

REVISION OF THE PHASIANIDS (AVES: GALLIFORMES) FROM THE LOWER MIOCENE OF SAINT-GÉRAND-LE-PUY (ALLIER, FRANCE)

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Abstract: A revision of the phasianids (Aves, Galliformes) from the Lower Miocene of St-Gérard-le-Puy (Allier, France) has been carried out. *Palaeortyx brevipes* Milne-Edwards, 1869, *Palaeortyx gallica* Milne-Edwards, 1869, *Palaeortyx phasianoides* Milne-Edwards, 1869, and *Palaeortyx intermedia* Ballmann, 1969 have been known before from this locality. St-Gérard-le-Puy is the type locality of the first three species. The four species of *Palaeortyx* represented at St-Gérard-le-Puy are distinguished by their size. Their separation and validity have recently been doubted with serious consequences for the systematics of *Palaeortyx*. Our investigation confirmed the separation and validity of the four species,

whereby *Palaeortyx intermedia* was recognized to be a junior synonym of *Palaeortyx prisca* and is synonymized with the latter here. These results are supported by investigations on variability statistics on some recent quails and partridges (*Coturnix*, *Perdix*, *Alectoris*). Comparisons with fossil phasianids from Quercy, Sansan, and La Grive (all France) and Wintershof-West (Germany) are made. New morphological and size differences between *Palaeortyx* and some species of *Palaeocryptonyx* are described.

Key words: Galliformes, phasianids, *Palaeortyx*, *Palaeocryptonyx*, Miocene, France.

THE galliforms from St-Gérard-le-Puy (Text-fig. 1) were first studied by Milne-Edwards (1867–71) in his monographic work on the fossil birds of France. Therein he described three new species of phasianids, *Palaeortyx brevipes* Milne-Edwards, 1869, *P. gallica* Milne-Edwards, 1869 and *P. phasianoides* Milne-Edwards, 1869, which he distinguished by their size. Later, these species were verified from several other localities in Europe (see below).

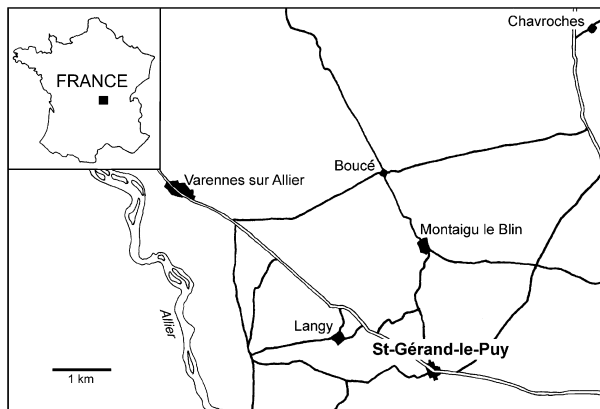
In 1992 Mourer-Chauviré first mentioned also the presence of *Palaeortyx intermedia* Ballmann, 1969 in St-Gérard-le-Puy, a taxon that was originally described by Ballmann (1969b) from the Lower Miocene of Wintershof-West (southern Germany). Besides these four species of *Palaeortyx*, which are typical Phasianidae, a more primitive galliform species, *Ameripodius alexis* Mourer-Chauviré, 2000, belonging to the family Quercymegapodiidae, has been recognized.

Recently Mlíkovský (2000) systematically revised the phasianids of St-Gérard-le-Puy based on only a partial sample of the material housed in the MNHN (for explanation of this abbreviation and others, see below). According to his results, *Palaeortyx brevipes* was synonymized

with *P. gallica*; *P. intermedia* was synonymized with *P. longipes* (Milne-Edwards, 1869), a taxon described from Sansan (France), and *P. phasianoides* was transferred from the phasianids (Galliformes) to the anatids (Anseriformes) and synonymized with *Mionetta blanchardi*.

In the course of our investigation on Neogene European Phasianidae all of the phasianid material from St-Gérard-le-Puy in the collections of the FSL, ML, MNHN and BSP has been re-studied and compared. In the same collections, additionally, a large number of phasianids from La Grive (Middle Miocene, France), Vieux-Collonges (Lower/Middle Miocene, France), Sansan (Middle Miocene, France), Quercy (Upper Oligocene, France), Wintershof-West (Lower Miocene, Germany), Sandelzhausen (Middle Miocene, Germany) and several unpublished localities in southern Germany have been studied; these will not be discussed in this paper but they contribute to our osteological comparisons. Compared skeletons of recent birds came from the SAPM.

Abbreviations. Institutions: BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich; FSL, Faculté des Sciences



TEXT-FIG. 1. Location of the St-Gérard-le-Puy area, Allier, France (modified after Cheneval 1989).

de Lyon, Université Claude Bernard, Lyon 1 (= UCBL); ML, Muséum d'Histoire Naturelle, Lyon (= Musée Guimet); MNHN, Muséum National d'Histoire Naturelle, Paris; SAPM, Staatssammlung für Anthropologie und Paläoanatomie München; USTL, Université des Sciences et Techniques du Languedoc (Laboratoire de Paléontologie), Montpellier. Anatomy: cmc, carpometacarpus; dext., dexter; dist., distal; mc, metacarpalis; prox., proximal; sin., sinister; tmt, tarsometatarsus; tt, tibiotarsus.

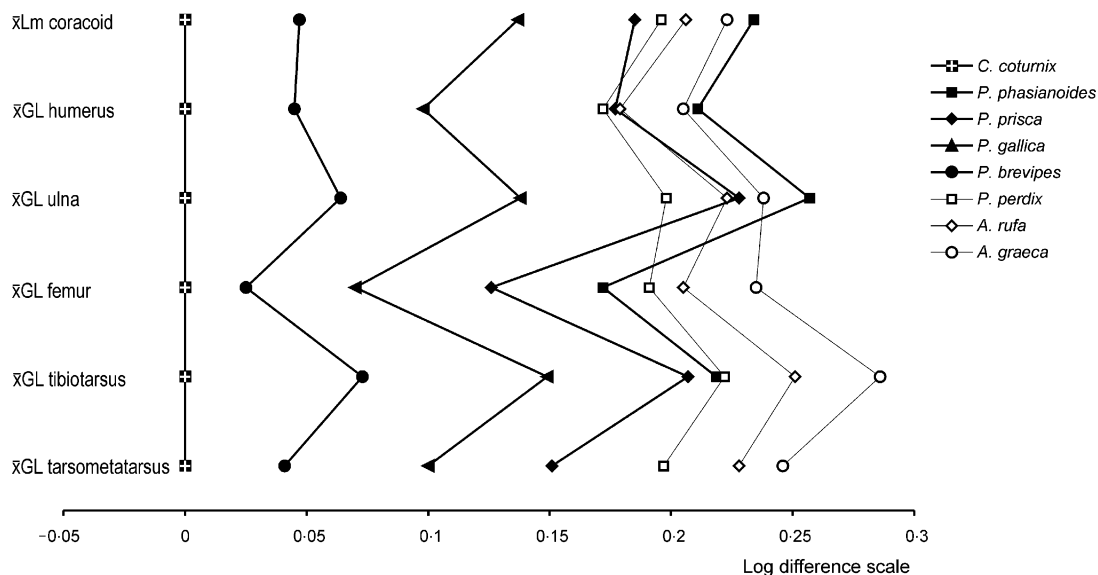
Methods. The osteological terminology principally follows Baemel *et al.* (1993) and occasionally Ballmann (1969a, b); measurements were taken after von den Driesch (1976). The stratigraphy

of the Miocene and the correlation with its 'Neogene Mammal-Unit' (MN-Units) follows Steininger (1999) and Mein (1990, 1999).

Text-figure 2 is a ratio diagram of the main long bones of several fossil and extant phasianid taxa. This kind of diagram was invented by Simpson (1941). It shows the differences in the measurements, converted into logarithms, of the main long bones as a ratio of those of a chosen standard taxon. The standard taxon chosen in our case is the extant *Coturnix coturnix*. In the diagram the horizontal distance between the points, marking the same elements of different taxa, is proportional to the ratio of their real dimensions. In addition, specimens or taxa, whose proportions of their long bones are similar, are illustrated by lines whose forms are alike. It is essentially: $\log(\text{measurement of compared taxon}) - \log(\text{measurement of standard taxon}) = \log(\text{measurement of compared taxon}/\text{measurement of standard taxon})$.

LOCALITY AND GEOLOGY

The site known as Saint-Gérard-le-Puy (Massif Central, Allier Department, France) combines several quarries in the St-Gérard-le-Puy area (Text-fig. 1), namely Montaigu-le-Blin (MN2a), and in a wider sense sometimes also Langy (principally MN2a), Chavroches (MN2a), Saulcet (MN1/2a), Poncenat (MN2), Cluzel (MN2a) and Billy (upper level, MN1) (Huguency *et al.* 2003). The fossiliferous limestone of the Saint-Gérard-le-Puy area is known as the 'Calcaire à Phryganes' or the 'Indusial Limestone',



TEXT-FIG. 2. 'Simpson diagram'; log differences of the lengths (in mm) of some long bones of the fossil taxa *Palaeortyx phasianoides*, *P. prisca*, *P. gallica* and *P. brevipes*, and the extant taxa *Coturnix coturnix*, *Perdix perdix*, *Alectoris rufa* and *A. graeca*. For further explanation of the diagram, see text. *Coturnix coturnix* was chosen as standard. Measurements of *Coturnix coturnix* are our own, those of *Perdix perdix*, *Alectoris rufa* and *A. graeca* are from Kraft (1972) (for data on *P. perdix* and *C. coturnix*; see also Table 2). GL, greatest length; Lm, medial length; \bar{x} , mean; $\log x - \log y = \log x/y$.

the latter is named after the caddisfly *Indusia tabulosa* (Insecta: Trichoptera) (Hugueney *et al.* 1990).

The quarries have been exploited for more than 150 years and have yielded an extraordinarily rich fossil assemblage. The predominantly aquatic (fluvatile-lacustrine) but also terrestrial faunal assemblages of St-Gérard-le-Puy contain mammals, birds, reptiles, some amphibians and insects, and gastropods. Due to its rich large and small mammal fauna, Montaigne-le-Blin is the reference locality of the European Mammal Neogene Unit MN2a (Mein 1999, p. 27).

The exceptional variety and abundance of fossil bird remains make St-Gérard-le-Puy the most important fossil bird locality of the Neogene. According to Cheneval (1983, p. 102) and Mourer-Chauviré (1995, pp. 339–342, 2000) the fossil birds at St-Gérard-le-Puy are represented by 18 orders, 48 genera and 61 species, most of them aquatic forms.

For more detailed information on the history of the site of St-Gérard-le-Puy and former studies on its geology and fossil fauna, see e.g. Cheneval (1983, 1989), Bucher *et al.* (1985) and Hugueney *et al.* (1990).

SYSTEMATIC PALAEONTOLOGY

Class AVES Linnaeus, 1758

Order GALLIFORMES Linnaeus, 1758

Family PHASIANIDAE Vigors, 1825

Subfamily PHASIANINAE Vigors, 1825

Genus PALAEORTYX Milne-Edwards, 1869

- p. 1869 *Palaeortyx* Milne-Edwards, vol. 2, p. 230.
- p. 1869 *Palaeoperdix* Milne-Edwards, vol. 2, p. 245.
- p. 1891 *Palaeortyx* Milne-Edwards; Lydekker, p. 136.
- p. 1891 *Palaeoperdix* Milne-Edwards; Lydekker, p. 139.
- p. 1892 *Palaeortyx* Milne-Edwards; Milne-Edwards, p. 71.
- p. 1892 *Rallus sensu* Milne-Edwards, p. 73.
- 1893 *Palaeortyx* Milne-Edwards; Lydekker, p. 519.
- p. 1908 *Palaeortyx* Milne-Edwards; Gaillard, p. 97.
- p. 1908 *Rallus* Brisson; Gaillard, p. 109.
- 1930 *Palaeortyx* Milne-Edwards; Ennouchi, p. 70.
- p. 1933 *Palaeortyx* Milne-Edwards; Lambrecht, p. 449.
- p. 1933 *Palaeoperdix* Milne-Edwards; Lambrecht, p. 431.
- p. 1933 *Quercyrallus* Lambrecht, p. 461.
- 1939 *Palaeortyx* Milne-Edwards; Gaillard, p. 21.
- 1964 *Palaeortyx* Milne-Edwards; Brodkorb, p. 298.
- p. 1964 *Ludiortyx* Brodkorb, p. 298.
- p. 1964 *Taoperdix sensu* Brodkorb, p. 301.
- 1967 *Palaeortyx* Milne-Edwards; Brodkorb, p. 112.
- p. 1967 *Quercyrallus* Lambrecht; Brodkorb, p. 118.
- 1969a *Palaeortyx* Milne-Edwards; Ballmann, p. 177.
- 1969b *Palaeortyx* Milne-Edwards; Ballmann, p. 30.
- 1973 *Palaeortyx* Milne-Edwards; Ballmann, p. 24.

- p. 1973 *Quercyrallus* Lambrecht; Cracraft, p. 20.
- p. 1977 *Quercyrallus* Lambrecht; Olson, p. 344.
- p. 1985 *Palaeoperdix* Milne-Edwards; Kurochkin, p. 86.
- 1992 *Palaeortyx* Milne-Edwards; Mourer-Chauviré, p. 83.
- 2000 *Palaeortyx* Milne-Edwards; Cheneval, p. 344.
- p. 2000 *Palaeoperdix* Milne-Edwards; Cheneval, p. 347.

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

Remarks. Linnaeus (1758, pp. 156–161) used the name Gallinae in the sense of today's order Galliformes, and thus can be accepted as the author of the order Galliformes.

Mlíkovský (2002a, p. 152f) synonymized *Palaeortyx* with the Recent genus *Coturnix*, arguing that they cannot be morphologically separated. Our own osteological comparisons of *Palaeortyx* with *Coturnix coturnix* led to the conclusion that *Palaeortyx* and *Coturnix* are distinguishable on the basis of several distinct characters (see differential diagnosis below); hence, we consider *Palaeortyx* to be a valid taxon.

Diagnosis. A detailed diagnosis of *Palaeortyx* has been given by Ballmann (1969b, p. 30f), which he himself emended in 1973 (p. 24f); Cheneval (2000, p. 344) gave a French translation of Ballmann's diagnosis from 1969. The following diagnosis is a translation from Ballmann (1969b, p. 30f), together with his additions from 1973 (p. 24f) (marked below with an asterisk, *) and, when possible, adapted to the osteological nomenclature of Baumel *et al.* (1993).

Small- to middle-sized representatives of galliforms

Tarsometatarsus. Slender shape, dainty to strong; proximal ending as wide as distal one or wider; spur missing; crista medianopolaris absent; hypotarsus situated slightly laterally; sulcus for musculus flexor hallucis longus shorter than crista lateralis hypotarsi [crista externa hypotarsi]; crista lateralis hypotarsi longer than crista medialis hypotarsi; sulcus hypotarsi separated into two parallel sulci; situated dorsally to the medial one there is a canal for the musculus flexor digitorum longus; fossa infracotylaris dorsalis deep. Sulcus for the musculus flexor hallucis longus weak*. Medial part of the tuberositas musculi tibialis cranialis stronger than lateral one. Fossa parahypotarsalis medialis distinct to deep; plantar side of the shaft raised and smooth. Dividing line between fossa abductoris digiti 4 and fossa flexoris hallucis brevis proximally runs into the hypotarsus; trochlea 4 distinctly surpasses trochlea 2 [Ballmann 1969b erroneously wrote 'trochlea 3' here] in distal direction; trochlea 2 more strongly bent plantarly than trochlea 4.

Tibiotarsus. Shaft and distal end slender; fossa plantaris and fossa flexoria separated by a longitudinal swelling; crista cnemialis cranialis reaches further distally than crista cnemialis lateralis; fossae retrocretales subdivided by a strong barrier; cross section of shaft at the level of the crista fibularis nearly an equilateral triangle.

Femur. Foramen pneumaticum absent; concerning the larger species the epicondylus medialis protruding hook-like.

Coracoid. Labrum interna sharp-edged in its caudal part. Foramen pneumaticum absent; on the medial side distal border of processus procoracoideus straight. Not pneumatized*.

Scapula. Nonpneumatic*.

Humerus. Proximal end wider than distal one; fossa pneumotricipitalis in two parts with large, very deep dorsal fossa and large ventral fossa; the latter without lamella, without substantia spongiosa, and without foramen pneumaticum; impressio of musculus entepicondylo-radialis sublimis situated on cranial edge of epicondylus ventralis; insertion of musculus extensor metacarpi radialis on processus supracondylaris dorsalis rounded; condylus ventralis strongly swollen distally; processus flexorius slender with caudal crest.

Ulna. Shaft short and strongly bent; proximal end ventrodorsally compressed; cross section triangular; margo interossea strongly developed, both cranial sides form an acute angle; olecranon blunt and situated in continuation of the shaft bending; impressio brachialis superficially and clearly bordered; tuberculum bicipitale ulnae weakly developed; trochlea carpalis orientated obliquely to the shaft, condylus ventralis ulnae distinctly larger than the flat condylus dorsalis ulnae; incisura tendinosa not clearly expressed; facies musculi ulni-metacarpalis ventralis deepened in the surface of the shaft.

Carpometacarpus. Processus intermetacarpalis strongly tooth-like; incisura interna present; facies articularis digitalis minor only a little more protruding distally than the convex part of the facies articularis digitalis minor, the latter overtops only slightly the flat part of the facies articularis digitalis minor.

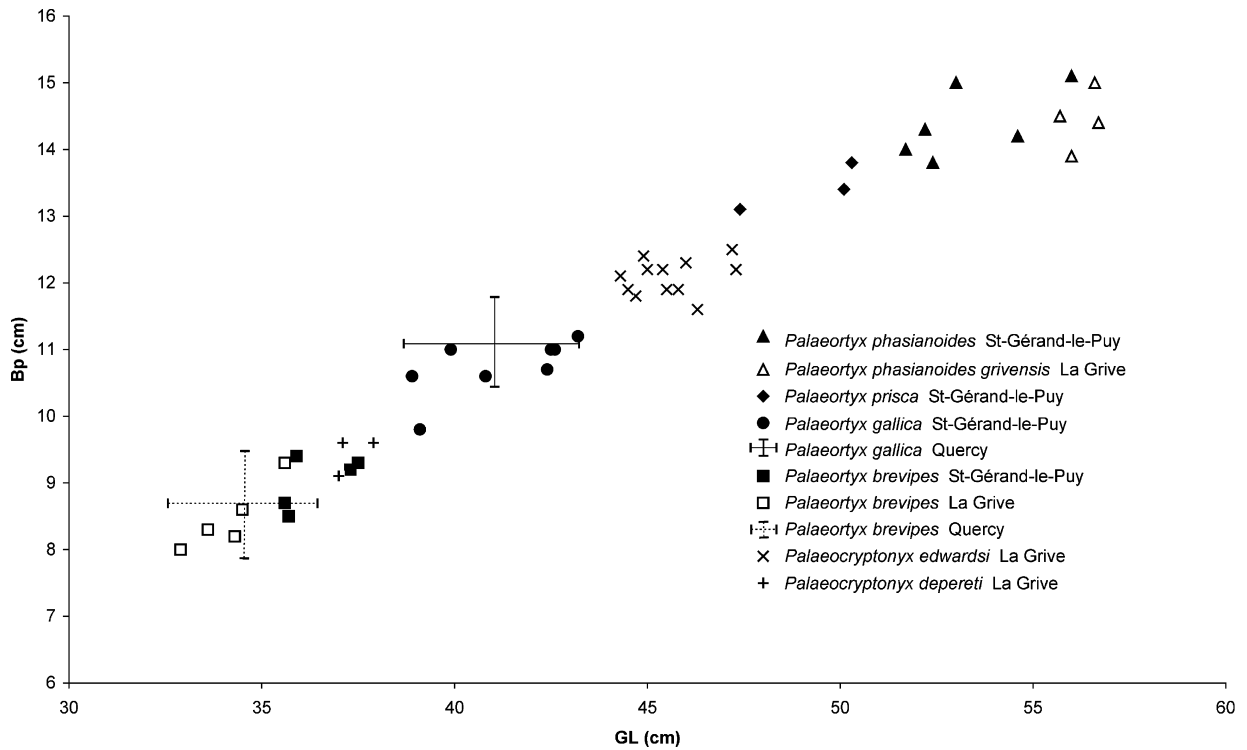
Synsacrum. Caudal to the fusing point the os lumbo-sacrale is dorsally swelled.*

Sternum. In its cranial part with two dents*

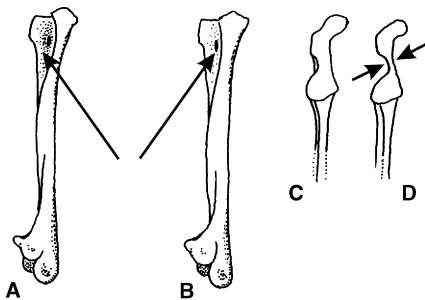
Differential diagnosis. *Palaeortyx* differs from *Coturnix coturnix* (SAPM 3, female; 9, male) by a humerus with a non-pneumatic ventral fossa pneumotricipitalis; the humerus shaft of *Coturnix* is straighter and not curved as in *Palaeortyx*; the proximal outline of the proximal extremity is characterized in *Palaeortyx* by an indentation between the caput humeri and the tuberculum ventrale, whereas this indentation is very weak or lacking in *Coturnix*. For the coracoid, the processus acrocoracoideus of

Palaeortyx is more hooked caudally, whereas it is not hooked in *Coturnix*; the dorsal side shows a fossa pneumatica in *Coturnix* (contrary to the coded character in the matrix of Dyke *et al.* 2003) but this is absent in *Palaeortyx*; the facies articularis sternalis seems to be less excavated in *Coturnix*. The scapula of *Palaeortyx* differs from that of *Coturnix* by the oblique orientation of the acromion, whereas it is right-angled to the proximal end in the latter. As shown in Text-figure 2 the relation of the limb bone length of *Coturnix coturnix* is different from the studied species of *Palaeortyx*; the ulna and tibiotarsus of *C. coturnix* are proportionally shorter in relation to the species of *Palaeortyx* and the humerus, the femur and the tarsometatarsus are proportionally longer (Text-fig. 2). At the tibiotarsus, both the crista cnemialis lateralis and cranialis are much more weakly developed in *Coturnix* than in *Palaeortyx*.

Palaeortyx and *Palaeocryptonyx* occur together in some localities, as in Petersbuch 2, Spitzberg (both Germany, unpublished), Sansan (France, see below), and La Grive (France); they have often been confused and are sometimes difficult to distinguish. A comparison of *Palaeortyx* with *Palaeocryptonyx edwardsi* (Depéret 1887) and *Palaeocryptonyx depereti* (Ennouchi 1930) from their type locality La Grive (Middle Miocene, MN7 +8, France), shows that the limb bones of *Palaeocryptonyx depereti* vary in size between *P. brevipes* and *P. gallica* (Text-fig. 3), but in some elements are more similar in size to *P. brevipes*; *Palaeocryptonyx edwardsi* is middle-sized between *P. gallica* and *P. prisca* (including *P. intermedia*) (Text-fig. 3), but corresponds in some bones more to *P. prisca*. *Palaeortyx* can be morphologically distinguished from *Palaeocryptonyx* in some bones. The humerus of *Palaeortyx* is characterized by a deeper dorsal fossa pneumotricipitalis and a non-pneumatized ventral fossa pneumotricipitalis, without a distal bony crest bordering the fossa. The scapula of *P. gallica* is similar in size to that of *Palaeocryptonyx edwardsi*, but (in proximal view) the bony connection between the tuberculum coracoideum and facies articularis humeralis is more robust than in *Palaeocryptonyx edwardsi*, where it is thin (Text-fig. 4). Concerning the tarsometatarsus, the fossa parahypotarsalis is deeper at the point of the opening of the proximal foramen in *P. gallica* and *P. prisca* than in *Palaeocryptonyx edwardsi* (Text-fig. 4), whereas the distal end of the tmt of *P. gallica* is morphologically indistinguishable from *Palaeocryptonyx edwardsi* (La Grive); *P. brevipes* is similar in size to *Palaeocryptonyx depereti*; the difference in the depth of their fossa parahypotarsalis is less distinguishable. The tibiotarsus of *Palaeocryptonyx edwardsi* (La Grive) can reach the length of *P. phasianoides*, but is rather more slender; the distal end of the tibiotarsus of *Palaeocryptonyx edwardsi* varies in size between those of *P. prisca* and *P. gallica*. The condylus medialis of *Palaeocryptonyx edwardsi*



TEXT-FIG. 3. Length/proximal width ratio diagram (own measurements) for the humeri of *Palaeortyx phasianoides*, *P. prisca*, *P. gallica* and *P. brevipes* from St-Gérand-le-Puy, La Grive and Quercy (all France), and *Palaeocryptonyx edwardsi* and *Palaeocryptonyx depereti* from La Grive. Cross-bars indicate the means and ranges for *P. brevipes* and *P. gallica* at Quercy.



TEXT-FIG. 4. Morphological differences between *Palaeortyx prisca* (A, C) and *Palaeocryptonyx edwardsi* (B, D). A–B, tarsometatarsus, lateral view. C–D, scapula, proximal view.

corresponds to that of *P. phasianoides*; both are proximodistally shorter than in *P. phasianoides grivensis* from La Grive (see differential diagnosis of *P. phasianoides*).

Mlíkovský (2002a, p. 158) referred the species *Palaeortyx prisca* to the extant genus *Alectoris*; our own comparisons led to the conclusion that there are distinct morphological differences between these taxa, which are described below under *P. prisca*.

Further species. Twenty species can be found under the name *Palaeortyx*, either originally attributed to this genus, or later

transferred to it: *P. gallica* Milne-Edwards, 1869; *P. brevipes* Milne-Edwards, 1869; *P. phasianoides* Milne-Edwards, 1869; *P. hoffmanni* (Gervais 1852); *P. blanchardii* Milne Edwards, 1869; *P. sansaniensis* (Milne-Edwards, 1869); *P. longipes* (Milne-Edwards, 1869); *P. edwardsi* Depéret, 1887; *P. media* Milne-Edwards, 1871; *P. ocyptera* Milne-Edwards, 1892; *P. cayluxensis* Lydekker, 1891; *P. prisca* (Milne-Edwards, 1869); *P. grivensis* Lydekker, 1893; *P. maxima* Lydekker, 1893; *P. depereti* Ennouchi, 1930; *P. joleaudi* Ennouchi, 1930; *P. gaillardii* Lambrecht, 1933; *P. miocaena* Gaillard, 1939; *P. major* Gaillard, 1939; *P. intermedia* Ballmann, 1969b.

All of these species have been described from the Upper Eocene of the Gypsum of Montmartre (France), the Upper Oligocene of Quercy (France), the Lower Miocene of St-Gérand-le-Puy (France) and Wintershof-West (Germany) up to the Middle Miocene of La-Grive-Saint-Alban and Sansan (both France). Most are not referred to *Palaeortyx* today.

P. edwardsi was recognized as belonging to *Palaeocryptonyx* by Ballmann (1969a, p. 182); later it was referred to *Alectoris* by Mlíkovský (2002a, p. 158f). *Palaeortyx depereti* was synonymized with *Coturnix gallica* by Mlíkovský (2002a, p. 154), but in our opinion it belongs to *Palaeocryptonyx* [not to be confused with *Palaeocryptonyx depereti* created by Gaillard (1908), which has been moved to *Quercymegapodius* by Mourer-Chauviré (1992, p. 81)]. *P. blanchardii* as well as *P. hoffmanni* were referred to *Ludiortyx* and turned out to be a rail (Cracraft 1973; Olson 1977). *P. sansaniensis* was placed in synonymy with *P. prisca* by Cheneval (2000, p. 345). *P. longipes* was considered to be

identical to *P. phasianoides* by Ballmann (1969a, p. 182), whereas Mlíkovský (2002a, p. 154) moved it to *Coturnix* and therein included *P. phasianoides grivensis* Ballmann, 1969 and most specimens of *P. phasianoides*, except for its syntypes; we agree with Ballmann (1969a) and place *P. longipes* in the synonymy of *P. phasianoides* (see below). *P. media* is a *nomen nudum* (Mourer-Chauviré 1995, p. 340). *P. ocyptera* was synonymized with *P. brevipes* and *P. cayluxensis* with *Paraortyx lorteti* by Mourer-Chauviré (1992, pp. 75, 83). *P. grivensis* was synonymized by Mlíkovský (2002a, p. 154) with *Coturnix gallica*, but we do not agree because it is clearly smaller than *P. gallica*. For the systematic position of *P. grivensis*, see discussion under *P. brevipes*. *P. maxima* was moved to *Miophasianus* by Brodkorb (1964, p. 315). *P. joleaudi* was transferred to *Plioperdix* by Brodkorb (1964, p. 317) and placed in synonymy with *Coturnix gallica* by Mlíkovský (2002a, p. 154); in our opinion it is too small to be synonymized with both *P. gallica* and *P. brevipes*. *P. gaillardii* was moved to *Ludiortyx* by Brodkorb (1964, p. 299) and synonymized with *Paraortyx lorteti* by Mourer-Chauviré (1992, p. 75). *P. miocaena* was placed in the synonymy of *Palaeocryptonyx edwardsi* by Ballmann (1969a; p. 182), but was recently moved to *Alectoris* by Mlíkovský (2002a, p. 158f). *P. major* was moved to *Pirortyx* by Brodkorb (1964, p. 300). *P. intermedia* is synonymized with *P. prisca* in this publication.

An additional point of confusion is that different species of different genera share the same species name: e.g. *Palaeortyx grivensis* and *Palaeocryptonyx grivensis*, and *Palaeocryptonyx depereti* (formerly *Palaeortyx*) and *Quercymegapodius depereti* (formerly *Palaeocryptonyx*).

***Palaeortyx gallica* Milne-Edwards, 1869**

Plate 1, figures 3, 6, 13, 17, 20; Plate 2, figures 3, 7, 16, 19

- *vp. 1869 *Palaeortyx gallica* Milne-Edwards, vol. 2, pp. 230–235, pls 128–129 [non pl. 129, figs 23–24].
- vp. 1869 *Palaeortyx brevipes* Milne-Edwards, vol. 2, pl. 130, fig. 13a–b.
- v. 1869 *Palaeoperdix? sansaniensis* Milne-Edwards, vol. 2, pp. 249–250, pl. 131, figs 18–23.
- vnon. 1891 (?)*Palaeortyx gallica* Milne-Edwards; Lydekker, p. 138, fig. 33.
- v. 1891 *Palaeoperdix? sansaniensis* Milne-Edwards; Lydekker, p. 139.
- 1892 *Rallus dasypus* Milne-Edwards, p. 73.
- 1908 *Rallus dasypus* Milne-Edwards; Gaillard, p. 112.
- 1912 *Palaeortyx brevipes* Milne-Edwards; Paris, p. 297.
- 1933 *Quercyrallus dasypus* (Milne-Edwards); Lambrecht, p. 461.
- v. 1933 *Palaeoperdix? sansaniensis* Milne-Edwards; Lambrecht, p. 432.
- 1964 *Taoperdix gallica* (Milne-Edwards); Brodkorb, p. 301.
- v. 1964 *Palaeoperdix sansaniensis* Milne-Edwards; Brodkorb, p. 313.
- 1967 *Palaeortyx gallica* Milne-Edwards, Brodkorb, p. 112.

- 1967 *Quercyrallus dasypus* (Milne-Edwards); Brodkorb, p. 118.
- vp. 1969b *Palaeortyx? intermedia* Ballmann, p. 33 [tt: BSP 1937 II 18106–7, scapula: BSP 1937 II 18096, 18109].
- vnon. 1972 ?*Palaeortyx gallica* Milne Edwards; Ballmann, p. 96.
- 1973 *Quercyrallus dasypus* (Milne-Edwards); Cracraft, p. 24, fig. 10d–e.
- 1977 *Quercyrallus dasypus* (Milne-Edwards); Olson, p. 334.
- vp. 1992 *Palaeortyx gallica* Milne-Edwards; Mourer-Chauviré, p. 87, fig. 10c–d. [non MNHN QU 15912, non USTL PDS 1288].
- vp. 1992 *Palaeortyx brevipes* Milne-Edwards; Mourer-Chauviré, p. 85 [MNHN QU 16964, USTL PDS 1225].
- vp. 1992 *Palaeortyx intermedia* Ballmann; Mourer-Chauviré, p. 87, fig. 10a–b [MNHN PFR 590, MNHN QU 16935].
- vp. 2000 *Palaeortyx prisca* (Milne-Edwards); Cheneval, p. 345, fig. 6.
- vp. 2000 *Palaeortyx gallica* Milne-Edwards; Mlíkovský, pp. 91–92 [non p. 94, table 1, MNHN AV 2897–2899, 2901, 2902, 2909, 2911, MNHN SG 10196–10198, the latter three Hoffstetter collection, formerly not numbered].
- non 2002a *Palaeortyx brevipes* Milne-Edwards; Mlíkovský, p. 153.
- vp. 2002a *Coturnix gallica* (Milne-Edwards); Mlíkovský, pp. 153–154.
- non 2002a *Palaeortyx Joleaudi* Ennouchi 1930; Mlíkovský, p. 154.

Lectotype. Humerus dext. (MNHN Av 2875), designated by Mlíkovský (2000, p. 92), figured inversely in Milne-Edwards (1867–71, pl. 129, figs 25–29).

Paralectotypes. Femur sin. (MNHN Av 2886, figured inversely in Milne-Edwards 1867–71, pl. 129, figs 12–17); femur dext. (MNHN Av 2888, figured inversely in Milne-Edwards 1867–71, pl. 129, figs 18–22); tt dext. (MNHN Av 2890, figured inversely in Milne-Edwards 1867–71, pl. 129, figs 1, 8–11); tmt dext. (MNHN Av 2894; figured inversely in Milne-Edwards 1867–71; pl. 129, figs 1–7).

Type locality and horizon. St-Gérard-le-Puy (Langy), France, Lower Miocene, MN2a.

Topotype material. Coracoid dext. (MNHN SG 10206); coracoid dext., dist. half (MNHN SG 10207); coracoid sin. (MNHN Av 2873); coracoid sin. (BSP 1993 IX 625); scapula sin., prox. three-quarters (FSL 444 201); scapula dext., prox. end (FSL 444 203); humerus sin., prox. end broken off (FSL 440 453); humerus sin., prox. end broken off (MNHN Av 2874); humerus sin., dist. end broken off (MNHN Av 2876); humerus sin. (MNHN Av 2877); humerus sin. (MNHN SG 10200); humerus

dext. (MNHN SG 10201); humerus sin. (FSL 444 189); humerus dext. (FSL 444 190); humerus dext. (FSL 444 191); humerus sin. (juv.) (FSL 444 192); humerus dext., prox. end broken off (FSL 444 193); humerus sin., prox. end broken off (FSL 444 194); humerus sin., prox. half (FSL 444 198); humerus dext. (ML StG 59); ulna dext. (MNHN 2902, figured in Milne-Edwards 1867–71, pl. 130, figs 13a–b, but referred to *P. brevipes*); ulna dext. (MNHN SG 10214); ulna dext. (MNHN SG 10216); ulna sin. (FSL 444 178); ulna dext. (FSL 444 179); ulna sin., prox. end broken off (FSL 442 383); femur sin. (MNHN SG 10195, Coll. Hoffstetter, formerly not numbered); femur sin. (MNHN Av 2887); femur sin. (MNHN SG 10217); femur dext., condylus medialis broken off (MNHN SG 10218); femur sin. (FSL 444 171); femur dext. (FSL 444 170); tt dext. (MNHN GS 10212); tt sin., prox. end broken off (MNHN Av 2889); tt sin., prox. end broken off (MNHN Av 2891); tt sin. (FSL 444 161); tmt dext. (MNHN SG 10220), tmt sin. (MNHN SG 10221).

Differential diagnosis. *P. gallica* is smaller than *P. phasianoides* and *P. prisca* but larger than *P. brevipes*. In comparison with these species the coracoid is proportionately longer (see Text-fig. 2).

Some elements of *P. gallica* are similar in size to *Palaeocryptonyx edwardsi*; the distal ends of the tarsometatarsus of *P. gallica* cannot be distinguished from those of *Palaeocryptonyx edwardsi* (La Grive), but proximally the fossa parahypotarsalis is deeper in *P. gallica*.

Dimensions. See Table 1.

Stratigraphical and geographical distribution. France: Phosphorites du Quercy (even though there are deposits from the Middle Eocene to the Upper Oligocene, phasianids are only known from the Upper Oligocene deposits of Quercy; Mourer-Chauviré 1992), St-Gérard-le-Puy (Lower Miocene, MN2; Milne-Edwards 1867–71), Sansan (Middle Miocene, MN6; *pars P. prisca* in Cheneval 2000); Germany: Wintershof-West (Lower Miocene, MN3, *pars P. intermedia* in Ballmann 1969b); Czech Republic: Tuchořice (Lower Miocene, MN3b; *Coturnix gallica* in Mlíkovský 2002b).

Discussion. Mlíkovský (2000, pp. 91–92) synonymized *P. gallica* and *P. brevipes*, arguing that the size differences of the syntypes are too small to distinguish these two species. Our study of the syntypes and several additional specimens of these taxa from St-Gérard-le-Puy (MNHN, FSL, ML, BSP) has resulted in the distinction of these two species. Comparisons with the extant species *Perdix perdix* and *Coturnix coturnix* led to the conclusion that the variability coefficients of several bone lengths of a unified species, *P. gallica* including *P. brevipes*, as proposed by Mlíkovský (2000), are much too large to represent only one zoological species of quail (Table 2), whereas the computed values of the variability coefficients of *P. gallica* and a separated *P. brevipes* correspond well with those of recent *P. perdix* and *C. coturnix* (Table 2).

For Mlíkovský's affiliation of the species *gallica* to the recent genus *Coturnix*, see the differential diagnosis for *Palaeortyx*. *Palaeortyx joleaudi* Ennouchi, 1930, described from La Grive (France), was put into synonymy with *P. gallica* by Mlíkovský (2002a, p. 154). However, following our own comparisons, the only known specimen of *P. joleaudi*, a humerus, although morphologically identical, is much too small to be synonymized with *P. gallica* or *P. brevipes*.

The tarsometatarsi of *P. gallica* from Quercy described by Mourer-Chauviré (1992, pp. 85–87, table 3) are slightly shorter than those from St-Gérard-le-Puy.

Palaeortyx brevipes Milne Edwards, 1869

Plate 1, figures 4–5, 10, 14, 18, 19; Plate 2, figures 4, 17, 20

- *vp. 1869 *Palaeortyx brevipes* Milne-Edwards, vol. 2, p. 235, pl. 130, figs 1–21 [*non* figs 7–11, 13a–b].
- p. 1891 *Palaeortyx brevipes* Milne-Edwards; Lydekker, p. 138 [*non* ulna].
- non* 1891 *Palaeortyx cayluxensis* Lydekker, p. 138.
- 1892 *Palaeortyx ocyptera* Milne-Edwards, p. 71.
- v. 1893 *Palaeortyx grivensis* Lydekker, pl. 41, fig. 12.
- 1908 *Palaeortyx ocyptera* Milne-Edwards; Gaillard, p. 98, fig. 27, pl. 5, figs 13–16.
- p. 1908 *Palaeortyx cayluxensis* Lydekker; Gaillard, p. 100, fig. 28; p. 103, fig. 29, pl. 6, figs 1–4.
- 1912 *Palaeortyx brevipes* Milne-Edwards; Paris, p. 297.
- non* 1933 *Palaeortyx cayluxensis* Lydekker; Lambrecht, p. 450.
- 1933 *Palaeortyx ocyptera* Milne-Edwards; Lambrecht, p. 451.
- 1933 *Palaeortyx brevipes* Milne-Edwards; Lambrecht, p. 451.
- 1939 *Palaeortyx* aff. *cayluxensis* Lydekker; Gaillard, p. 21, fig. 9.
- non* 1964 *Ludiortyx cayluxensis* (Lydekker); Brodkorb, p. 299.
- 1964 *Taoperdix brevipes* (Milne-Edwards); Brodkorb, p. 301.
- 1967 *Palaeortyx brevipes* Milne-Edwards; Brodkorb, p. 112.
- v. 1972 ?*Palaeortyx gallica* Milne Edwards; Ballmann, p. 96.
- non* 1992 *Palaeortyx brevipes* Milne-Edwards; Mourer-Chauviré, p. 85 [MNHN QU 16964, USTL PDS 1225].
- vp. 1992 *Palaeortyx gallica* Milne-Edwards 1869; Mourer-Chauviré, p. 87 [USTL PDS 1288, MNHN QU 15912 = *P. brevipes*]
- vp. 2000 *Palaeortyx gallica* Milne-Edwards; Mlíkovský, pp. 91–92 [p. 94, table 1, MNHN AV 2897–2899, 2901, 2902, 2909, 2911, MNHN SG 10196, 10197, 10198, the last three Hoffstetter collection, formerly not numbered].

vp? 2000 *Palaeortyx prisca* (Milne-Edwards 1869–71) nov. comb.; Cheneval, p. 345 [MNHN Sa 1416, 14019, 14016, see remarks].

Lectotype. Humerus dext. (MNHN Av 2898), designated by Mlíkovský (2000, p. 92), figured (inversely) in Milne-Edwards (1867–71, pl. 130, figs 12–16: (wrongly written on the original label: figs 12–13).

Paralectotypes. Coracoid sin. [MNHN Av 2897, figured (inversely) in Milne-Edwards 1867–71, pl. 130, figs 17–21]; tt dext. (MNHN Av 2909, figured inversely in Milne-Edwards 1867–71; pl. 130, fig. 21a–b); tmt dext. (MNHN Av 2911, figured in Milne-Edwards 1867–71; pl. 130, figs 1–6).

Type locality and horizon. St-Gérard-le-Puy (Langy), France, Lower Miocene, MN2a.

Topotype material. Coracoid dext. (FSL 440 605); coracoid sin. (MNHN SG 10196, Coll. Hoffstetter, formerly not numbered); scapula sin., prox. half (FSL 444 202); scapula dext., prox. three-quarters (MNHN SG 10209), humerus sin. (FSL 444 199); humerus dext. (FSL 444 200); humerus dext., dist. end broken off (MNHN Av 2899); humerus dext. (MNHN Av 2901); humerus sin. (MNHN SG 10197, Coll. Hoffstetter, formerly not numbered); ulna dext. (MNHN SG 10198, Coll. Hoffstetter, formerly not numbered); ulna sin. (FSL 444 180); ulna sin., prox. end broken off (FSL 444 181); ulna sin. (FSL 444 183); ulna sin. (FSL 444 184); cmc dext., os mc minus broken off (MNHN Av 2904); femur dext. (FSL 444.172); tt dext., dist. half (MNHN Av 2910); tmt dext. (MNHN SG 10222); tmt dext., dist. end broken off (MNHN SG 10223); tmt dext. (FSL 444 157).

Differential diagnosis. *P. brevipes* is smaller than *P. gallica*, *P. prisca* and *P. phasianoides*. The femur of *P. brevipes* is relatively longer than in *P. gallica*, *P. prisca* and *P. phasianoides*, as well as the humerus, which is proportionally longer than in *P. gallica* and *P. phasianoides* (Text-fig. 2).

P. brevipes sometimes overlaps in size with the somewhat larger *Palaeocryptonyx depereti*. In comparison with *Palaeocryptonyx depereti*, the humerus of *P. brevipes* is characterized by a deep dorsal and a deep ventral fossa pneumotricipitalis, whereby the ventral fossa pneumotricipitalis is not pneumatic.

The tmt of *P. brevipes* is somewhat shorter than that of *P. depereti*. The fossa parahypotarsalis is slightly deeper in *P. brevipes* than in *Palaeocryptonyx depereti*, but the difference in the depth of the fossa parahypotarsalis is not as distinct as in *P. prisca* and *Palaeocryptonyx edwardsi*. The extremitas omalis of the coracoid rises less steeply proximally in *P. brevipes* than in *P. gallica*, *P. prisca* and *P. phasianoides*.

Dimensions. See Table 1.

Remarks. The specimens (MNHN Sa 1416, 14019, 14016, see synonymy) from Sansan cannot be referred with certainty to *P. brevipes*; a possible affiliation to *Palaeocryptonyx depereti* cannot be excluded, although the latter is not definitively proved in Sansan.

Stratigraphical and geographical distribution. France: Phosphorites du Quercy (Upper Oligocene; Mourer-Chauviré 1992), Créchy (Upper Oligocene; Mourer-Chauviré *et al.* 2004), St-Gérard-le-Puy (Lower Miocene, MN2; Milne-Edwards 1867–71), Sansan (Middle Miocene, MN6, *P. prisca partim*; Cheneval 2000), Vieux-Collonges, MN5 (Lower/Middle Miocene, *P. intermedia partim*; Ballmann 1972), La Grive (Middle Miocene, MN7+8; own investigation); Germany: Petersbuch 2 (Lower Miocene, MN2; own investigation), Spitzberg (Middle Miocene, MN6; own investigation).

Discussion. Five femora housed in the MNHN [femur dext. (MNHN Av 2906, figured inversely in Milne-Edwards 1867–71, pl. 130, figs 7–11); femur sin. (MNHN Av 2908); femur dext., distal end broken off (MNHN Av

EXPLANATION OF PLATE 1

- Figs 1, 8–9, 11, 15, 22. *Palaeortyx phasianoides* Milne Edwards, 1869. 1, scapula dext. (MNHN SG 10203), lateral view. 8, coracoid sin. (MNHN SG 10208), dorsal view. 9, carpometacarpus sin. (MNHN SG 10210), ventral view. 11, 15, humerus sin. (ML StG 1430); 11, caudal view; 15, cranial view. 22, ulna sin. (FSL 444 177), ventral view.
- Figs 2, 7, 12, 16, 21. *Palaeortyx prisca* Milne Edwards, 1869. 2, scapula sin. (MNHN SG 10205), lateral view. 7, coracoid dext. (FSL 444 204), dorsal view. 12, 16, humerus sin. (FSL 91 803); 12, caudal view; 16, cranial view. 21, ulna sin. (MNHN SG 10215), ventral view.
- Figs 3, 6, 13, 17, 20. *Palaeortyx gallica* Milne Edwards, 1869. 3, scapula sin. (MNHN SG 10206), lateral view. 6, coracoid dext. (FSL 444 201), dorsal view. 13, 17, humerus dext. (ML StG 59); 13, caudal view; 17, cranial view. 20, ulna dext. (MNHN SG 10216), ventral view.
- Figs 4–5, 10, 14, 18–19. *Palaeortyx brevipes* Milne Edwards, 1869. 4, scapula dext. (FSL 440 605), lateral view. 5, coracoid dext. (MNHN SG 10209), dorsal view. 10, carpometacarpus dext. (MNHN Av 2904), ventral view. 14, 18, humerus sin. (FSL 444 199); 14, caudal view, 18, cranial view. 19, ulna sin. (FSL 444 184), ventral view.
- All specimens from St-Gérard-le-Puy, Allier, France (Early Miocene, Mammal Neogene zone MN2a).



GÖHLICH and MOURER-CHAUVIRÉ, *Palaeortyx*

2905); femur dext. (MNHN Av 2907); femur sin. (MNHN Av 2908)] are labelled *P. brevipes*, but differ in detail from the general *Palaeortyx* morphology, even if they seem to belong to phasianids.

They differ from the femur of *P. brevipes* in the following ways: distal end (1) in medial view without any prominence proximally on the condylus medialis; (2) lateral crista of trochlea fibularis reaching less caudally; (3) in distal view sulcus intercondylaris shallower; proximal end (4) in proximal view with an incisura of facies articularis antetrochanterica narrower; (5) with a collum caudally less or not incised in lateral view; (6) smaller size. This femur morphology can also be observed in three other small femora from Quercy (MNHN QU 17002, 17027, 16934). For the synonymy of *P. gallica* and *P. brevipes* postulated by Mlíkovský (2000), see discussion of *P. gallica*.

An additional small taxon, *Palaeortyx grivensis* Lydekker, 1893 was described from La Grive (Middle Miocene, France). The holotype, a humerus, is morphologically identical with, and only a little smaller than, the humeri of *P. brevipes* from St-Gérard-le-Puy, but it fits in the size variations of *P. brevipes* described by Mourer-Chauviré (1992) from Quercy, which are slightly smaller. Hence, a synonymy of *P. brevipes* with *P. grivensis* is possible. Ballmann (1973, 1976) also described *P. grivensis* from the Upper Miocene of Gargano (Italy), but current investigations on new phasianid material from Gargano by one of us (UBG) and M. Pavia (University of Turin) indicate that the phasianid taxon of Gargano and *P. brevipes* from St-Gérard-le-Puy are probably distinct. Thus, the systematic identity and validity of *P. grivensis* may be clarified with the study of the phasianids from Gargano.

Ballmann (1973, p. 25; 1976, p. 8) put *Palaeocryptonyx depereti* (Ennouchi, 1930) in synonymy with *Palaeortyx grivensis* Lydekker, 1893; however, following our comparisons of both holotype humeri, they can be morphologically separated from each other by the non-pneumatization of the ventral fossa pneumotricipitalis in *P. grivensis*.

Palaeortyx prisca (Milne-Edwards, 1869)

Plate 1, figures 2, 7, 12, 16, 21; Plate 2, figures 2, 6, 8–15, 18

- *vp. 1869 *Palaeoperdix prisca* Milne-Edwards, pp. 246–248, pl. 131, figs 1–8, 15–17 [non figs 11–14].
- p. 1891 *Palaeoperdix prisca* Milne-Edwards; Lydekker, p. 139.
- p. 1912 *Palaeoperdix prisca* Milne-Edwards; Paris, p. 296.
- p. 1933 *Palaeoperdix prisca* Milne-Edwards; Lambrecht, p. 423.

- p. 1964 *Palaeoperdix prisca* [sic] Milne-Edwards; Brodkorb, p. 313.
- 1969b *Palaeortyx? intermedia* Ballmann, pp. 33–34, pl. 1, figs 1–2.
- 1972 *Palaeortyx intermedia* Ballmann 1966 [sic]; Ballmann; p. 96.
- vp. 1992 *Palaeortyx intermedia* Ballmann 1966 [sic]; Mourer-Chauviré, p. 87 [non fig. 5h–i, MNHN Qu 15582; MNHN Qu 16962 = *P. phasianoides*].
- vp. 2000 *Palaeortyx prisca* (Milne-Edwards); Cheneval, p. 345 [non MNHN Sa 14013, 14016–14019, 14024, MNHN Sa 1416].
- vp. 2002a *Alectoris prisca* (Milne-Edwards); Mlíkovský, p. 158.
- v. 2002 *Palaeortyx intermedia* Ballmann 1969; Göhlich, pp. 182–185, pl. 2, figs 5–9.
- v. 2003 cf. *Palaeortyx intermedia* Ballmann 1969; Göhlich, p. 244, fig. 4.

Lectotype. Tarsometatarsus dext., prox. half (MNHN Sa 1236), lectotype designation by Cheneval (2000, p. 345), figured (inversely) in Milne-Edwards (1867–71, pl. 131, figs 1–4) and in Cheneval (2000, fig. 4).

Paralectotypes. Coracoid dext. prox. end broken off (MNHN Sa 1239) (figured inversely in Milne-Edwards 1867–71, pl. 131, figs 15–17 and in Cheneval 2000, fig. 5); tt sin., dist. half (MNHN Sa 1237) (figured inversely in Milne-Edwards 1867–71, pl. 131, figs 5–8).

Type locality and horizon. Sansan (Gers), France, Middle Miocene, MN6.

Material. Coracoid dext. (MNHN SG 10202); coracoid dext. (MNHN SG 10205); coracoid dext., processus lateralis broken off (FSL 444 174); coracoid sin., distal half (FSL 444 175); coracoid sin. (BSP 1993 IX 624); scapula sin., prox. third (FSL 444 204); humerus sin., proximal end broken off (FSL 444 187); humerus sin. (FSL 91 803); humerus dext. (ML StG 1627); humerus dext. (MNHN Av 2913); ulna dext. (FSL 440 608); ulna sin. (MNHN SG 10215); femur dext. (FSL 444 163); femur dext. (FSL 444 164); femur dext. (FSL 444 165); femur dext. (FSL 444 166); femur dext. (FSL 444 167); femur dext., prox. end damaged (FSL 444 168); femur dext., prox. end broken off (FSL 444 169); femur dext. (ML StG 1464); tt dext. (MNHN SG 10211); tt dext., shaft (MNHN SG 10213); tmt sin. (MNHN SG 10219).

Differential diagnosis. *P. prisca* is smaller than *P. phasianoides* but larger than *P. gallica* and *P. brevipes*. In some bones (e.g. tmt, femur, coracoid) it is similar in size to *Palaeocryptonyx edwardsi*; the scapula of *P. prisca* is somewhat larger than that of *Palaeocryptonyx edwardsi* and the bony connection between the tuberculum coracoideum and facies articularis humeralis (in proximal view) is more robust than in *Palaeocryptonyx edwardsi*.

(Text-fig. 4), in which it is thin. The humerus of *P. prisca* differs from that of *Palaeocryptonyx edwardsi* in having a deep lateral and medial fossa pneumotricipitalis, whereas the medial fossa pneumotricipitalis is not pneumatic. The fossa parahypotarsalis on the tarsometatarsus is deeper at the point of the opening of the proximal foramen than in *Palaeocryptonyx edwardsi* (Text-fig. 4), while the distal end is morphologically indistinguishable. The tibiotarsi are shorter than those of *P. phasianoides*, although both the dimensions and the morphology of their distal ends seem to be virtually identical.

Dimensions. See Table 1.

Remarks. The type of *Palaeoperdix? sansaniensis* Milne-Edwards, 1869 (figured inversely in Milne-Edwards 1867–71, pl. 131, figs 18–23), which has been referred to *P. prisca* and listed under the paralectotypes by Cheneval (2000, p. 345) and Mlíkovský (2002a, p. 158), is referred to *P. gallica* herein. The distal humerus, described by Milne-Edwards (1867–71, pl. 131, figs 11–14) as belonging to *P. prisca*, was determined by Cheneval (2000) to be the rallid *Palaeoaramides beaumonti*. It was impossible to find the fragmentary furcula figured in Milne-Edwards (1867–71, pl. 131, figs 9–10).

Stratigraphical and geographical distribution. France: Phosphorites du Quercy (Upper Oligocene, *P. intermedia*; Mourer-Chauviré 1992), St-Gérard-le-Puy (Lower Miocene, MN2; Mourer-Chauviré 1992), Vieux-Collonges (Lower/Middle Miocene, MN5, *P. intermedia*; Ballmann 1972), Sansan (Middle Miocene, MN6; Cheneval 2000); Germany: Wintershof-West (Lower Miocene, MN3, *P. intermedia*; Ballmann 1969b), Sandelzhausen (early Middle Miocene, MN5, *P. intermedia*; Göhlich 2002); Austria: Grund (early Middle Miocene, MN5, cf. *P. intermedia*; Göhlich 2003).

Discussion. It was Mourer-Chauviré (1992), who first mentioned the presence of *P. intermedia* Ballmann, 1969 in St-Gérard le Puy. It was described by Ballmann (1969b) based on material from the fissure filling of Wintershof-West (Lower Miocene, MN3) in Germany. Mlíkovský (2000) did not agree that *P. intermedia* occurs in St-Gérard-le-Puy and put it into synonymy with *Palaeoperdix longirostris* from Sansan, to which he also referred the *P. phasianoides* material from St-Gérard-le-Puy except for the two syntypes of *P. phasianoides* (see under *P. phasianoides*).

Comparisons of the material of *P. prisca* from Sansan (Middle Miocene, MN6, France) with the material of *P. intermedia* from St-Gérard-le-Puy (Lower Miocene, MN2, France) and its type locality Wintershof-West (Lower Miocene, MN3, Germany) led to the conclusion of their synonymy. It was Cheneval (2000, p. 345) who

moved the species *P. prisca* to *Palaeortyx*. The lectotype of *P. prisca*, a proximal end of a tarsometatarsus, unfortunately cannot be compared with a syntype-tarsometatarsus of *P. intermedia* from Wintershof-West because there is only a distal tarsometatarsus of *P. intermedia*, described by Ballmann (1969b), but a direct comparison of both specimens side by side shows a correspondence in size. However, a tarsometatarsus from St-Gérard-le-Puy (MNHN SG 10219), formerly determined by us to be a *P. intermedia*, corresponds exactly, both morphologically and in size, to the lectotype of *P. prisca* (Pl. 2, figs 8–12). Although the lectotype tarsometatarsus of *P. prisca* is only a proximal end, it clearly shows a deep fossa parahypotarsalis and the structure of the hypotarsus corresponds exactly with those of the other represented species of *Palaeortyx*. Unfortunately, no tarsometatarsus of '*P. intermedia*' is known from the deposits of Quercy (Mourer-Chauviré 1992).

Cheneval (2000, p. 345) described as the most distinctive feature (in comparison with *P. gallica*) of the lectotype tarsometatarsus of *P. prisca* a medial sharp-edged crest below the cotyla medialis. In fact, this medial crest, which is present in all tarsometatarsi of *Palaeortyx*, only gives the impression of being sharp-crested, because a small part along the crest is splintered. Furthermore, the holotype of *P. intermedia* from Wintershof-West, a coracoid (BSP 1937 II 18103, figured in Ballmann, pl. 1, figs 1–2), morphometrically corresponds to the coracoid paralectotype of *P. prisca* (figured in Cheneval 2000, fig. 5). Unfortunately the latter lacks the proximal process acroracoides; therefore, no measurement of the length can be given, but the two specimens have been studied side by side and correspond to each other.

The diagnostic features for the coracoid of *P. intermedia* from Wintershof-West were given by Ballmann (1969b, p. 33, translated from German) as follows: 'small and slender; foramen pneumaticum lacking; crista articularis sternalis (= facies articularis sternalis) slightly arched and strongly enlarged medially; caudal and dorsal facies articulares sternales developed; linea intermuscularis runs to processus externus (= processus lateralis); margo interna not curved; in the caudal third labrum internum protruding medially as a sharp crest; medially the caudal edge of tuber brachialis (= processus acroracoides) is straight'. All of these features are included in the morphological variability of the coracoids from St-Gérard-le-Puy, formerly determined by us to be *P. intermedia*, and in the coracoid paralectotype of *P. prisca* from Sansan. Therefore, we put *P. intermedia* Ballmann, 1969 in the synonymy of *P. prisca* Milne-Edwards, 1869 on the basis of priority of publication.

Two tibiotarsi from Wintershof-West (BSP 1937 II 18106 and 18107) that were referred to *P. intermedia* by

Ballmann, are too small to belong to *P. prisca* and correspond in size to *P. gallica* from St-G erand-le-Puy.

Some of the material from Sansan that has been referred to *P. prisca* (Cheneval 2000, p. 345) belongs to different galliform taxa: a coracoid (MNHN Sa 14017) and an ulna (MNHN Sa 14013) can be determined as cf. *P. prisca*; the humeri (MNHN Sa 1416, 14024) belong to *Palaeocryptonyx edwardsi*; two coracoids (MNHN Sa 1416, 14019) and a tarsometatarsus (MNHN Sa 14016) cannot definitely be referred to *Palaeortyx brevipes* or *Palaeocryptonyx depereti*; a coracoid (MNHN Sa 14018) is determined hereby as cf. *P. phasianoides*.

Our study of the material of *P. phasianoides* and *P. prisca* (including '*P. intermedia*') from St-G erand-le-Puy results in the distinction of these two species because of their size difference. Comparisons with the present-day species *Perdix perdix* and *Coturnix coturnix* led us to the conclusion that the variability coefficients, especially of the coracoids and the humeri of a unified species like *P. longipes* (= *P. phasianoides* in the sense of Ml kovsk y 2000, 2002a) including *P. intermedia*, as proposed by Ml kovsk y (2000, p. 93), are too large to represent only one species of quail (Table 2), whereas the computed values of the variability coefficients of the two distinguished taxa, *P. phasianoides* and a separated *P. prisca* (= *P. intermedia* in our sense) correspond well to those of recent *P. perdix* and *C. coturnix* (Table 2).

Ml kovsk y (2002a, p. 158) moved *prisca* to the recent genus *Alectoris*, but our comparisons of *Palaeortyx* with extant *A. rufa* (SAPM 19, male; 21, female) and *A. graeca* (SAPM 3, male; 26, female) show the following differences: in *Alectoris* the male tarsometatarsi are characterized by a spur, which is always absent in *Palaeortyx*; the ventral fossa pneumotricipitalis is pneumatized in *Alectoris*, while it is not pneumatized in *Palaeortyx*; in contrast to the deep dorsal fossa pneumotricipitalis of *Palaeortyx* it is moderately deep in *Alectoris*. The processus pisiformis on the carpometacarpus is very thin, pointed, and distally elongated in *Palaeortyx*, whereas it is thicker and

not distally elongated in *Alectoris*. At the ulna the tuberculum carpale is more pointed in *Palaeortyx* and blunter in *Alectoris*. As shown in Text-figure 2 the proportions of the length of the limb bones of *Alectoris* are different from those of *Palaeortyx*; the leg bones especially are relatively longer in *Alectoris*.

Palaeortyx phasianoides Milne-Edwards, 1869

Plate 1, figures 1, 8–9, 11, 15, 22; Plate 2, figures 1, 5

- *vp. 1869 *Palaeortyx?* *phasianoides* Milne-Edwards 1867–71, p. 237, pl. 130, figs 22–25 (*non* pl. 130, figs 26–27).
- v. 1869 *Palaeoperdix longipes* Milne-Edwards, vol. 2, p. 245; pl. 130, figs 28–31 (= holotype of *P. longipes*).
- vp. 1887 *Palaeortyx edwardsi* Dep ret, pp. 285–286 (ML LGr 42d) [*non* Dep ret, pl. 13, fig. 51 (ML LGr 42b); fig. 52 (ML LGr 42a); ML LGr 42c].
- p. 1891 *Palaeortyx* (?) *phasianoides* Milne-Edwards; Lydekker, p. 139 (*non* humerus).
- 1891 *Palaeoperdix longipes* Milne-Edwards; Lydekker, p. 139.
- vp. 1893 *Palaeortyx edwardsi* Dep ret; Lydekker, p. 519, pl. 41, figs 9, 9a, 10.
- 1912 *Palaeoperdix longipes* Milne-Edwards; Paris, p. 296.
- p. 1933 *Palaeortyx* (?) *phasianoides* Milne-Edwards 1871; Lambrecht, p. 452 (*non* humerus).
- vp. 1939 *Palaeortyx edwardsi* Dep ret; Gaillard, p. 49, fig. 24.
- v. 1939 *Palaeortyx miocaena* Gaillard, p. 52, fig. 27 (= syntype).
- vp. 1964 *Taoperdix phasianoides* (Milne-Edwards); Brodkorb, p. 301 (*non* humerus).
- 1967 *Palaeortyx phasianoides* Milne-Edwards; Brodkorb, p. 112.
- v. 1969b *Palaeortyx phasianoides* Milne-Edwards; Ballmann, p. 31–33, pl. 1, figs 5–6.

EXPLANATION OF PLATE 2

Figs 1, 5. *Palaeortyx phasianoides* Milne Edwards, 1869. 1, femur sin. (FSL 444 162), caudal view. 5, tibiotarsus sin. (FSL 444 158), cranial view.

Figs 2, 6, 8–15, 18. *Palaeortyx prisca* Milne Edwards, 1869. 2, femur sin. (FSL 444 172), caudal view. 6, tibiotarsus dext. (MNHN SG 101211), plantar view. 8–12, tarsometatarsus dext., lectotype (MNHN SA 1236) from Sansan; 8, proximal view; 9, dorsal view; 10, plantar view; 11, medial view; 12, lateral view. 13–15, 18, tarsometatarsus sin. (MNHN SG 10219); 13, proximal view; 14, medial view; 15, plantar view; 18, dorsal view.

Figs 3, 7, 16, 19. *Palaeortyx gallica* Milne Edwards, 1869. 3, femur sin. (FSL 444 170), caudal view. 7, tibiotarsus sin. (FSL 444 161), cranial view. 16, 19, tarsometatarsus dext. (MNHN SG 10220); 16, plantar view; 19, dorsal view.

Figs 4, 17, 20. *Palaeortyx brevipes* Milne Edwards, 1869. 4, femur dext. (FSL 444 172), caudal view. 17, 20, tarsometatarsus dext. (FSL 444 157); 17, plantar view; 20, dorsal view.

Specimens in 1–7, 13–20 from St-G erand-le-Puy, Allier, France (Early Miocene, Mammal Neogene zone MN2a); those in 8–12 from Sansan, Gers, France (Middle Miocene, Mammal Neogene zone MN6).



GÖHLICH and MOURER-CHAUVIRÉ, *Palaeortyx*

TABLE 1. Measurements (in mm) of *Palaeortyx phasianoides*, *P. prisca*, *P. gallica* and *P. brevipes* from St-Gérard-le-Puy given as mean (\bar{x}), range (min – max), and standard deviation (S); n, number of specimens. Measurements of bones that are slightly worn or damaged are given in parentheses. GL, greatest length; Lm, medial length; Wp, proximal width; Dp, proximal depth; Ws, smallest width of shaft; Wd, distal width; Dd, distal depth. Coracoid: Wdf, width of distal facies; Lp, proximal length from distal margin of facies articularis humeralis to proximal end; Wpa, width of processus acrocoracoideus. Scapula: W, proximal width from caudal margin of facies articularis humeralis to acromion; Wc, smallest width of the corpus caudally to facies articularis humeralis. Ulna: Ddp, proximal diagonal depth from processus cotylaris dorsalis to olecranon; Wtr, width of distal trochlea (condylus dorsalis ulnaris); Dtr, depth of distal trochlea; Dmax, maximal diagonal of distal trochlea. Radius: Wpmax, maximal width proximal. Carpometacarpus: Lc, cranial length from trochlea carpalis to cranial distal end; LS, length of spatium; Dmc, depth (craniocaudally) of os metacarpale majus; Wmc, width (dorsoventrally) of os metacarpale majus. Tibiotarsus: L, length from proximal articulation surface (without crista cne-mialis) to distal end; Ddp, proximal diagonal depth. All specimens except MNHN SG 10206, a coracoid of *P. gallica*, are adult. The original measurements are available from the authors on request.

	<i>Palaeortyx phasianoides</i>				<i>Palaeortyx prisca</i>				<i>Palaeortyx gallica</i>				<i>Palaeortyx brevipes</i>			
	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n
coracoid																
GL	39.4	(38)–41.7	1.383	5	35.3	34.5–36.9	1.386	3	(31)	–	–	1	26.3	25.7–26.9	0.849	2
Lm	37.4	36.3–39.5	1.417	4	33.5	32.7–34.5	0.750	4	30.0	29.5–(30.5)	0.503	3	24.4	23.4–25.6	1.106	3
Wd	13.3	12.6–13.8	0.643	3	10.8	10.1–11.5	0.990	2	–	–	–	–	8.9	7.8–9.9	1.485	2
Wdf	8.9	8.0–9.6	0.700	4	7.2	6.4–7.7	0.602	4	–	(> 6)–(6.5)	–	3	5.8	5.4–6.6	0.666	3
Lp	12.1	11.2–12.8	0.670	4	10.9	10.4–11.3	0.377	4	9.6	9.5–9.7	0.141	2	7.7	7.2–8.5	0.700	3
Wpa	7.5	–	–	1	6.2	–	–	1	5.55	5.5–5.6	0.071	2	4.45	4.3–4.6	0.212	2
scapula																
GL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
W	10.6	10.2–10.8	0.321	3	9.6	–	–	1	8.05	8.0–8.1	0.071	2	6.5	6.2–6.8	0.424	2
Wc	3.4	3.3–3.6	0.173	3	3.1	–	–	1	2.75	2.7–2.8	0.071	2	2.6	2.4–2.8	0.283	2
humerus																
GL	53.3	51.7–(56)	1.652	6	49.3	47.4–50.3	1.620	3	41.1	38.9–43.2	1.614	9	36.4	35.6–37.5	0.922	5
Wp	14.5	13.8–15.1	0.499	8	13.4	13.1–13.8	0.351	3	10.7	10.0–11.2	0.457	10	8.9	8.1–9.4	0.516	6
Ws	4.7	4.4–5.4	0.307	8	4.4	4.3–4.5	0.082	4	3.7	3.1–4.9	0.396	14	2.9	2.6–3.2	0.219	6
Wd	11.1	10.8–11.4	0.216	6	10.3	10.0–10.4	0.191	4	8.1	7.9–8.6	0.259	13	7.1	6.8–7.3	0.217	5
ulna																
GL	(51)	–	–	1	47.7	47.6–47.8	0.141	2	38.7	38.4–40.5	1.737	5	32.7	32.0–33.6	0.833	3
Ddp	(9.0)	–	–	1	8.2	7.8–8.6	0.566	2	7.1	(6.8)–7.4	0.228	5	5.7	(5.1)–6.1	0.479	4
Wp	7.0	–	–	1	6.3	6.1–6.5	0.283	2	4.8	(4.7)–5.0	0.152	5	4.2	(3.8)–4.4	0.263	4
Ws	2.8	–	–	1	2.7	2.7–2.7	0.000	2	2.3	2.0–2.5	0.187	6	2.0	2.0–2.0	0.000	5
Wtr	6.0	–	–	1	5.55	5.4–5.7	0.212	2	4.6	4.3–4.9	0.219	6	3.9	3.9–4.0	0.058	3
Dtr	5.8	–	–	1	5.3	5.3–5.3	0.000	2	4.5	4.3–4.8	0.175	6	4.2	4.1–4.3	0.115	3
Dmax	7.2	–	–	1	6.3	6.2–6.4	0.141	2	5.4	5.0–5.8	0.279	6	4.8	4.5–(5.1)	0.248	6
cmc																
GL	29.2	–	–	1	–	–	–	–	–	–	–	–	18.7	–	–	1
Lc	28.3	–	–	1	–	–	–	–	–	–	–	–	17.6	–	–	1
Dp	8.7	–	–	1	–	–	–	–	–	–	–	–	5.3	–	–	1
Dd	5.2	–	–	1	–	–	–	–	–	–	–	–	3.7	–	–	1
LS	14.3	–	–	1	–	–	–	–	–	–	–	–	10.0	–	–	1
Dmc	2.6	–	–	1	–	–	–	–	–	–	–	–	1.7	–	–	1
WMc	2.8	–	–	1	–	–	–	–	–	–	–	–	1.8	–	–	1
femur																
GL	53.2	–	–	1	47.9	45.9–49.4	1.077	7	42.1	39.1–44.2	1.764	7	37.9	–	–	1
Lm	49.8	–	–	1	45.5	44.0–47.3	1.191	6	40.3	37.9–41.9	1.143	6	36.9	–	–	1
Wp	10.2	–	–	1	8.7	8.3–9.6	0.500	6	7.4	6.5–8.2	0.725	7	6.9	–	–	1
Dp	6.6	–	–	1	5.6	5.4–5.9	0.183	6	4.7	4.2–5.1	0.354	6	4.4	–	–	1
Ws	4.0	–	–	1	3.6	3.4–4.6	0.396	8	3.4	2.6–4.3	0.538	7	2.7	–	–	1
Wd	10.0	–	–	1	7.9	7.7–8.4	0.239	8	6.8	6.1–7.4	0.456	6	6.3	–	–	1
Dd	8.7	–	–	1	6.8	(6.1)–7.2	0.378	8	5.9	5.3–6.5	0.439	5	5.3	–	–	1

TABLE 1. Continued

	<i>Palaeortyx phasianoides</i>				<i>Palaeortyx prisca</i>				<i>Palaeortyx gallica</i>				<i>Palaeortyx brevipes</i>			
	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n	\bar{x}	min – max	S	n
tt																
GL	70.3	69.1–71.5	1.697	2	67.3	–	–	1	59.8	58.6–60.8	1.114	3	50.1	–	–	1
L	68.8	66.6–70.0	1.882	3	64.4	–	–	1	57.8	56.5–59.3	1.419	3	48.5	–	–	1
Ddp	12.5	11.9–13.0	0.778	2	12.4	–	–	1	9.8	9.1–10.2	0.635	3	7.1	–	–	1
Wp	8.2	7.5–8.9	0.702	3	8.1	–	–	1	6.6	5.9–(7.1)	0.624	3	4.8	–	–	1
Ws	3.4	3.0–3.7	0.277	5	3.4	3.3–3.5	0.141	2	2.8	2.6–3.1	0.192	5	2.2	2.2–2.2	0.000	2
Wd	7.1	6.7–7.3	0.251	5	7.1	–	–	1	5.6	5.3–6.3	0.472	4	4.5	4.2–4.7	0.354	2
Dd	7.3	7.0–7.7	0.274	5	7.0	–	–	1	5.6	5.2–6.0	0.462	4	4.3	4.1–4.5	0.283	2
tmt																
GL	–	–	–	–	37.1	–	–	1	33.0	31.7–34.4	1.358	3	28.8	27.2–30.1	1.464	3
Wp	–	–	–	–	7.4	–	–	1	6.2	5.8–6.5	0.379	3	5.7	4.9–6.0	0.535	4
Dp	–	–	–	–	(7.4)	–	–	1	6.1	5.4–6.7	0.666	3	5.1	(4.1)–6.1	1.414	2
Ws	–	–	–	–	3.5	–	–	1	3.1	2.7–3.4	0.351	3	2.8	2.4–3.1	0.294	4
Wd	–	–	–	–	8.0	–	–	1	6.7	6.0–7.2	0.624	3	6.1	5.5–6.7	0.603	3

vp. 1992 *Palaeortyx intermedia* Ballmann 1966 [sic]; Mourer-Chauviré, p. 87 [fig. 5h–i (MNHN Qu 15582); (MNHN Qu 16962)].

vp. 2000 *Palaeortyx longipes* Milne-Edwards; Mlíkovský, pp. 92–93 (*non* MNHN Av 2873, MNHN Av 2913).

vp. 2000 *Palaeortyx longipes* Milne-Edwards 1867–71; Cheneval, p. 347, fig. 7 (= MNHN Sa 1224), and referred material (tmt MNHN Sa 14013–14015), (*non* humeri, MNHN Sa 1281, MNHN Sa 10299; coracoid, MNHN Sa 1462).

Neotype. Göhlich and Mourer-Chauviré (2003) applied to the International Commission on Zoological Nomenclature to designate the syntype-scapula dext. (prox. half) (MNHN Av 2895, figured inversely in Milne-Edwards 1867–71, pl. 130, figs 22–25) to be the neotype. See remarks below.

Type locality and horizon. St-Gérard-le-Puy (Langy), France, Lower Miocene, MN2a.

Topotype material. Coracoid sin. (MNHN SG 10203); coracoid dext., angulus medialis and processus lateralis broken off (MNHN SG 10204); coracoid sin. (FSL 440 604); coracoid sin., processus acroracoides broken off (FSL 444 173); coracoid sin. (MNHN SG 10196, Coll. Hoffstetter, formerly not numbered); scapula sin., prox. half (FSL 91 844); scapula dext., sub-complete (MNHN SG 10208); humerus dext., distal end broken off (FSL 444 188); humerus dext., prox. end (FSL 444 196); humerus dext., prox. end (FSL 444 197); humerus sin. (ML StG 1430, cast); humerus dext., dist. 2/3 (MNHN Av 2916); humerus sin. (MNHN Av 2912); humerus sin. (MNHN Av 2914); humerus dext. (MNHN Av 2915); humerus dext. (BSP 1993 IX 622); humerus dext. (BSP 1993 IX 623); ulna sin. (FSL 444 177); cmc sin., os metacarpale minus broken off (MNHN SG 10210); femur sin. (FSL 444 162); tt sin. (FSL 440 600); tt sin. (FSL 444 158); tt sin., dist. 2/3 (FSL 444 159); tt sin., dist. 2/3 (FSL 331 150); tt dext. (ML StG 3700).

Differential diagnosis. *P. phasianoides* is larger than *P. brevipes*, *P. gallica* and *P. prisca*. It differs from the subspecies *P. phasianoides grivensis* Ballmann, 1969 from La Grive at the distal tibiotarsus by a proximodistally shorter condylus medialis (Text-fig. 5A–B) (in medial view). The same shape, with a proximodistally shorter condylus medialis, can be found in *Palaeocryptonyx edwardsi*. At the distal femur (in distal view) the sulcus intercondylaris is narrower and slightly deeper, the lateral side of the condylus lateralis inclines more obliquely in cranial direction in *P. phasianoides* (Text-fig. 5G–H) and the condylus lateralis is not flattened distally as in *P. phasianoides grivensis* (Text-fig. 5I–J); *P. phasianoides* has a somewhat more slender distal shaft. Concerning the scapula, the swelling below the collum scapulae on the margo dorsalis is weak in *P. phasianoides*, whereas it is often (but not always) stronger in *P. p. grivensis* (Text-fig. 5E–F).

The tibiotarsus of *Palaeocryptonyx edwardsi* can be similar in length to *P. phasianoides*, but is somewhat more slender, whereas its distal end varies in size between those of *P. prisca* and *P. gallica*. The tt of *P. phasianoides* differs from *P. phasianoides grivensis* from La Grive in having a proximodistally shorter condylus medialis (in medial view), a proximodistally narrower pons supratendineus, and a canalis extensorius with a somewhat more distally situated distal opening.

Dimensions. See Table 1.

Remarks. Milne-Edwards (1867–71) created *Palaeortyx phasianoides* based on a scapula (MNHN Av 2895) and an attributed humerus fragment (MNHN Av 2896) (both figured inversely in Milne-Edwards 1867–71, pl. 130, figs 22–27) from St-Gérard-le-Puy, France. Ballmann

TABLE 2. Standard deviation (S) and coefficient of variation (V) of the fossil taxa *Palaeortyx phasianoides*, *P. prisca*, *P. gallica* and *P. brevipes* from St-Gérard-le-Puy. For comparison, the standard deviation and coefficient of variation of the extant taxa *Perdix perdix* and *Coturnix coturnix* and of the combined taxa as proposed by Mlíkovský (2000, 2002a) are also given: *Palaeortyx longipes* (including *P. phasianoides* and *P. intermedia*) and *Palaeortyx gallica* (including *P. brevipes*). n, number of specimens; \bar{x} , mean; GL, greatest length (in mm).

		<i>Palaeortyx phasianoides</i>				<i>Palaeortyx prisca</i>				<i>Palaeortyx gallica</i>				<i>Palaeortyx brevipes</i>			
		\bar{x}	S	V	n	\bar{x}	S	V	n	\bar{x}	S	V	n	\bar{x}	S	V	n
coracoid	GL	39.4	1.383	3.513	5	35.3	1.386	3.925	3	–	–	–	–	26.3	0.849	3.226	2
scapula	GL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
humerus	GL	53.3	1.652	3.100	6	49.3	1.620	3.286	3	41.1	1.614	3.927	9	36.4	0.922	2.533	5
ulna	GL	–	–	–	–	47.7	0.141	0.297	2	38.7	1.737	4.488	5	32.7	0.833	2.547	3
radius	GL	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
cmc	GL	29.2	–	–	1	–	–	–	–	–	–	–	–	18.7	–	–	1
femur	GL	53.2	–	–	1	47.9	1.077	2.248	7	42.1	1.764	4.190	7	37.9	–	–	1
tt	GL	70.3	1.697	2.414	2	67.3	–	–	1	59.8	1.114	1.862	3	50.1	–	–	1
tmt	GL	–	–	–	–	37.1	–	–	1	33.0	1.358	4.116	3	28.8	1.464	5.083	3

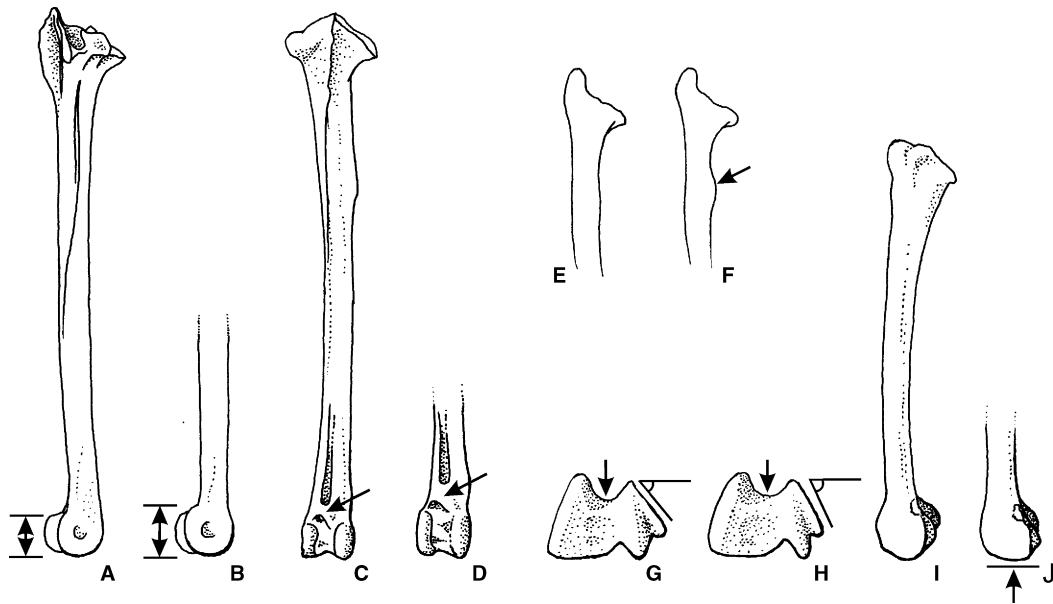
		<i>Perdix perdix</i>				<i>Coturnix coturnix</i>				<i>Palaeortyx longipes</i> (= <i>P. phasianoides</i> + <i>P. 'intermedia'</i> , after Mlíkovský 2000)				<i>P. gallica</i> (= <i>P. gallica</i> + <i>P. brevipes</i> , after Mlíkovský 2000)			
		\bar{x}	S ♀+♂	V ♀+♂	n	\bar{x}	S	V	n	\bar{x}	S	V	n	\bar{x}	S	V	n
coracoid	GL	37.2	1.035	3.495	59	23.7	0.836	3.526	7	37.84	2.461	6.505	8	83.6	2.779	9.962	3
scapula	GL	52.8	1.465	4.974	60	35.4	–	–	5	–	–	–	–	–	–	–	–
humerus	GL	48.8	0.92	3.807	48	32.8	0.745	2.271	7	52.0	2.542	4.917	9	39.4	2.717	6.896	14
ulna	GL	44.5	0.915	3.878	47	28.2	0.862	3.056	8	–	–	–	–	29.1	3.426	9.387	8
radius	GL	40	0.885	3.66	48	25.4	0.904	3.567	4	–	–	–	–	–	–	–	–
cmc	GL	26.9	0.695	2.826	49	17.9	0.319	1.782	7	–	–	–	–	–	–	–	–
femur	GL	55.6	0.85	4.375	61	35.8	1.306	3.647	7	48.5	2.132	4.395	8	41.5	2.212	5.330	8
tt	GL	70.3	1.48	6.374	46	42.4	0.947	2.239	7	69.5	1.790	2.576	3	57.4	4.935	8.597	4
tmt	GL	41.2	0.955	4.012	48	26.2	0.752	2.869	7	–	–	–	–	30.7	2.631	8.569	6

(1969b, p. 31) first recognized that the syntype humerus (MNHN Av 2896) is too large to belong to *Palaeortyx phasianoides*. Unfortunately he failed to name the only remaining specimen of Milne-Edwards syntypes, the scapula (MNHN Av 2895), as the lectotype. Notwithstanding Ballmann's restriction, Mlíkovský (2000, p. 93) fixed the humerus fragment as the lectotype of *P. phasianoides*, but subsequently determined it to be a pathological humerus of the anatid *Mionetta blanchardi* (Milne-Edwards, 1863). As a consequence, he synonymized *Palaeortyx phasianoides* with *Mionetta blanchardi*. Additionally Mlíkovský (2000, p. 91) did not accept the syntype scapula to be phasianid.

After re-studying the syntypes and the large topotype material of *P. phasianoides* from St-Gérard-le-Puy and further Cenozoic European localities we came to the conclusion that the syntype scapula is typical of the Phasianidae, and that the syntype humerus fragment is not a

pathological humerus but belongs to the galliform *Ame-ripodius alexis*, described by Mourer-Chauviré (2000) from St-Gérard-le-Puy. Owing to these taxonomic confusions, which are based on incorrect determinations, and with the intention of preserving the well-known taxon *P. phasianoides*, we applied (Göhlich and Mourer-Chauviré 2003, 2004) to the ICZN to set aside the previous designation of the lectotype and to designate as a neotype the syntype scapula (MNHN Av 2896). Therefore we continue to use the name *P. phasianoides* as a valid taxon until a decision is taken by the ICZN.

Stratigraphical and geographical distribution. France: Quercy (Upper Oligocene; two humeri formerly determined as *P. intermedia* by Mourer-Chauviré 1992), St-Gérard-le-Puy (Lower Miocene, MN2; Milne-Edwards 1867–71), La Grive (Middle Miocene, MN7+8, subspecies *P. phasianoides grivensis*; Ballmann 1969a). Germany: Wintershof-West (Lower Miocene, MN3;



TEXT-FIG. 5 Morphological differences between *Palaeortyx phasianoides* (A, C, E, G, I) from St-Gérard-le-Puy and *Palaeortyx phasianoides grivensis* (B, D, F, H, J) from La Grive (Middle Miocene, MN7+8, France). A–B, tibiotarsus, lateral view. C–D, tibiotarsus, cranial view. E–F, scapula, lateral view. G–H, femur, distal view. I–J, femur, lateral view.

Ballmann 1969b). Czech Republic: Dolnice (Lower Miocene, MN4; Švec 1980: *P. cf. phasianoides*).

Discussion. For the synonymy of *P. longipes* (including *P. phasianoides* in the sense of Mlíkovský 2000) and *P. intermedia*, postulated by Mlíkovský (2000, p. 93), see the discussion under *P. prisca*.

The species *Palaeoperdix longipes* Milne-Edwards, 1869 has been described only from the proximal end of a tarsometatarsus (MNHN Sa 1224, figured in Milne-Edwards 1867–71, pl. 130, figs 28–31) from Sansan (Middle Miocene, MN6), France. As proposed by Ballmann (1969a, p. 182), we accept that the holotype of *P. longipes* is referable to *P. phasianoides*.

Milne-Edwards (1867–71, pp. 245–246) as well as Cheneval (2000, p. 347) pointed out, as a diagnostic feature of *P. longipes*, that the crista medianoplantaris, situated plantarly on the proximal tarsometatarsus, is very sharp-edged. This is correct, but comparative studies on several tarsometatarsi of *P. phasianoides* from La Grive and Wintershof-West (there is no tmt of *P. phasianoides* known from St-Gérard-le-Puy) show that this feature is variable; the crista medianoplantaris was observed to be less sharp-edged (FSL 330 895–330 899; FSL 62 267-12–62 267-17, FSL 62 267-22, ML LGr 6067i, BSP 1937 II 18046) to more sharp-edged (FSL 62 267-19, ML LGr 6035c, ML LGr 6067h). Moreover, the three additional proximal topotype tarsometatarsi from Sansan that have also been referred to *P. longipes* by Cheneval (2000, p. 348), are not characterized by a very sharp-edged crista medioplantaris. In

conclusion we accept *P. longipes* as a junior synonym of *P. phasianoides*.

Mlíkovský (2000, p. 93) accepted neither of the two syntypes of *Palaeortyx phasianoides* Milne-Edwards, 1869 from St-Gérard-le-Puy as phasianids (see remarks above) and put the topotype material into synonymy with *Palaeoperdix* [= *Palaeortyx*] *longipes*. Additionally he (Mlíkovský 2000, p. 93) synonymized *Palaeortyx intermedia* Ballmann, 1969 with *Palaeoperdix* [= *Palaeortyx*] *longipes* (including *Palaeortyx phasianoides*), arguing that the measurement of the proximal width of the tmt of *P. longipes* corresponds in size to the same element of *P. intermedia* Ballmann, 1969, but in fact, no proximal tarsometatarsus has been described for *P. intermedia* from Wintershof-West, its type locality. Unfortunately no tarsometatarsus of *P. phasianoides* is known from St-Gérard-le-Puy. However, in comparison with the proximal width of the tarsometatarsi of *P. phasianoides* from La Grive and Wintershof-West, and of *P. longipes* from Sansan, the tarsometatarsi of *P. prisca* from St-Gérard-le Puy (= *P. intermedia*, see above) and Sansan are distinctly smaller.

PHASIANIDAE indet.

Remarks. There is only one complete radius of *Palaeortyx* known from St-Gérard-le-Puy, but because there is no possibility of size comparison, it cannot be referred to any of the species described.

Three additional tarsometatarsi of galliforms are known from St-Gérard-le-Puy, and these are morphologically different from the tarsometatarsi of the *Palaeortyx* species described. The tmt dext., prox. end damaged (FSL 330 999) is the same length as in *P. gallica*, but its shaft and distal end are more slender. Because of this it resembles that of the Rallidae, but the fossae on both sides of the hypotarsus indicate that it is galliform. The fossa parahypotarsalis medialis is shallower in comparison with *Palaeortyx* and thus closer to *Palaeocryptonyx depereti*. We found a tarsometatarsus of *P. depereti* from La Grive (ML LGr 51) to which our specimen corresponds but which is a little shorter. Because our specimen cannot be identified with certainty, and because there is no other proof of *P. depereti* in St-Gérard-le-Puy, we determine it as *Galliiformes indet.*

There is a similar problem pertaining to a tmt sin. with a damaged hypotarsus (ML StG 238). Its length is similar to that of *P. intermedia*, but it seems to be somewhat more robust. Unlike in the tarsometatarsi of *Palaeortyx* the fossa parahypotarsalis is shallower, which is a characteristic of *P. edwardsi*. Without any other proof of the presence *P. edwardsi* at St-Gérard-le-Puy an affiliation with this species seems to be too uncertain.

The tmt dext (FSL 444 156), with its hypotarsus broken off, corresponds in morphology and size with *P. gallica*, but it differs in having a shallower fossa parahypotarsalis, and stronger cristae plantares medialis and lateralis.

CONCLUSIONS

Our revision of the phasianids from the Lower Miocene of St-Gérard-le-Puy confirms the presence of four different species of *Palaeortyx*: *P. gallica*, *P. brevipes*, *P. phasianoides* and *P. prisca*. The last of these is described for the first time from St-Gérard-le-Puy and was found to be the senior synonym of *P. intermedia*. Thus, *Palaeortyx intermedia* is synonymized in this study with *Palaeortyx prisca* (Milne-Edwards, 1869), described from the Middle Miocene of Sansan (France). *Palaeortyx brevipes* was synonymized by Mlíkovský (2000) with *Palaeortyx gallica*, and *Palaeortyx intermedia* with *Palaeortyx longipes* (Milne-Edwards 1869). *P. longipes* was described from the Middle Miocene of Sansan (France) and was formerly a junior synonym of *Palaeortyx phasianoides*. Our study of the skeletal remains of the phasianids from St-Gérard-le-Puy and investigations on variability statistics of some recent quails and partridges (*Coturnix*, *Perdix*, and *Alectoris*) led to differing conclusions: *Palaeortyx brevipes*, *P. gallica*, *P. prisca* and *P. phasianoides* are separated and valid taxa; *P. longipes* is a junior synonym of *P. phasianoides*.

Whereas it was proposed by Mlíkovský (2002a) to refer *P. gallica* to the recent genus *Coturnix* and *P. prisca* to extant *Alectoris*, our comparisons with the extant quails and partridges noted above add up to osteological differences between these Recent and Miocene taxa, and confirm the distinction of the Tertiary genus *Palaeortyx*. In addition, some new morphological and size differences between *Palaeortyx* and *Palaeocryptonyx* were discovered, including a more robust bony catwalk between the tuberculum coracoideum and facies articularis humeralis in the scapula and a deeper shallow fossa parahypotarsalis on the proximal tarsometatarsus of *Palaeortyx*.

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