, Ennouchi (1930) referred three more humeri to *P. grivensis* (ML LGr 52-54), and he described a second small sized species of *Palaeortyx* from La Grive, *P. depereti* (Ennouchi 1930). Following the opinion of Ballmann (1969a, 1973, 1976) the latter is a junior synonym with *P. grivensis*. Recently, Mlíkovský (2002) designated a lectotype for *P. depereti*, selecting a complete humerus (ML LGr 50), that shows the morphological characteristics of *Palaeocryptonyx* (Göhlich & Mourer-Chauviré, 2005). For this reason, *"depereti"* must be treated as a valid taxon in the genus *Palaeocryptonyx* and therefore can no longer be considered as synonym of *Palaeortyx grivensis*

After evaluating the material, we agree with Ballmann that all of the *Palaeortyx* material from La Grive-Saint-Alban belongs to one species. Recently Göhlich and Mourer-Chauviré (2005) suggested that this species might be a synonym of *Palaeortyx brevipes*. However, this study supports the validity of *P. grivensis* in La Grive and distinguishes it from *P. brevipes* from Saint-Gérand-le-Puy,

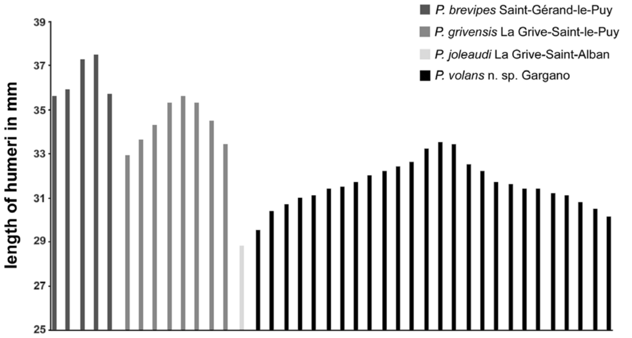

Figure 4 – Total length of the humeri of small *Palaeortyx*: *P. brevipes* from Saint-Gérand-le-Puy, *P. grivensis* and *P. joleaudi* from La Grive-Saint-Alban, *P. volans* n. sp. from Gargano (data for *P. brevipes* from Göhlich & Mourer-Chauviré, 2005).

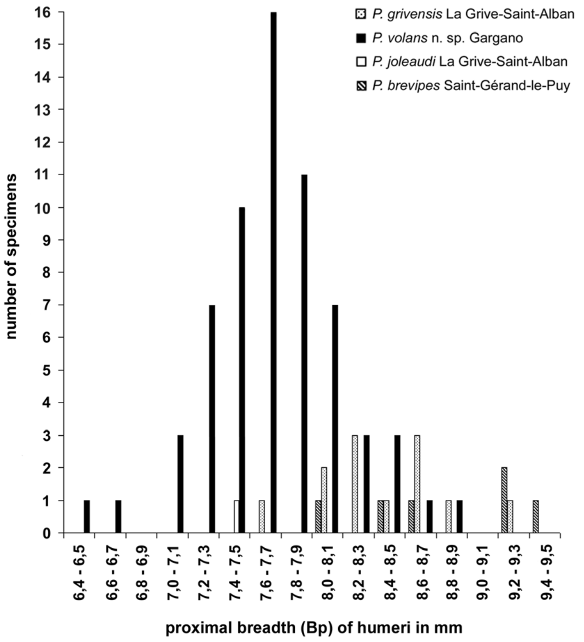

Figure 5 – Value distribution of the proximal breadth of the humerus in small *Palaeortyx*: *P. brevipes* from Saint-Gérand-le-Puy, *P. grivensis* and *P. joleaudi* from La Grive-Saint-Alban, *P. volans* n. sp. from Gargano (data for *P. brevipes* from Göhlich & Mourer-Chauviré, 2005).

as shown in fig. 4. To determine the validity of *Palaeortyx volans* n. sp. we compared the holotype humerus (RGM 178899) with the holotype humerus of *P. grivensis* and the referred humeri from La Grive-Saint-Alban. The humeri of *P. volans* are morphologically and metrically very similar to those of *P. grivensis*; however, the humerus of *P. volans* n. sp. is somewhat smaller (fig. 4) and more slender; its proximal width and, especially, its distal width differ significantly from those of *P. grivensis* (figs. 5, 6).

CONCLUSIONS

Previous work on the fossil bird material from Gargano by Ballmann (1973, 1976) indicated *Palaeortyx grivensis* to be the only species of galliforms in the whole assemblage. However, the analyses presented here reveals that this material belongs to the new species *Palaeortyx volans* n. sp.. This species is, up to now, only found in the Neogene Gargano vertebrate assemblage, as shown in a recent revision of the Miocene galliforms from France (Göhlich & Mourer-Chauviré, 2005) where no similar forms were detected. Based on these data, *P. volans* n. sp. appears to be endemic to that insular bioprovince.

However, limb proportions of different long bones suggest that, compared to the other forms of the genus, *Palaeortyx volans* n. sp. possessed good flying capabilities (fig. 3). In fact, the wing and leg and the relative dimensions of the different bones are more similar to those of species of the genus *Coturnix*, even if in *Palaeortyx volans* n. sp. the shortness of the tarsometatarsus, typical of the genus *Palaeortyx*, is evident. The genus *Coturnix* comprises a large number of living species, widespread in different parts of the world. Some of them show a good flying ability that allows them to migrate, even over long distance, as the case of the Common Quail, *Coturnix coturnix*, and to colonize islands, even those far from the continent (Del Hoyo et al., 1994). In general, galliforms are absent from islands, even from those close to the mainland (Alcover et al., 1992; Mourer-Chauviré et al., 2001). If they are present, it indicates the end of isolation of the island, as the case of the arrival of *Alectoris graeca* in Sicily (Bonfiglio et al., 2002). The only confirmed endemic species of galliform is *Coturnix gomerae*, from the Pleistocene of Canary Islands. This species is clearly derived from *C. coturnix*, and it shows wing and leg proportions that clearly indicate a reduction of its flying ability (Jaume et al., 1993).

The abundant fossil material of the new species *Palaeortyx volans* n. sp. allows us to understand some of its ecology. In fact, the presence of various remains of young individuals, not yet able to fly and, at the same time, the presence of medullary bone in some of the remains, clearly indicate that this species was breeding in the Gargano area (Ballmann, 1979; Matthiesen, 1990). The presence of a breeding species on a island with no endemic characteristics is normally interpreted as the proof of its migratory habit, for this reason we suggest here that *Palaeortyx volans* n. sp. was a migratory galliform, with an ecology very similar to the living *Coturnix coturnix*, which is characterized by annual migrations.

The good flying ability of *Palaeortyx volans* n. sp. is the only way to explain its colonization of the Gargano archipelago, probably quite far from the mainland, as demonstrated by the high degree of endemism of the vertebrate association. On the other hand the good flying ability sug-

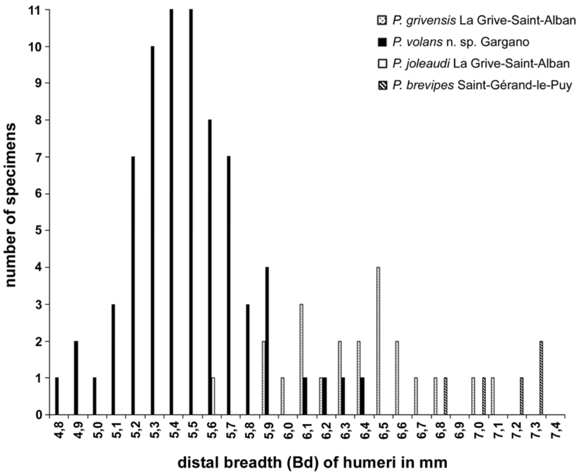

Figure 6 - Value distribution of the distal breadth of the humerus in small *Palaeortyx*: *P. brevipes* from Saint-Gérand-le-Puy, *P. grivensis* and *P. joleaudi* from La Grive-Saint-Alban, *P. volans* n. sp. from Gargano (data for *P. brevipes* from Göhlich & Mourer-Chauviré, 2005).

gests that this species was not strictly endemic to the Gargano area, in that case, in fact, the flying ability was expected to be reduced, as observed in *Coturnix gomerae*. *Palaeortyx volans* n. sp. can be expected to be found in some other fossil assemblages of the Neogene, probably of the Mediterranean area, as it was not recognised in France and Central Europe (Göhlich & Mourer-Chauviré, 2005). In conclusion, this species represents the most abundant bird taxon of the Gargano Neogene vertebrate assemblages, where it was probably an important food source for the numerous birds of prey, mostly strigiforms, present in the association (Ballmann, 1973, 1976; Pavia & Göhlich, 2004). On the other hand, *Palaeortyx volans* n. sp. indicates an open environment with low vegetation and grassland for the Gargano archipelago during the Neogene.

ACKNOWLEDGEMENTS

First of all we would like to thank in particular M. Freudenthal (Leiden), F. Masini (Firenze), C. Petronio (Roma) and M. Rummel (Augsburg) for putting the studied material at our disposal. Special thank to L. van den Hoek Ostende (Leiden) for the possibility to work on the material published by Ballmann and housed in Leiden. We warmly thank C. Mourer-Chauviré for continuous discussions and suggestions and for translating the French abstract. Many thanks are also given to K. Campbell (Los Angeles) for the improvement of the English. We are grateful to S. Chapman (London) and J. Cooper (Tring) for making the holotype of *P. grivensis* available; photo of the holotype of *P. grivensis* was made by P. Crabb of the Photographic Unit of the Natural History Museum, London. This research received support from the SYNTHESYS Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme, in particularly with NL-TAF-2904 to M. Pavia; work supported by Italian MIUR PRIN 2006 to G. Pavia. While conducting this study U. Göhlich was a Humboldt Fellow in the Feodor Lynen Program at the Université Claude Bernard, Lyon 1, France. The authors also thank C. Mourer-Chauviré and an anonymous referee for helpful comments on the manuscript.

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ANNEX - LIST OF EXAMINED MATERIAL OF *PALAEORTYX VOLANS* N. SP.

Scapula—RGM 425952, left prox. half; RGM 425529, right prox half; RGM 425758, right prox. half; RGM 425988, left prox. half; RGM 335994, left prox. half; PU 102078, left prox. end.

Coracoid—PU 102045, left, lacking proc. lateralis; RGM 425513, left, almost complete; RGM 425729, left, lacking proc. acrocoracoideum and proc. lateralis; IGF 112, right, almost complete; RGM 425665, right, almost com-

		GL	Lm	Bp	Dp	Bd	Did	BF	SC	DC
Coracoid										
IGF 112		20,8	20,0	6,2	2,6	-	-	4,4	1,4	2,0
PU 102045		-	21,7	6,7	2,7	-	-	5,0	1,6	2,1
RGM 424729		-	22,3*	-	-	-	-	(4,5)	1,7	2,1
RGM 425513	Paratype	-	20,2	6,7	2,3	-	-	-	1,5	2,1
RGM 425665		21,4	20,4	7,1	2,5	-	-	4,7	1,7	2,2
RGM 425720		-	20,5	6,7			2,6	-		
RGM 425967		22,7	22,1	7,2	2,6	-	-	5,2	1,7	2,3
Humerus										
PU 102022		32,5	-	8,1	-	5,7	-	-	2,7	-
PU 102031		33,4	-	8,5	-	-	-	-	2,9	
RGM 177582		31,1	-	7,7	-	5,3	-	-	2,5	-
RGM 177615		29,5	-	7,0	-	5,2	-	-	2,8	-
RGM 178676		32,4	-	7,9	-	5,4	-	-	2,5	-
RGM 178757		30,7	-	7,4	-	5,4	-	-	2,5	-
RGM 178897		31,4	-	7,6	-	5,5	-	-	2,8	-
RGM 178899	Holotype	32,0	-	7,6	-	5,4	-	-	2,7	-
RGM 178900		30,1	-	7,3	-	5,0	-	-	2,7	-
RGM 178901		32,2	-	8,4	-	5,7	-	-	2,7	-
RGM 178903		30,8	-	7,1	-	5,1	-	-	2,6	-
RGM 178904		32,2	-	8,1	-	5,5	-	-	2,6	-
RGM 178907		31,5	-	7,5	-	5,4	-	-	2,4	-
RGM 178909		30,4	-	7,6	-	5,4	-	-	2,5	-
RGM 178912		33,2	-	7,8	-	5,9	-	-	2,7	-
RGM 178913		31,4	-	7,5	-	5,3	-	-	2,6	-
RGM 178914		31,0	-	-	-	5,2	-	-	2,6	-
RGM 178915		31,4	-	7,3	-		-	-	2,5	-
RGM 178916		31,7	-	7,9	-	5,3	-	-	2,6	-
RGM 178918		31,2	-	7,6	-	5,2	-	-	2,5	-
RGM 178924		31,6	-	7,9	-	5,7	-	-	2,6	-
RGM 178925		31,1	-	7,6	-	5,5	-	-	2,6	-
RGM 178930		30,5	-	7,3	-	4,9	-	-	2,5	-
RGM 178964		33,5	-	-	-	5,5	-	-	2,8	-
RGM 425850		32,6	-	7,7			-	5,7	-	-
RGM 425851		31,7	-	7,8	-	-	-	-	2,7	-
Ulna										
IGF 026		31,6	-	3,5	4,9	2,7	3,1	-	1,5	3,7
PU 102027		26,3	-	3,5	5,0	3,3	3,2	-	1,5	3,8
PU 102069		26,5	-	3,3	4,5	3,0	2,9	-	1,4	3,5
RGM 425493	Paratype	29,8	-	3,4	4,9	3,2	3,2	-	1,5	3,7
RGM 425523		26,8	-	3,2	4,7	3,1	2,9	-	1,6	3,5
Radius										
RGM 425969	Paratype	25,6	-	1,9	2,4	2,8	-	-	1,1	-
Carpometacarpus										
IGF 200		19,4	18,6	5,2	-	-	3,7	-	-	-
PU 102029		19,7	18,7	5,2	-	-	3,5	-	-	-
RGM 425504	Paratype	-	16,2	4,6	-	-		-	-	-
RGM 425552		16,2	15,8	4,5	-	-	3,1	-	-	-
RGM 425728		17,6	16,5	4,9	-	-	3,2	-	-	-
RGM 425977		17,1	16,7	-	-	-	3,1	-	-	-
RGM 425985		17,3	16,9	4,8	-	-	3,2	-	-	-

Table 1 – Measurements of the complete bones of the forelimbs of *Palaeortyx volans* n. sp. Lm for the carpometacarpus is the length of the os metacarpale major. * indicates estimated values.

plete; RGM 425967, left, almost complete; RGM 425720, right, lacking proc. lateralis; PU 102046, left, lacking dist. end; RGM 425891, right, lacking the dist. end; RGM 425645, left, lacking dist. end; RGM 335982, left, lacking proc. acrocoracoideum and proc. lateralis; RGM 425492, left, lacking proc. acrocoracoideum; IGF 201, right, lacking dist. end; RGM 425642, left, lacking dist. end; RGM 425667, left, lacking dist. end; RGM 335981, left, lacking dist. end; RGM 425560, right, lacking dist. end; RGM 425735, right, lacking dist. end; RGM 425732, left, lacking dist. end; RGM 425524, left, lacking dist. end; RGM 335990, left, lacking dist. end; RGM 425674, left, lacking dist. end; RGM 425997, left, prox. half; RGM 335983, left, prox. half; RGM 425904, right, prox. half; RGM 425677, right, prox. half; RGM 425630, right, prox. half; RGM 335992, right, prox. half; RGM 425633, right, prox. half; RGM 425691, right, prox.

		GL	Lm	Bp	Dp	Bd	Did	SC
Femur								
PU 102026		35,0	32,4	6,3	3,7	5,8	5,0	2,4
PU 102081		33,8	32,1	5,9	3,8	5,7	4,8	2,5
RGM 425490	Paratype	34,1	32,1	6,3	4,1	5,7	(4,6)	2,4
RGM 425608		34,0	33,3	6,2	4,1	5,8	4,9	2,6
Tibiotarsus						-	-	
IGF 061+057		41,2*	40,0*	4.8	6.3	-	-	2.2
Tarsometatarsus						-	-	
IGF 131		23,5	-	-	4,0*	-	-	2,4
IGF 99		22,1*	-	-	-	-	-	2,2
NMA 507/1801		23,9	-	5,0	4,9	-	-	2,4
RGM 425514	Paratype	24,0	-	4,8	4,4	-	-	2,4
RGM 425533		22,6	-	4,6*	-	-	-	2,3
RGM 425553		22,2	-	4,6	4,3	5,0	-	2,2
RGM 425586		22,0	-	4,6	4,3	5,2	-	2,3
RGM 425778		24,5	-	5,1	4,8	5,4	-	2,5
RGM 425817		25,0	-	4,9	4,7	-	-	2,4
RGM 425968		22,4	-	4,1*	-	-	-	2,4

Table 2 – Measurements of the complete bones of the hindlimbs of *Palaeortyx volans* n. sp.   * indicates estimated values.

half; RGM 425983, right, prox. half; RGM 425958, left, prox. half; RGM 425682, right, prox. half; RGM 335995, right, prox. half; RGM 425745, right, prox. half; IGF 222, right, prox. half; RGM 425559, left, prox. half; IGF 142, left, prox. half; RGM 425746, left, prox. half; RGM 425989, right, prox. half; RGM 425646, left, prox. half; IGF 36, left, prox. half; RGM 425681, left, prox. half; RGM 425727, left, prox. half; IGF 206, right, prox. end; IGF 65, left, prox. half; RGM 335993, right, prox. half; RGM 425731, right, prox. half; RGM 425738, right, prox. end; RGM 425717, right, prox. half; PU 102079, right, prox. half; RGM 425683, left, prox. half.

Humerus—PU 102022, right, complete; RGM 178897, right, complete; RGM 178900, right, complete; RGM 178903, right, complete; RGM 178907, right, complete; RGM 178916, right, complete; RGM 177582, left, complete; RGM 177615, left, complete; RGM 178768, left, complete; RGM 178757, left, complete; RGM 178899, left, complete; RGM 178901, left, complete; RGM 178904, left, complete; RGM 178909, left, complete; RGM 178912, left, complete; RGM 178913, left, complete; RGM 178918, left, complete; RGM 178924, left, complete; RGM 178925, left, complete; RGM 178930, left, complete; RGM 425850, left, complete; PU 102031, right, lacking epicondylus ventralis; RGM 425851, left, almost complete; RGM 178929, right, prox. part broken; RGM 178905, left, prox. part broken RGM 178908, left, prox. part broken; RGM 178914, left, prox. part broken; RGM 178964, left, prox. part broken RGM 425854, right, lacking dist. end; RGM 178921, right, prox. half; RGM 178917, right, prox. half; RGM 178926, right, prox. half; RGM 178902 right, prox. half; RGM 178967, right, prox. half; RGM 178968, right, prox. half; RGM 177769, right, prox. half; RGM 177749, right, prox. half; RGM 179018 right, prox. half; RGM 425845, left, prox. half; PU 102025, right, prox. half; IGF 204, right prox. half; RGM 425636, left, prox. half; RGM 425518, right, prox. end; RGM 425890, right, prox. end; IGF 133, right, lacking prox. end; RGM 425953, left, lacking prox. end; RGM 425815, left, dist. half; RGM 425635, right, dist. half; RGM 425540, right, dist. end; PU 102064, left, prox. half; RGM 425776, left, prox. half; RGM 425889, right, prox. half, lacking ventral tuberculum; PU 102062, right, prox. half; IGF 229, right, prox. half; RGM 425503, right, prox. half; PU 102060, right, prox. half; PU 102063, right, prox. half; PU 102061, right, prox. half, lacking tuberculum ventrale; PU 102080, right, prox. half, lacking tuberculum ventrale; RGM 425978, left, prox. half, lacking tuberculum ventrale; IGF 70, left, prox. half, lacking tuberculum ventrale; RGM 425516, left, prox. end; RGM 425578, right, prox. end; RGM 425510, right, prox. end; IGF 113, right, prox. end; RGM 425814, right, prox. end; IGF 6, right, prox. end; RGM 178920, left, prox. part; RGM 178911, left, prox. half; RGM 178910, left, prox. part; RGM 178906, left, prox. half; RGM 178898, left, prox. part; RGM 178896, left, prox. half; RGM 178895, left, lacking dist. end; RGM 177699, left, prox. half; RGM 178942, left, prox. part; RGM 177731, left, prox. half; RGM 178951, left, prox. half; RGM 178922, left, prox. half; RGM 179010, left, prox. part; RGM 425602, left, prox. end; RGM 425519, left, prox. end; RGM 425520, left, prox. end; RGM 425855, left, prox. end; RGM 335571, left, prox. half, lacking tuberculum ventrale; RGM 425530, left, prox. end; PU 102065, right, lacking prox. end; IGF 139, left, lacking prox. end; RGM 425783, left, lacking prox. end; IGF 189, right, lacking prox. end; PU 102067, left, lacking prox. end; RGM 335984, right, dist. half; RGM 425703, right, dist. half; IGF 12, right, dist. half; RGM 335962, right, dist. half; IGF 100, right, dist. half; RGM 425491, right, dist. half; PU 102068, right, dist. half; RGM 425970, right, dist. half; RGM 425576, right, dist. half; RGM 178927, right, dist. half; RGM 178947, right,

Taxon	CORACOID			HUMERUS			ULNA			CARPOMETACARPUS			FEMUR			TIBIOTARSUS			TARSOMETATARSUS		
	x Lm	n°	log diff.	x GL	n°	log diff.	x GL	n°	log diff.	x GL	n°	log diff.	x GL	n°	log diff.	x GL	n°	log diff.	x GL	n°	log diff.
Coturnix coturnix	23,7	7	**0**	32,8	7	**0**	28,2	8	**0**	17,9	7	**0**	35,8	7	**0**	42,4	7	**0**	26,2	7	**0**
Coturnix gomerae	22,7	2	**0,016**	35,8	5	**0,038**	29,1	4	**0,014**	-	-	-	40,9	12	**0,058**	48,8	5	**0,061**	27,3	5	**0,018**
Coturnix delegorguei	21,6	1	**-0,006**	33,7	1	**0,012**	29,7	1	**0,023**	-	-	-	35,3	1	**-0,006**	43,6	1	**0,012**	26,5	1	**0,005**
Coturnix coromandelica	21,0	2	**-0,018**	32,9	5	**0,001**	27,6	3	**-0,009**	17,3	2	**-0,015**	32,6	3	**-0,041**	40,9	2	**-0,016**	24,7	3	**-0,026**
Palaeortyx volans n. sp.	21,7	9	**-0,004**	31,6	26	**-0,017**	28,5	6	**0,005**	17,6	12	**-0,006**	34,0	12	**-0,022**	41,4	4	**-0,010**	22,8	18	**-0,060**
Palaeortyx grivensis	24,4	1	**0.013**	34,0	5	**0,014**	-	-	-	-	-	-	37,7	2	**0,023**	-	-	-	-	-	-
Palaeortyx phasianoides	37,5	4	**0,234**	53,3	6	**0,211**	(51)	1	**0,257**	29,2	1	**0,213**	53,2	1	**0,172**	70,3	2	**0,219**	-	-	-
Palaeortyx prisca	33,5	4	**0,185**	49,3	3	**0,177**	47,7	2	**0,228**	-	-	-	47,9	7	**0,126**	68,3	1	**0,207**	37,1	1	**0,151**
Palaeortyx gallica	30,0	3	**0,137**	41,1	9	**0,098**	38,7	5	**0,138**	-	-	-	42,1	7	**0,070**	59,8	3	**0,149**	33,0	3	**0,100**
Palaeortyx brevipes	24,4	3	**0,047**	36,4	5	**0,045**	32,7	3	**0,064**	18,7	1	**0,019**	37,9	1	**0,025**	50,1	1	**0,073**	28,8	3	**0,041**
Perdix perdix	34,9	62	**0,202**	48,8	48	**0,172**	44,5	47	**0,198**	26,9	49	**0,176**	55,6	61	**0,191**	70,3	46	**0,222**	41,2	48	**0,197**
Alectoris graeca	38,0	26	**0,239**	52,6	21	**0,205**	48,8	20	**0,238**	30,4	20	**0,230**	61,5	23	**0,235**	81,9	20	**0,286**	45,8	19	**0,246**

Table 3 - Mean values of the greatest length (GL) and internal length (Lm, only for the coracoid) of the long bones of *Coturnix coturnix*, *C. gomerae*, *C. delegorguei*, *C. coromandelica*, *Palaeortyx volans* n. sp., *P. grivensis*, *P. phasianoides*, *P. prisca*, *P. gallica*, *P. brevipes*, *Perdix perdix*, *Alectoris graeca* and the values of the log differences with *Coturnix coturnix*, selected as standard (data from Kraft, 1974; Jaume et al., 1993; Göhlich & Mourer-Chauviré, 2005).

dist. half; RGM 178928, right, dist. half; RGM 179019,right, dist. half; RGM 178704, right, dist. half; RGM 425532, left, dist. half; IGF 121, left, dist. half; RGM 335969, left, dist. half; IGF 134, left, dist. half; RGM 425640, left, dist. half; RGM 335972, left, dist. half; RGM 425521, left, dist. half; RGM 425580, left, dist. half; RGM 178898, left, dist. half; RGM 178933, left, dist. half; RGM 177603, left, dist. half; RGM 177602, left, dist. half; RGM 177729, left, dist. part; RGM 177644, left, dist. part; RGM 177645, left, dist. part; RGM 177621, left, dist. part; RGM 178919, left, dist. half; RGM 425541, left. dist. end; RGM 425670, left. dist. end; RGM 425696, left. dist. end; IGF 44, left. dist. end; RGM 425893, left. dist. end; IGF 135, left. dist. end; RGM 425663, left. dist. end; RGM 425964, left. dist. end; RGM 425902, right, dist. end; RGM 425790, right, dist. end; IGF 120, left, lacking prox. end; IGF 29, right, prox. shaft; RGM 425708, left shaft; RGM 178923, left shaft; RGM 177654, left shaft; RGM 425951, left shaft; IGF 211, left shaft; IGF 224, left shaft.

Ulna— IGF 26, right, complete; PU 102027, right, complete; RGM 425493, left, complete; RGM 425523, left, complete; PU 102069, left, complete; PU 102030, left, prox. half; RGM 425796, right, prox. end; IGF 80, right, dist. half; RGM 425971, left, prox. and dist. ends damaged; IGF 87, left, lacking dist. end and acromion; RGM 425581, left, prox. end; IGF 81, left, dist. half; RGM 335987, left, dist. half; RGM 425789, right, dist. half; IGF 147, left, dist. half; RGM 425484, right, dist. end; RGM 425747, right, dist. end; RGM 335991, right, dist. end; PU 102070, left, proximal half, lacking the acromion.

Radius—RGM 425969, left, complete.

Carpometacarpus—PU 102029, left, lacking os mc minus; IGF 200, right, lacking os mc minus; RGM 425728, left, lacking os mc minus; RGM 425552, left, lacking os mc minus; RGM 425504, right, lacking os mc minus; RGM 335977, right, lacking os mc minus; RGM 425985, right, lacking os mc minus; IGF 146, left, prox. end damaged, lacking os mc minus; RGM 425517, left, lacking proc. extensorius and os mc minus, dist. end damaged; RGM 425898, right, dist. end damaged, lacking os mc minus; RGM 425675, right, lacking os mc minus and the dist. end; RGM 425998, left, prox. half, lacking proc. extensorius, os mc minus; RGM 425896, left, prox. half, lacking os mc minus; IGF 187, left, proximal half, lacking the trochlea carpalis and os mc minus; RGM 425736, right, prox. half, lacking os mc minus; RGM 425858, right, lacking prox. end and os mc minus; RGM 425737, right, prox. half, prox. end damaged and lacking os mc minus; RGM 425692, right, prox. half, prox. end damaged and lacking os mc minus.

Femur—RGM 425608, left, complete; PU 102026, right, complete; RGM 425490, left, complete; RGM 425607, right, almost complete; RGM 425785, right prox. half; IGF 193, right, prox. half; RGM 335967, left, dist. 2/3; RGM 425792, right, dist. end; PU 102081, left, complete; PU 102071, right, prox. half, prox. end slightly damaged; IGF 136, right, prox. half; IGF 25, right, damaged prox. half; RGM 425712, right, damaged prox. half; RGM 425981, left, damaged prox. half; RGM 425566, left, damaged prox. half; RGM 425575, left, damaged prox. half; RGM 425724, left, damaged prox. half; RGM 425959, right, prox. half; RGM 425960, left, damaged prox. half; RGM 425525, left, prox. half; RGM 425754, left, damaged prox. half; RGM 425721, left, damaged prox. half; RGM 425714, left, damaged prox. half; RGM 425973, right, damaged prox. half; PU 102082, right, prox. half; RGM 425511, right, prox. half; RGM 425900, right, prox. end; PU 102073, right, dist. half; PU 102072, right, lacking the prox. end; RGM 425705, left, dist. half; RGM 425515, left, dist. half; IGF 122, left, dist. half; RGM 425730, left, dist. half; RGM 425568, right, dist. half; IGF 186, right, dist. half; RGM 425573, left, dist. end; IGF 118, left, dist. end; IGF 140, left, dist. end; RGM 425962, right, dist. end; IGF 35, right, dist. end; RGM 425871, right, dist. end; RGM 425874, right, dist. end; RGM 425966, left, shaft; RGM 425666, right, dist. end; RGM 425899 right, dist. end.

Tibiotarsus—PU 102024, right, lacking prox. end; IGF 61+57, right, complete; PU 102047, right, prox. end; RGM 335978, left, dist. half; RGM 425509, right, prox. 2/3; RGM 335976, left, prox. half; IGF 194 left, prox. end; RGM 425631, left, prox. end; RGM 335960, left, prox. end; RGM 425563, left, prox. end; RGM 425711, left, prox. end; RGM 335964, left, dist. half; PU102074, right, dist. half; IGF 108, right, dist. half; IGF 145, left, dist. half, lacking condylus medialis; IGF 91, left, dist. half; RGM 425690, left, dist. half; RGM 425527, left, dist. end; RGM 425744, right, dist. end; IGF 141, left, dist. end; RGM 425956, left, dist. end; RGM 335978, right, dist. end; RGM 425924, right, dist. end; RGM 425938, right, dist. end; RGM 425808, left, dist. end; RGM 335968, right, dist. end; RGM 425980, left, dist. end; RGM 425673, right, dist. end; RGM 425522, left, dist. end; RGM 425671, right, dist. end; RGM 335974, right, dist. end; RGM 425528, right, dist. end; RGM 425722, left, dist. end; RGM 425488, right, dist. end; RGM 425995, left, dist. end; RGM 425680, left, dist. end; RGM 425501, left, dist. end; IGF 178, right, dist. end; RGM 425784, right, dist. end; IGF 167, right, dist. end; RGM 425644, left, dist. end; IGF 67, right, dist. end; RGM 425498, right, dist. end; RGM 425852, right shaft.

Tarsometatarsus—RGM 425778, right, complete; RGM 425992, left, complete; RGM 425817, right, lacking trochlea IV; RGM 425514, right, lacking trochlea II; RGM 425533, right, almost complete; RGM 425968, right, lacking trochlea II, prox. end damaged; IGF 131, right, lacking trochlea II, prox. end damaged; RGM 425553, left, complete; RGM 425586, right, almost complete; PU 102028, left, dist. half; IGF 99, left, lacking trochlea IV, prox. end damaged;

PU 102076, right, lacking prox. end and trochleae II and IV; PU 102075, left, lacking dist. end; RGM 425506, right, shaft; IGF 97, right, lacking dist. end; RGM 425632, right, lacking trochleae III and IV; RGM 425799, left, lacking dist. end; RGM 335985, left, prox. half; RGM 425669, left, prox. half; IGF 182, left, prox. half; RGM 425647, left, prox. half; RGM 335975, right, prox. half, prox. end damaged; RGM 425993, right, prox. half; RGM 425972, right, dist. half, lacking trochlea IV; RGM 425707, right, dist. half; RGM 425986, right, dist. half, lacking trochlea II; RGM 425939, right, dist. half; RGM 425788, right, dist. half, lacking trochlea IV; RGM 425963, right, dist. end; RGM 425679, right, dist. end, lacking trochlea IV; RGM 425716, right, dist. end, lacking trochlea IV; RGM 425957, right, dist. end, lacking trochleae II and IV; RGM 425987, right, dist. end, lacking trochlea II; RGM 425557, left, dist. half, lacking trochlea IV; RGM 425734, left, dist. end; RGM 425994, left, dist. half, lacking trochlea III; RGM 425892, left, dist. half, lacking trochleae II and III; RGM 335986, left, dist. half, lacking all trochleae; NMA 507/1801, left, almost complete, lacking trochlea IV.

Sternum—RGM 425485, cranial half; RGM 425496, cranial half; RGM 425507, cranial portion; IGF 102, cranial fragment; IGF 198, cranial fragment.

Furcula—RGM 425787, fragment with apophysis furculae.