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The Fossil Galliform Bird *Paraortygoides* from the Lower Eocene of the United Kingdom

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ABSTRACT

A new fossil species assigned to the galliform genus *Paraortygoides* Mayr is described from the Lower Eocene (Ypresian Stage) London Clay Formation of the United Kingdom. *Paraortygoides radagasti*, n. sp., is referred to the genus on the basis of comparisons with other specimens from the Middle Eocene deposit of Messel (Hessen, Germany). Because of the three-dimensional preservation of this fossil material, *P. radagasti* contributes new information pertaining to the morphology of the genus *Paraortygoides*, in particular with regard to the thoracic vertebrae, tarsometatarsus, and toes. This genus, for example, is distinguished from other currently known fossil and extant galliform birds by the presence of deep pneumatic excavations in the lateral sides of the thoracic vertebrae. The results of a preliminary phylogenetic analysis suggest that *Paraortygoides* is basal within Galliformes (as already proposed by Mayr [2000]); monophyly of the order is supported with Megapodiidae as the basal sister taxon with respect to the Cracidae and Phasianidae. *Paraortygoides radagasti* is one of the oldest galliform birds described to date; its age and degree of preservation provide a reliable early phylogenetic constraint for the divergence of a basal clade within the order Galliformes.

INTRODUCTION

The avian order Galliformes has generally been considered one of the more basal clades of modern birds (= Neornithes sensu Cracraft, 1988). Current classifications suggest that the order comprises five distinct families, namely Megapodiidae (megapodes and relatives), Numididae (guinea fowl), Phasianidae (pheasants and relatives), Odonto-

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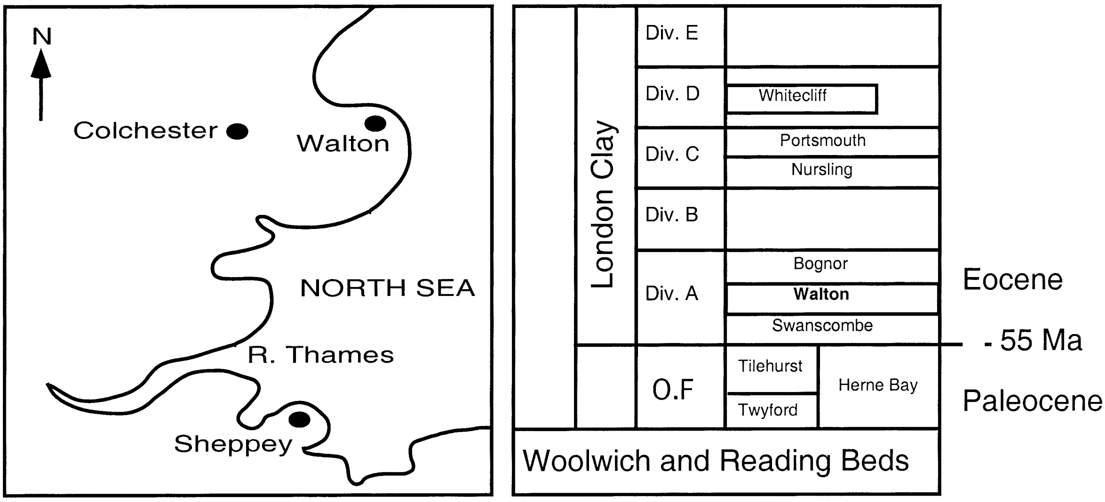

Fig. 1. Map of southeast coast of the United Kingdom showing the principal outcrops of the London Clay Formation at Walton-on-the-Naze and the Isle of Sheppey (left side) as well as a simplified stratigraphy of the formation (right side).

phoridae (New World quails), and Cracidae (currasows and relatives; Wetmore, 1964; Cracraft, 1981; Sibley and Ahlquist, 1990). Most often, Galliformes have been placed within a basal neornithine clade along with Anseriformes (waterfowl) that has been termed the Galloanserae (e.g., Cracraft, 1988; Dzerzhinsky, 1995; Livezey, 1997; Groth and Barrowclough, 1999; see Zusi and Livezey, 2000 and Cracraft and Clarke, 2001 for further commentaries; but see also Ericson, 1996, for an alternative view).

The described fossil record of this order appears extensive if taken at face value; putative remains of ‘‘galliform’’ birds have been described from deposits that range in age from latest Cretaceous to Recent (e.g., Brodkorb, 1963; Unwin, 1993; Hope, 2002). However, since the exact affinities of the fossil records from the Cretaceous are uncertain because of their incompleteness (Hope, 2002) and the resultant problems with the polarization of few phylogenetically informative characters (Clarke, 1999), the oldest certain record of the order [described to date] is likely from the Lower Eocene Green River Formation of the United States (Grande, 1984). This taxon, *Gallinuloides wyomingensis* Eastman, 1900, was placed within the extinct family Gallinuloididae by Lucas (1900), now also considered to contain a number of somewhat younger and incompletely known taxa (Milne-Edwards, 1867–1871; Tordoff and Macdonald, 1957; Crowe and Short, 1992; Mayr, 2000). A number of other named taxa of galliform birds from the Tertiary have been described, but these have also largely been based on incomplete skeletal material (see Olson, 1985; Mayr, 2000, for further discussion). Most importantly, these specimens have never been considered within a cladistic analysis along with extant galliforms.

The remains of fossil birds have been known from the Eocene of the United Kingdom for more than a hundred years (e.g., Koenig, 1825; Owen, 1841, 1846; Andrews, 1899). A number of specimens were described from the Lower Eocene (Ypresian Stage) London Clay Formation by Harrison and Walker (1977), and were referred to Galliformes as the types of the taxa *Argillipes*, *Percolinus*, and *Coturnipes*. However, and as will be discussed below, since these taxa were named on the basis of single fossil elements, their exact affinities remain uncertain (Dyke, 2000).

In this paper we present the description of a new species of the fossil galliform *Paraortygoides* Mayr from the base of the London Clay Formation outcropped at the locality of Walton-on-the-Naze, Essex, UK (King, 1981; Collinson, 1983: fig. 1). The genus *Paraortygoides* was named by Mayr (2000) for the reception of the type species, *P. messelensis*, known from the Middle Eocene deposit of Messel, Hessen, Germany (Schaal and Ziegler, 1988). Originally this taxon was based on a single articulated individual (SMF-ME 1303; lacking the skull; Mayr, 2000), but subsequent collections have yielded a number of additional specimens that are also referrable to *P. messelensis* (G. Mayr, personal commun.; see below). The new fossil material described here is one of the oldest currently known certain records for the order. We also consider the phylogenetic position of *Paraortygoides* using a number of osteological features within a cladistic character analysis. Hence, this material is the oldest galliform bird to be investigated within a strict cladistic framework.

MATERIALS AND METHODS

The fossil specimens discussed herein are housed in the collections of the Palaeontology Department of The Natural History Museum, London, United Kingdom (BMNH PAL); the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF); and the Staatliches Museum für Naturkunde, Karsruhe, Germany (SMNK). Recent comparative material was examined at the American Museum of Natural History, Department of Ornithology (AMNH). We have used the anatomical terminology outlined by Baumel and Witmer (1993), with some modifications to English after Howard (1929).

SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758

GALLIFORMES TEMMINCK, 1820

GALLINULOIDIDAE? LUCAS, 1900

(see Mayr, 2000, and Discussion)

Paraortygoides Mayr, 2000

Paraortygoides radagasti, new species

ETYMOLOGY: For the wizard of Middle Earth, Radagast the Brown, rabid communicator with birds (Tolkien, 1954: 269).

HOLOTYPE: BMNH PAL A 6217 (figs. 2, 3, 4), partial associated specimen consisting of four cervical vertebrae; one sternal fragment; one sacral vertebra; eight rib fragments; three thoracic vertebrae; proximal right scapula; proximal end of right carpometacarpus; distal end of left femur; proximal end of left femur; caput of right femur; left distal femur; proximal end of left tibiotarsus; two fragmentary distal condyles of tibiotarsus; proximal end of left tarsometatarsus; right distal tarsometatarsus; ten pedals; and eleven indeterminate but associated bone fragments (including fragments of? skull bones). This specimen was referred to as a ‘‘small gamebird’’ by Harrison (1983).

PARATYPE: BMNH PAL A 5234, distal end of left tarsometatarsus.

LOCALITY AND HORIZON: Walton-on-the-Naze, Essex, southeast England (fig. 1). Bed A2 of the London Clay Formation, Lower Eocene (Ypresian Stage; King, 1981). Both specimens were collected in 1977 by Mr. Steve Vincent (see Harrison, 1983).

DIAGNOSIS: As discussed by Mayr (2000), *Paraortygoides* exhibits a number of osteological characters that allow its placement within Galliformes. The new species described here, albeit less completely preserved than the known specimens of *P. messelensis*, does preserve characters, including a cranially shifted processus pisiformis of carpometacarpus and an asymmetric plantar side of trochlea metatarsi III, that confirm its placement within the order (see Mayr, 2000). However, none of the characters listed by Mayr (2000: 47) as uniquely diagnostic for this genus are preserved in BMNH PAL A 6217; hence, our referral of this fossil material to *Paraortygoides* is based on its clear similarity to the currently known specimens of *P. messelensis* (Fig. 4, below). Further generic diagnoses for *Paraortygoides* with respect to other well-represented Tertiary taxa (e.g., *Quercymegapodius*, *Gallinuloides*) are given in Mayr (2000).

Paraortygoides radagasti, n. sp., is differentiated from *P. messelensis* Mayr on the basis of the following characters: facies articularis humeralis of scapula larger and more robust; processus extensorius of carpometacarpus narrower and more proximally upturned; processus pisiformis more prominent. Measurements of preserved elements are given in table 1.

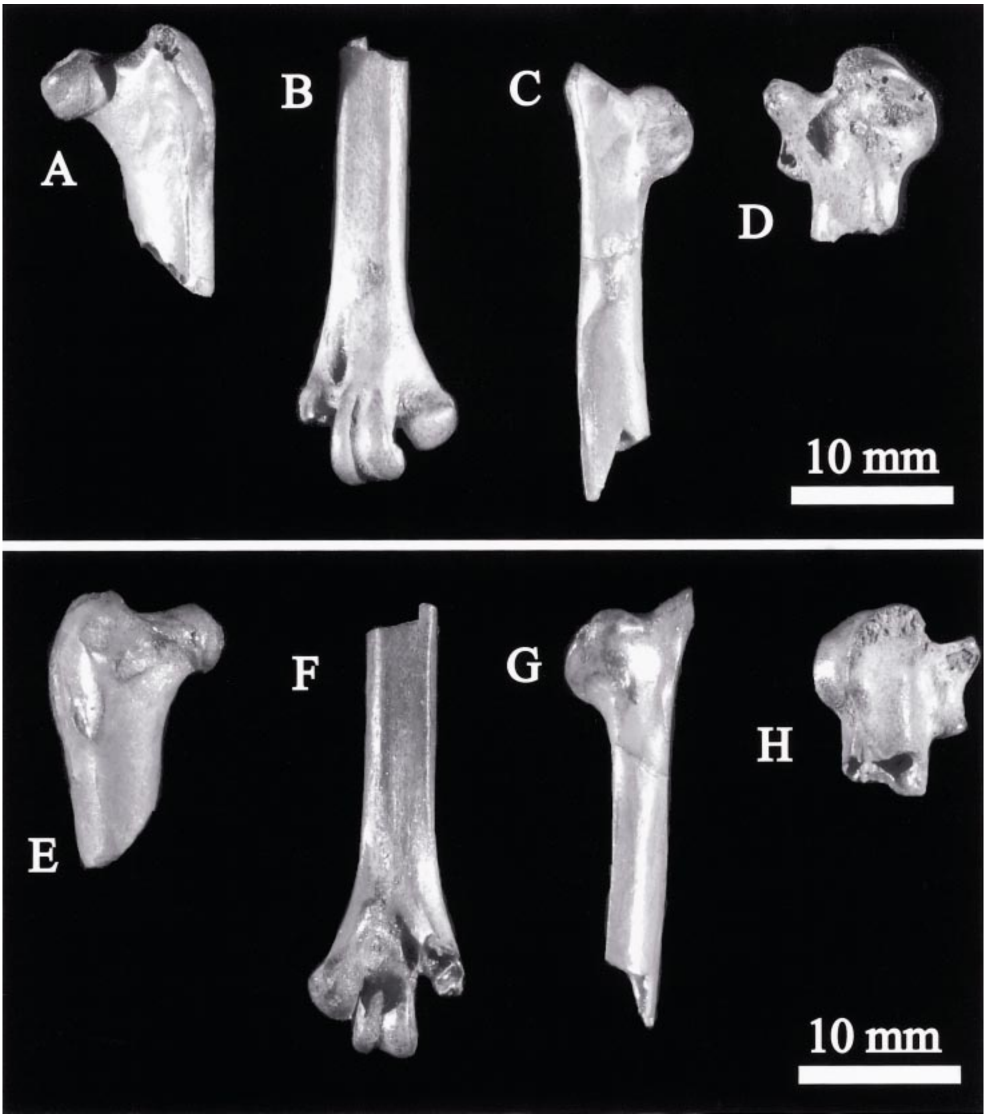

Fig. 2. Preserved elements of *Paraortygoides radagasti* (BMNH PAL A 6217). **A, E,** proximal left femur in cranial (**A**) and caudal (**E**) views; **B, F,** distal right tarsometatarsus in dorsal (**B**) and plantar (**F**) views; **C, G,** proximal right scapula in medial (**C**) and lateral (**G**) views; **D, H,** proximal right carpometatacarpus in ventral (**D**) and dorsal (**H**) views.

DESCRIPTION AND COMPARISONS

VERTEBRAE

Because of the crushed nature of the known specimens of *Paraortygoides messelensis*, few details of vertebral morphology were provided by Mayr (2000). One of the advantages of the fossil material from the London Clay is that most often it is preserved in three dimensions.

CERVICALS: Four incomplete cervical vertebrae (of indeterminate position) form part of the holotype of *P. radagasti*. The arci vertebrae are not markedly raised dorsally and the sulcus caroticus is small.

THORACICS: Three partially preserved, approximately mid-series, thoracic vertebrae are represented. They are very similar in their morphology to those of living galliforms, having well-developed spinous pro-

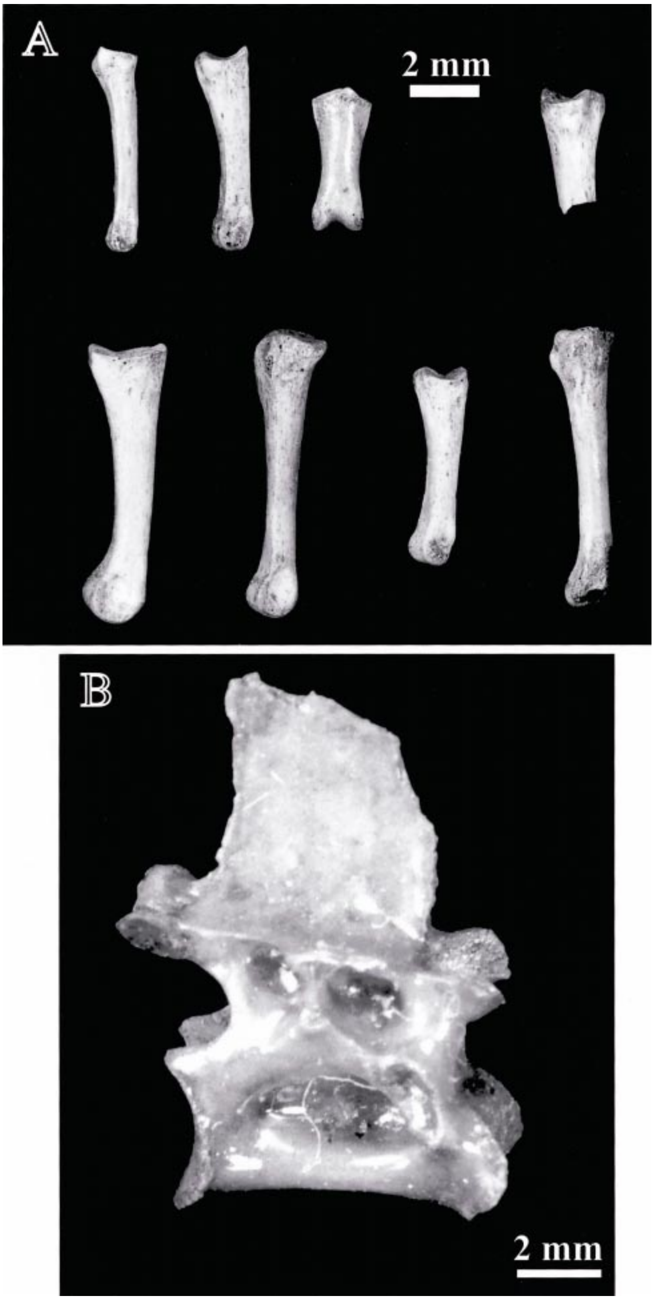

Fig. 3. Preserved elements of *Paraortygoides radagasti* (BMNH PAL A 6217). **A,** preserved tarsals; **B,** one of three preserved thoracic vertebrae (note the large pneumatic fossa). For measurements, see table 1.

cesses and prezygapohyses. Most intriguingly, clear lateral excavations (fossae) are seen in the centra of the preserved thoracic vertebrae of *P. radagasti*. These are not seen in the type of *P. messelensis* (SMF-ME 1303) because of its preservation. However, they can be seen on other, as yet undescribed specimens referable to the genus (e.g., SMNK-ME 1025). Such large, lateral excavations of the vertebrae are not present in

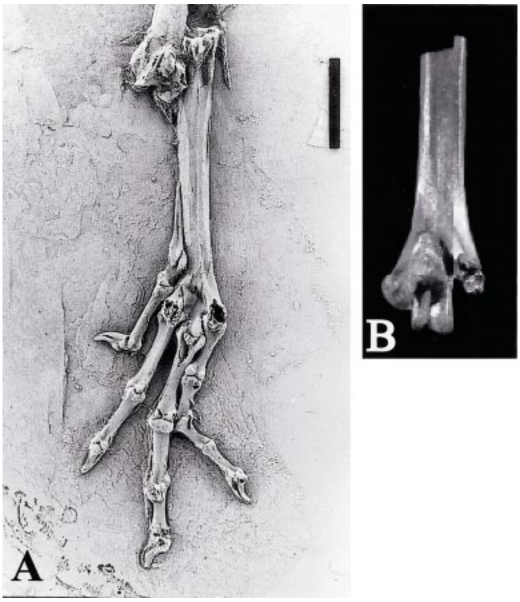

Fig. 4. Comparisons of the preserved tarsometatarsi of *Paraortygoides messelensis* (holotype, SMF-ME 1303; **A**) and *P. radagasti* (holotype, BMNH PAL A 6217; **B**). Figure 4A courtesy of G. Mayr and the Senckenberg Museum, Frankfurt am Main.

extant galliforms, but are seen in a number of Mesozoic non-neornithines (e.g., *Hesperornis* and *Ichthyornis*; Norell and Clarke, 2001; Chiappe, 2002) and other neornithine birds (although they are highly variable in distribution). In addition, the thoracic centra of *P. radagasti* are depressed and approximately as wide as they are tall. In most living galliforms, the thoracic centra are less depressed and are much wider than they are tall. Although the prezygapophyses are incompletely preserved in BMNH PAL A 6217, they appear to be orientated at a less acute angle with respect to the processus spinosus than is the case in Recent taxa.

SACRAL: A single, incomplete sacral vertebra (lacking zygapophyses) is preserved as part of the holotype of *P. radagasti*.

FORELIMB ELEMENTS

SCAPULA: Only the proximal one-third of the right scapula is preserved (fig. 2C, G) and is very similar to that already described for *P. messelensis* (Mayr, 2000). The acromion is curved, but is not as marked as is the case in Recent galliforms; it is also longer and narrower. Compared to specimens referred to *P. messelensis* (i.e., SMNK-ME 3663[4]), the scapula of *P. radagasti* is larger and has a more pointed acromion. The facies articularis humeralis is semicircular in shape, as opposed to being subcircular, as is the case in some extant taxa; this surface is also larger and more robust than in *P. messelensis* (SMNK-ME 3663). The facies articularis humeralis is orientated parallel to the corpus scapulae contrasting with extant taxa where this angle is more acute. The separation between the acromion and the facies articularis humeralis is small and smooth in *Paraortygoides*; in Recent galliforms this area is often depressed and rugose. As noted by Mayr (2000), a small tubercle is present on the dorsal side of the corpus scapulae (also seen in many anseriform birds); this is generally located on the lateral surface or is less pronounced in extant galliforms.

CARPOMETACARPUS: Only the proximal portion of the right carpometacarpus is preserved in A 6217 (fig. 2D, H), broken distal to the proximal margination of the os metacarpale majus. The morphology of this element in *P. messelensis* was described in detail by Mayr (2000); in A 6217 it is very similar. However, the processus extensorius of *P. radagasti* is narrower and more upturned than is the case in *P. messelensis*, and the processus pisiformis is more marked and prominent. Compared to extant galliforms the proximal indentation between the trochlea carpalis and the facies articularis ulnaris is much less pronounced in *Paraortygoides* (in living galliforms the trochlea carpalis is markedly raised proximally), and the fovea carpalis cranialis is shallower. In ventral view, next to the processus pisiformis, there is a distinct indentation in *P. radagasti* that is not seen in *P. messelensis* (or in other fossil and extant galliforms). An alular phalanx of the right wing is also preserved as part of this specimen.

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[4] SMNK-ME 3663 is somewhat smaller in comparison with the holotype (SMF-ME 1303) of *P. messelensis* (i.e., respective lengths of humeri− 38:48.5 mm); hence, this specimen may represent another smaller species of *Paraortygoides*, or could be a female of *P. messelensis*, since few osteological differences are discernible (G. Mayr, personal commun.).

TABLE 1

Measurements (mm) of Preserved Elements of Holotype Specimen of *Paraortydoides radagasti* (BMNH PAL A 6217)

Cervical vertebrae (most complete example)	
Total length	8.0
Total width	5.5
Thoracic vertebra (most complete example)	
Total length	6.2
Total preserved width	5.5
Width of centrum	4.2
Length of lateral fossa	2.9
Height of lateral fossa	1.2
Height of neural spine	3.2
Sacral vertebra	
Total preserved length	9.2
Width of proximal articulation	1.9
Width of distal articulation	3.3
Proximal femur	
Total preserved length	12.9
Distance, facies articularis acetabularis to trochanteris femora	7.5
Distal femur	
Total preserved length	10.1
Proximal tibiotarsus	
Total preserved width	8.7
Length of caput fibula	3.2
Distal tarsometatarsus	
Total preserved length	21.3
Width trochlea metatarsi III	3.1
Width trochlea metatarsi II	2.1
Proximal tarsometatarsus	
Total preserved width across hypotarsus	6.7
Width, cotyla medialis	2.5
Width, cotyla lateralis	2.3
Scapula	
Total preserved length	20.5
Distance, facies articularis humeralis to acromion	6.0
Carpometacarpus	
Total preserved length	8.5
Medial width (including processus alularis)	4.1
Medial width (including processus extensorius)	7.5

HIND-LIMB ELEMENTS

FEMUR: The femur of *P. radagasti* is known on the basis of incomplete portions of both proximal (fig. 2A, E) and distal ends. As noted by Mayr (2000), the trochlea fibularis is grooved and bordered by cristae. On the proximal end, the trochanter femoris is raised as a distinct ridge and the facies articularis antitrochanteris is shallow. No clear differences with the femora of *P. messelensis* could be ascertained (although this element is not well preserved in the Messel specimens). On the distal end, the fossa poplitea differs from extant taxa in that it is less excavated and lacks a distinct pneumatic foramen on its proximal margin. Additional comparisons with extant galliforms show that the condylus medialis is flatter in medial view, the impressio ligamenti collateralis lateralis is more marked, the margin of the condylus medialis projects farther distally, and the fovea ligamenti capitis is deeper in *P. radagasti*. Interestingly, *P. radagasti* does not appear to possess the distinct pneumatic foramen distal to the caudal margin of the facies articularis antitrochanterica that is seen in extant galliforms; the distribution of this character in other fossil taxa remains to be investigated.

TIBIOTARSUS: Only two distal condyles of the tibiotarsus (side indeterminate) are preserved as part of the type specimen of *P. radagasti*.

TARSOMETATARSUS AND TOES: The tarsometatarsus of *P. radagasti* is known on the basis of both proximal and distal portions (no complete element has yet been recognized in existing collections; fig. 2B, F), and agrees very well in its morphology with the corresponding elements of *P. messelensis* (fig. 4; see also Mayr, 2000). As is the case in all extant and fossil galliform birds (Mayr, 2000), the plantar side of the articulating surface of trochlea metatarsi III is distinctly asymmetric; the lateral ridge protrudes farther proximally than does the medial ridge. The foramen vasculare distale is oval and of intermediate size. Detailed features of the hypotarsus are not visible on the holotype specimen of *P. messelensis* (SMF-ME 1303) because of flattening during preservation. The incomplete hypotarsus of *P. radagasti* is relatively flat (as is the case in all galliforms), the eminentia intercotylaris is not markedly raised above the surface of the cotylae (less so than in extant galliforms), and the crista medialis hypotarsi is short. In extant galliforms both cristae are abbreviate, but the medialis is generally somewhat longer than the lateralis. In BMNH PAL A 6217 the crista lateralis is not preserved, and the fossa infracotylaris dorsalis is shallow (as is the case in extant taxa). The foramina vascularia proximalia are not preserved. The plantar projection of trochlea metatarsi II is much less pronounced and more separated from the body of the trochlea in *P. radagasti* than in extant galliforms.

Ten complete but disarticulated tarsals (fig. 3A) are preserved as part of the holotype, including the proximal tarsals of digits II, III, and IV. A number of additional distal tarsal fragments (digits uncertain) are also preserved as part of this specimen. No claws are preserved in BMNH PAL A 6217.

DISCUSSION

Phylogenetic Analysis

Initial consideration of the phylogenetic position of *Paraortygoides messelensis* was given by Mayr (2000). On the basis of a few characters, Mayr (2000) hypothesized that *Paraortygoides* is the sistertaxon of all Recent galliforms (i.e., Megapodiidae, Cracidae, Phasianidae) as well as the extinct family Quercymegapodiidae that is considered to contain a number of other incompletely known fossil taxa from the Tertiary (i.e., *Quercymegapodius* Mourer-Chauviré, 1992, and *Ameripodius* Alvarenga, 1995; see Mourer-Chauviré, 1992; Mayr, 2000; not discussed further here). On the basis of the more completely preserved specimens of *P. messelensis*, Mayr (2000) listed a number of osteological characters that distinguish this genus from the known members of the Quercymegapodiidae (e.g., presence of a marked second fossa pneumotricipitalis on the proximal humerus and short processus procoracoideus on the proximal coracoid). Mayr (2000) tentatively placed *Paraortygoides* within the Gallinuloididae (along with the incompletely known *G. wyomingensis* Eastman); the two genera are of similar size and correspond in the morphology of a number of overlapping skeletal elements (where preserved, see Mayr, 2000, for details; this taxon is currently under study; T. Crowe, personal commun.).

In order to further elucidate the phylogenetic position of *Paraortygoides* we conducted a phylogenetic analysis including a number of exemplar taxa from families of galliform birds (i.e., Megapodiidae, Cracidae, and Phasianidae) and the osteological characters listed in appendix 1. The resultant data set (appendix 2) was analyzed by use of parsimony in the standard software for phylogenetic analysis, PAUP * 4.0b1 (Swofford, 1998), and employing branch-and-bound searches (that guarantee to recover all shortest or most-parsimonious-trees [MPTs]; Hendy and Penny, 1982).

Some of the characters utilized and discussed here are amended or developed from those presented by previous workers (e.g., Holman, 1964; Olson, 1974; Cracraft, 1981; Mayr, 2000; Cracraft and Clarke, 2001), but the majority are based on our own observations, and at this stage have been restricted primarily to the postcranial skeleton (with the exception of characters 51 and 52; Cracraft, 1981; Mayr, 2000). Since the aim of this paper is soley to highlight additional character evidence pertaining to the phylogenetic relationships of *Paraortygoides*, a more comprehensive analysis of extant and fossil galliforms and discussion of relevant osteological characters will be presented elsewhere.

Parsimony analysis of this preliminary osteological data set (appendix 2; following the removal of uninformative characters) resulted in the production of 3 MPTs, each 186 steps in length (summary topology from strict consensus shown in fig. 5). In these trees *Paraortygoides* is hypothesized to occupy a basal position within a monophyletic Galliformes (in agreement with Mayr, 2000); the Megapodiidae is the sistertaxon to a clade comprising the Cracidae and Phasianidae (fig. 5). Based at this stage on outgroup comparisons with the basalmost extant anseriform genus, the Magpie-Goose *Anseranas* (Livezey, 1997), monophyly of Galliformes is supported at this level on the basis of the following characters: double incisurae laterales of sternum (character 32; see Holman, 1964; not preserved in *Paraortygoides*), and trochlea metatarsi III distinctly asymmetric (character 46; i.e., lateral ridge protrudes farther proximally than does the medial; see Mayr, 2000). To the exclusion of *Paraortygoides*, monophyly of the three extant galliform clades (i.e., Phasianidae, Cracidae, and Megapodiidae) is supported by the absence of a prominent and projected processus pro-

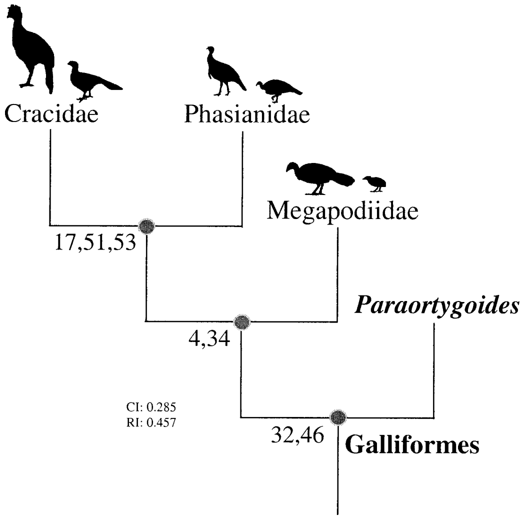

Fig. 5. Phylogenetic hypothesis presented on the basis of the analyses described herein. For list of osteological characters and character-taxon data set, see appendices 1 and 2. CI, consistency index; RI, retention index. Numbers beneath nodes refer to unambigously optimized characters listed in appendix 1.

coracoideus on the scapular end of the coracoid (character 4), and the absence of pneumatic fossae on the lateral surfaces of the thoracic vertebrae (character 34). In agreement with Mayr (2000), we find support for the position of Megapodiidae as the basal sister-taxon of the Phasianidae and Cracidae (contra Holman, 1964); monophyly of the latter grouping is supported by presence of a V-shaped furcula (character 17), ectethmoidale reduced or absent (character 51; see Cracraft, 1981), and spatium intermetacarpale of carpometacarpus wide (os metacarpale minus distinctly bowed; character 53; see Mayr, 2000).

Other Fossil Galliforms from the Eocene of the United Kingdom

As noted above, a number of other putative fossil galliform birds have been described previously from the London Clay Formation of the United Kingdom. Harrison and Walker (1977) described four genera and species of putative phasianid galliforms from outcrops at the Isle of Sheppey, Warden Point, and Burnham-on-Crouch, Essex (fig. 1), namely: *Argillipes aurorum* (holotype, BMNH PAL 3130, proximal end of right tarsometatarsus; paratype, BMNH PAL 4283, proximal end of right tarsometatarsus [incomplete]; BMNH PAL 4282, distal end of left humerus), *Argillipes paralectoris* (holotype, BMNH PAL 3604, proximal end of left tarsometarsus), *Percolinus venablesi* (holotype, BMNH PAL 3680, proximal end of left tarsometatarsus; paratype, BMNH PAL 2140, cast of proximal end of left tarsometatarsus; also BMNH PAL 3321, cast of same specimen), and *Coturnipes cooperi* (holotype, BMNH PAL 3706, distal end of left tarsometatarsus). All of this incomplete fossil material was placed in the Phasianidae by Harrison and Walker (1977) on the basis of comparisons with Recent osteological specimens. For example, and with regard to the galliform affinities of the distal tarsometatarsus represented in this collection (BMNH PAL 3706), Harrison and Walker (1977) noted that this element has a ‘‘large distal foramina that is distoproximally elongate and set in a long extensor groove, almost to [the level of] the inter-trochlea notch’’, as is the case in phasianids.

Of further possible relevance to the affinites of Harrison and Walker's *Coturnipes cooperi* is the description of a number of isolated specimens from the Palaeocene Nanjemoy Formation of Virginia by Olson (1999). This material, including the distal ends of right and left tibiotarsi, and the distal end of a right tarsometatarsus was considered by Olson (1999) as possibly referable to *Coturnipes* (Olson, 1999: fig. 3f–i). Olson (1999) conceded that although the tibiotarsi resemble those of the Phasianidae, the remainder of the skeleton is reminiscent of the Recent Falconidae, hence ‘‘as strange and inexplicable mosaic as might be imagined’’ (Olson, 1999: 127). Further work (and clearly more complete material) is required to positively resolve the affinities of the enigmatic *Coturnipes cooperi*; the presence of an asymmetric trochlea metatarsi III in the available specimens provides single-character evidence for the galliform affinities of this taxon. Interestingly, all of the tarsometatarsi referred thus far to the genus *Paraortygoides* are much smaller than is the holotype specimen of *Coturnipes* (G. Dyke, personal obs.). The two taxa can also be distinguished on the basis of the tarsometatarsus, because in *Coturnipes* the distal end is wider, there are marked ridges present medially and laterally on the plantar surface, and the foramen vasculare distale is longer and wider.

The holotype specimens of the two other genera described by Harrison and Walker (1977), *Argillipes* and *Percolinus*, are both incomplete proximal tarsometatarsi that differ from each other in the shape of the cotylar area, in the extent that the cotyla medialis and lateralis overhang the dorsal surface of the shaft, and in the size of the sulcus hypotarsi (Harrison and Walker, 1977; pl. 8 F–O; Dyke, 2000). The proximal surfaces of the tarsometatarsi are not clearly visible in the known specimens of *Paraortygoides messelensis*, but the proximal left tarsometatarsus of *P. radagasti* shows that this element is distinguishable from the holotypes of both *Argillipes* and *Percolinus*. Although this area is incompletely preserved in BMNH PAL A 6217, the fossa infracotylaris dorsalis is shallower than in either *Argillipes* or *Percolinus*; further, the eminentia intercotylaris is flatter and the crista lateralis is not hooked (the latter is the case in the holotype of *Percolinus venablesi*, BMNH PAL 3680). Unfortunately, both the genera *Argillipes* and *Percolinus* were founded on the basis of fossil specimens that lack any of the characters that have been proposed as diagnostic of the order (e.g., Dzerzhinsky, 1995; Mayr, 2000). No distinctive features of the proximal tarsometatarsus have yet been proposed as unique to Galliformes. On this basis alone it remains unclear whether this fossil material can indeed be referred to Galliformes, let alone the Phasianidae. As reported here, Dyke (2000) was unable to find convincing character evidence to refer any of this material to the fossil taxa discussed above; at this stage we consider these specimens? Galliformes incertae sedis until more material becomes available and it is possible to further evaluate their affinities.

Paraortygoides radagasti is the first certain record for the order Galliformes described to date from the Lower Eocene of the United Kingdom. Since our phylogenetic hypothesis is based on a large number of osteological characters and includes representative extant taxa, this genus is reliably placed near to the base of the galliform ingroup. This implies that basal clades within the order had diverged by the Lower Eocene, some 60 million years ago. Fossils, such as *Paraortygoides*, for which both adequate skeletal material and some degree of phylogenetic control are available, should be used to further elucidate the pattern and extent of the evolutionary radiation of modern birds (in the calibration of molecular clocks, for example).

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REFERENCES

Alvarenga, H. 1995. Um primitivo membro da ordem Galliformes (Aves) do Terciário Médio da Bacia de Taubaté, Estado de São Paulo, Brasil. Annals Academia Brasil Ciencas 67: 33–44.

Andrews, C.A. 1899. On the remains of a new bird from the London Clay of Sheppey. Proceedings of the Zoological Society of London 1899: 776–785.

Baumel, J.J., and L.M. Witmer. 1993. Osteologica. *In* J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (editors), Handbook of avian anatomy: nomina anatomica avium. Publications of the Nuttall Ornithological Club (23): 45–132.

Brodkorb, P. 1963. Birds from the Upper Cretaceous of Wyoming. Proceedings of the 3rd International Ornithological Congress: 55–70.

Chiappe, L.M. 2002. Basal bird phylogeny: problems and solutions. *In* L.M. Chiappe and L.D. Witmer (editors), Mesozoic birds, over the heads of the dinosaurs: Berkeley: University of California Press.

Clarke, J.A. 1999. New information on the type material of *Ichthyornis*: of chimeras, characters and current limits of phylogenetic taxonomy. Journal of Vertebrate Paleontology 19: 38A.

Clarke, J.A., and L.M. Chiappe. 2001. A new carinate bird from the late Cretaceous of Argentina. American Museum Novitates 3323: 1–23.

Collinson, M.E. 1983. Fossil plants of the London Clay: Fieldguide to fossils 1. London: Palaeontological Association.

Cracraft, J. 1981. Towards a phylogenetic classification of the recent birds of the world (Class Aves). Auk 98: 681–714.

Cracraft, J. 1988. The major clades of birds. *In* M.J. Benton (editor), The phylogeny and classification of the tetrapods, vol. 1: amphibians, reptiles, birds: 333–355. Oxford: Systematics Association.

Cracraft, J., and J.A. Clarke. 2001. The basal clades of modern birds. *In* J.A. Gauthier (editor), New perspectives on origin of birds: proceedings of the Ostrom Symposium. Postilla: 143–156.

Crowe, T.M., and L.L. Short, Jr. 1992. A new gallinaceous bird from the Oligocene of Nebraska, with comments on the phylogenetic position of the Gallinuloididae. Natural History Museum of Los Angeles County, Science Series 36: 179–185.

Dyke, G.J. 2000. Taxonomy and phylogenetics of fossil modern birds: the early radiation of Neornithes. Unpublished Ph.D. diss., University of Bristol, United Kingdom, 450 pp.

Dzerzhinsky, F.Y. 1995. Evidence for common ancestry of the Galliformes and Anseriformes. Courier Forschungsinstitut Senckenberg 181: 325–336.

Eastman, C.R. 1900. New fossil bird and fish remains from the Middle Eocene of Wyoming. Geological Magazine 7: 54–58.

Ericson, P.G.P. 1996. The skeletal evidence for a sister-group relationship of anseriform and galliform birds—a critical evaluation. Journal of Avian Biology 27: 195–202.

Grande L. 1984. Paleontology of the Green River Formation, with a review of the fish fauna. Geological Survey of Wyoming Bulletin, 63.

Groth, J.G., and G.F. Barrowclough. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. Molecular Phylogenetics and Evolution 12: 115–123.

Harrison, C.J.O. 1983. Fossil birds from the London Clay of Essex: the W. George and S. Vincent collections. Tertiary Research 5: 81–83.

Harrison, C.J.O., and C.A. Walker. 1977. Birds of the British Lower Eocene. Tertiary Research Special Paper 3: 1–52.

Hendy, M., and D. Penny. 1990. Branch and bound algorithms to determine minimal evolutionary trees. Mathematical Biosciences 59: 277–290.

Holman, J.A. 1964. Osteology of gallinaceous birds. Quarterly Journal of the Florida Academy of Sciences 27: 230–252.

Hope, S. 2002. The Mesozoic fossil record of Neornithes. *In* L.M. Chiappe and L.D. Witmer (editors), Mesozoic birds: above the heads of the dinosaurs. Berkeley: University of California Press, in press.

Howard, H. 1929. The avifauna of Emeryville Shellmound. University of California Publications in Zoology 32: 301–394.

King, C. 1981. The stratigraphy of the London Clay and associated deposits. Tertiary Research Special Paper 6: 1–158.

Koenig, E. 1825. Icones fossilium sectiles. London, 44 pp.

Livezey, B.C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis* and the interordinal relationships of waterfowl. Zoological Journal of the Linnean Society 121: 361–428.

Lucas, F.A. 1900. Characters and relations of *Gallinuloides wyomingensis* Eastman, a fossil Gallinaceous bird from the Green River Shales of Wyoming. Bulletin of the Museum of Compative Zoology 36: 79–84.

Mayr, G. 2000. A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany). Senckenbergiana lethaea 80: 45–57.

Milne-Edwards, A. 1867–1871. Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France [4 volumes]. Paris: Victor Masson.

Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): systematics and biostratigraphy. Natural History Museum of Los Angeles County, Science Series 36: 67–95.

Norell, M.A., and J.A. Clarke. 2001. Fossil that fills a critical gap in avian evolution. Nature 409: 181–184.

Olson, S.L. 1974. *Telecrex* restudied: a small Eocene guineafowl. Wilson Bulletin 86: 246–250.

Olson, S.L. 1985. The fossil record of birds. *In* D.S. Farner, J.R. King, and K.C. Parkes (editors), Avian biology vol. 8: 79–256. New York: Academic Press.

Olson, S.L. 1999. Early Eocene birds from eastern North America: a faunule from the Nanjemoy Formation of Virginia. Publications of the Virginia Division of Mineral Resources 152: 123–132.

Owen, R. 1841. Description of the fossil remains of a mammal (*Hyracotherium leporinum*) and of a bird (*Lithornis vulturinus*) from the London Clay. Transactions of the Geological Society of London (ser. 2) 6: 203–208.

Owen, R. 1846. A history of British fossil mammals and birds. London: John Van Voorst.

Schaal S., and W. Ziegler. 1988. Messel-Ein Schaufenster in die Geschichte der Erde und des Lebens. Frankfurt am Main: Kramer.

Sibley, C.G., and J.E. Ahlquist. 1990. Phylogeny and classification of birds: a study in molecular evolution. New Haven, CT: Yale University Press, 756 pp.

Swofford, D.W. 1998. PAUP—phylogenetic analysis using parsimony, version 4.0b for PPC. Washington, DC: Smithsonian Institution.

Tolkien, J.R.R. 1954. The fellowship of the ring. Boston: Houghton Mifflin, 423 pp.

Tordoff, H.B., and J.R. Macdonald. 1957. A new bird (family Cracidae) from the early Oligocene of South Dakota. Auk 74: 174–184.

Unwin, D.M. 1993. Aves. *In* M. J. Benton (editor), The fossil record II. London: Chapman and Hall.

Weber, E., and A. Hesse. 1995. The systematic position of *Aptornis*, a flightless bird from New Zealand. Courier Forschungsinstitut Senckenberg 181: 293–301.

Wetmore, A. 1960. A classification for the birds of the world. Smithsonian Miscellaneous Collections 139: 1–37.

Zusi, R.L., and B.C. Livezey. 2000. Homology and phylogenetic implications of some enigmatic cranial features in galliform and anseriform birds. Annals of the Carnegie Museum 69: 157–193.

APPENDIX 1

LIST OF OSTEOLOGICAL CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS (ALL ARE UNORDERED)

1. Coracoid, cotyla scapularis: shallow, not excavated (a); cuplike, excavated (b).
2. Coracoid, processus acrocoracoideus: hooked sternally (a); straight, not hooked sternally (b).
3. Coracoid, distinct pneumatic fossa on dorsal surface of sternal end: present (a); absent (b).
4. Coracoid, processus procoracoideus: present and projected (a); absent (b).
5. Coracoid, sulcus articularis humeralis: located on dorsal surface (a); turned dorsolaterally (b).
6. Coracoid, processus acrocoracoideus, medial view: surface depressed (a); not bearing marked depression (b).
7. Coracoid, processus lateralis, sternal margin: pointed (a); rounded (b).
8. Coracoid, processus lateralis, scapular margin: prominent and upturned (a); rounded (b).
9. Coracoid, facies articularis sternalis: distinctly excavated (a); smooth, not excavated (b).
10. Scapula, dorsal side of corpus bearing distinct tubercle: present (a); absent (b).
11. Scapula, caudal end tapered: present (a); absent (b).
12. Scapula, acromion: hooked (a); flat (b).
13. Scapula, facies articularis humeralis: semicircular (a); circular or subcircular (b).
14. Scapula, facies articularis humeralis: parallel to the corpus scapulae (a); acute with respect to corpus (b).
15. Scapula, separation between acromion and the facies articularis humeralis: small and smooth (a); large, depressed, and rugose (b).
16. Scapula, dorsal surface of facies articularis humeralis: excavated by fossa (a); not excavated, fossa absent (b).
17. Furcula, corpus: U-shaped (a); V-shaped (b).
18. Furcula, scapus claviculae: stout, widening toward extremitas omalis (a); of uniform thickness towards extremitas omalis (b).
19. Furcula, apophysis: pronounced and pointed (a); small or obsolete, not pronounced (b).
20. Humerus, condylus dorsalis: hooked proximally (a); rounded (b).
21. Humerus, second fossa pneumotricipitalis: present (a); absent (b).
22. Humerus, processus flexorius: reaches as far dorsally as does condylus ventralis (a); reachs farther dorsally than condylus ventralis (b).
23. Ulna shorter than or subequal to humerus (a); ulna longer than humerus (b).
24. Ulna, distinct indentation under distal margin of condylus dorsalis: present (a); absent (b).
25. Ulna, incisura tendinosa: distinct (a); obsolete (b).
26. Carpometacarpus, processus intermetacarpalis present and overlapping os metacarpale minus: present (a); absent (b).
27. Carpometacarpus, tip of processus exten-

sorius: pointed cranially (a); not directed cranially (b).

28. Carpometacarpus, facies articularis digitalis major: divided (a); single (b).
29. Carpometacarpus, proximal end of os metacarpale minus: projected (a); no projection (b).
30. Carpometacarpus, processus pisiformis: single (a); divided (b).
31. Sternum, apex carinae: distinctly pointed cranially (a); rounded (b).
32. Sternum, incisurae laterales: single (a); double (b).
33. Sternum, pneumatic foramen on dorsal surface distal to apex: penetrates corpus sternum (a); no foramen or foramen does not penetrate corpus sterni (b).
34. Lateral pneumatic fossae on thoracic vertebrae: present (a); absent (b).
35. Thoracic centra: mediolaterally depressed (a); flat, undepressed (b).
36. Thoracic centra: approximately as wide as tall (or taller than wide) (a); distinctly wider than tall (b).
37. Cervical vertebrae: groove on caudal surface of hypapophysis present (a); absent (b).
38. Number of vertebrae fused to notarium: four (a); five (b).
39. Femur, trochlea fibularis bordered by two cristae of equal height: present (a); absent (b).
40. Femur, facies articularis antitrochanteris: distal pneumatic foramen present (a); absent (b).
41. Tibiotarsus, trochlea cartilaginis tibialis: asymmetrical (a); symmetrical (b).
42. Tibiotarsus, condyles: of equal size (a); unequal size (b).
43. Tibiotarsus, fibula: extends two-thirds or less the length of tibiotarsus (a); more than two-thirds (b).
44. Tibiotarsus, crista cnemialis lateralis: pointed (a); rounded (b).
45. Tarsometatarsus, trochleae metatarsorum II and IV of similar length (a); trochlea metatarsi II distinctly shorter than IV (b).
46. Tarsometatarsus, plantar surface of trochlea metatarsi III: distinctly asymmetric (a); symmetrical (b).
47. Tarsometatarsus, plantar projection of trochlea metatarsi II: separated from remainder of trochlea by distinct indentation (a); not clearly separated, no indentation (b).
48. Claws: bearing distinct sulcus on lateral surface (a); no distinct groove (b).
49. Scapula, fossa between acromion and facies articularis humeralis: present (a); absent (b).
50. Humerus, transerve ridge at beginning of incisura capitis: absent (a); present (b) [Mayr, 2000].
51. Ecthemoidale, reduced or lost: absent (a); present (b) [Cracraft, 1981].
52. Quadrate, processus orbitalis long and thin: present (a); absent (b) [Cracraft, 1981].
53. Carpometacarpus, wide spatium intermetacarpale: absent (a); present (b) [Mayr, 2000].

APPENDIX 2

Data Set Used In The Phylogenetic Analysis

?, condition not preserved. Coding for *Paraortygoides* based on BMNH PAL A 6217 (holotype of *P. radagasti*) and SMR-ME 1303 (holotype of *P. messelensis*)

	Characters																																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Anseranas (outgroup)	b	b	a	a	a	b	a	a	a	b	a	b	a	a	a	b	a	b	b	a	b	a	a	b	b	b	a	b	b	a	b	a	b	a	a	b	a	b	b	a	b	b	a	a	a	b	b	a	a	a	a	b	a
Macrocephalon	a	a	b	b	b	b	a	b	b	a	a	a	a	b	a	a	a	a	a	a	b	b	b	a	b	b	b	a	a	a	a	b	b	b	a	b	a	a	a	a	b	b	b	b	a	a	b	b	a	b	a	a	a
Alectura	a	a	b	b	b	b	b	b	a	a	a	a	a	b	a	a	b	a	a	a	b	b	b	b	b	b	b	a	b	b	b	b	b	b	b	b	b	a	b	a	a	b	a	b	a	a	a	b	b	b	a	b	a
Crax	a	a	a	b	b	b	b	b	a	b	a	b	a	b	b	a	b	a	a	a	b	a	b	b	b	b	a	a	b	a	b	b	a	b	a	a	b	a	b	b	b	b	a	b	a	a	b	a	b	b	b	b	b
Numida	a	a	b	b	a	a	a	a	a	a	b	a	b	b	a	b	b	b	a	a	b	b	a	a	b	b	a	a	b	a	b	b	a	b	a	a	a	a	b	a	a	b	a	a	b	a	a	b	b	b	b	a	b
Agelastes	a	a	b	b	a	a	a	b	b	b	a	a	b	b	a	b	b	b	a	a	b	b	a	a	b	b	a	a	b	a	b	b	a	b	a	a	a	a	b	b	a	b	a	b	b	a	a	a	b	b	a	a	b
Colinus	a	a	b	b	a	a	a	a	b	a	a	a	b	b	a	b	b	a	a	b	a	b	a	b	b	a	a	a	a	a	b	b	b	b	b	b	a	a	b	b	b	b	a	a	b	a	a	a	b	b	b	a	b
Cyrtonyx	a	a	b	b	b	a	a	a	b	b	b	b	b	b	a	b	b	a	a	b	a	b	a	b	b	a	a	a	b	a	b	b	b	b	a	a	b	a	b	b	a	b	b	a	b	a	a	a	b	b	b	b	b
Oreortyx	a	a	b	b	b	a	a	a	b	b	b	b	b	b	a	b	b	a	a	b	a	b	a	a	a	a	a	a	b	a	b	b	b	b	a	b	a	a	b	b	b	b	b	b	b	a	a	b	b	b	b	b	b
Lophortyx	a	a	b	b	b	a	a	a	b	b	b	b	b	b	a	b	b	a	a	b	a	b	a	b	a	a	a	a	b	a	b	b	b	b	b	b	a	a	b	b	a	b	b	a	b	a	a	a	b	b	b	b	b
Polyplectron	a	a	a	b	b	a	b	a	a	a	b	a	a	b	a	b	a	b	a	b	b	b	a	b	a	a	a	a	b	b	b	b	b	b	b	b	a	a	b	a	b	b	b	a	b	a	a	a	b	b	b	a	b
Coturnix	a	b	b	a	a	a	a	a	b	a	b	a	b	a	a	b	b	b	a	a	a	b	a	b	a	a	a	a	a	a	b	b	b	b	a	b	a	a	b	b	a	b	a	b	b	a	a	a	b	b	b	a	b
Francolinus	a	a	a	b	a	a	a	a	a	a	b	a	b	b	a	b	b	a	a	b	a	b	a	a	b	a	a	a	a	a	b	b	b	b	b	b	b	a	b	a	a	b	b	a	b	a	b	a	b	b	b	a	b
Alectoris	a	a	b	a	a	a	a	a	b	a	b	a	b	b	a	b	b	a	a	b	a	b	a	b	b	a	a	a	a	b	b	b	b	b	a	a	a	a	b	a	b	b	a	a	b	a	a	a	a	b	b	a	b
Lophura	a	a	a	b	a	a	b	b	a	a	b	b	b	b	a	b	a	a	a	a	b	b	b	a	b	a	a	a	b	b	b	b	b	b	a	b	a	a	b	b	a	b	a	a	b	a	a	a	b	b	a	a	b
Pavo	a	a	a	b	a	b	a	b	a	a	b	a	b	a	b	b	b	b	a	a	b	b	a	b	b	a	a	a	b	a	b	b	b	b	b	b	a	b	a	a	a	b	b	b	a	a	a	a	a	b	b	a	b
Tetrao	a	a	a	b	b	a	a	a	a	a	b	a	a	b	b	b	b	a	a	a	b	a	a	a	b	a	a	b	b	b	b	b	b	b	a	a	b	a	b	a	a	b	b	a	b	a	b	a	a	b	b	a	b
Phasianus	a	a	a	b	a	a	a	a	b	a	b	a	a	b	a	b	b	a	a	b	b	b	a	b	b	a	a	a	b	a	b	b	b	b	b	b	b	a	a	a	b	b	a	b	b	a	a	a	b	b	b	a	b
Gallus	a	a	b	b	b	a	b	b	a	a	b	b	b	b	a	b	b	a	a	a	b	b	a	b	b	a	a	a	b	a	b	b	b	b	a	b	b	a	b	b	a	b	b	b	b	a	a	a	b	b	a	a	b
Meleagris	a	a	a	b	b	a	b	b	a	a	b	b	b	b	a	b	b	b	a	a	b	b	a	a	b	a	a	a	b	a	b	b	b	b	b	b	a	a	a	b	a	b	a	a	b	a	a	a	b	b	b	a	b
Tetraogallus	a	b	b	b	b	a	a	b	a	a	a	a	a	b	b	b	b	b	a	b	b	b	a	a	b	a	a	a	b	a	b	b	b	b	b	a	b	a	b	b	b	b	a	a	a	a	a	a	b	b	b	a	b
Paraortygoides	b	b	?	a	a	?	?	?	?	a	a	a	a	a	a	b	a	a	a	?	a	a	a	a	a	b	a	?	b	a	a	?	?	a	a	b	?	?	a	b	a	a	a	b	a	a	a	a	b	a	?	?	a

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