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A small stem-galliform bird (Aves: Paraortygidae) from the Eocene of Uzbekistan

Un petit oiseau de souche galliforme (Aves : Paraorygidae) de l'Éocène de l'Ouzbékistan

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A B S T R A C T

Landfowl (order Galliformes) are among the most characteristic birds of the modern avian faunas, but their early evolutionary history is insufficiently known. The diversity of previously described Eocene galliforms implies a great role of Eocene diversification in the early evolution of this group. However, almost nothing is known about the Eocene diversity of galliforms in Asia, even though this large continent with a variety of habitats might have played a significant role in their early evolution. Here we describe a partial coracoid from the Lutetian–Bartonian of Uzbekistan, which is the oldest diagnosable galliform bird in Asia, and is further the first landbird known from this geographical area. The specimen displays a unique morphology with few autapomorphies and an unexpected combination of similarities with the African genus *Scopelortyx* and Eurasian *Paraortyx*, and hence is described as a new taxon, *Xorazmortyx turkestanensis* gen. et sp. nov., within the extinct family Paraortygidae, being the first Asian representative of this clade. Similarities with the African genus *Scopelortyx* indicate a connection of land bird faunas between northern Africa/Arabia and Asia in the middle Eocene. Better dispersal abilities of the early galliforms Paraortygidae are inferred from the osteology of their pectoral girdle and the humerus, which do not show adaptations to the powerful burst take off (escape flight), characteristic of most modern Phasianidae.

R É S U M É

Les gallinacés (ordre des Galliformes) sont parmi les oiseaux les plus caractéristiques des faunes d'oiseaux modernes), mais leur histoire évolutive précoce est insuffisamment connue. La diversité des galliformes éocènes décrits jusqu'à présent implique un grand rôle de la diversification à l'Éocène dans l'évolution précoce de ce groupe. Cependant, presque rien n'est connu quant à la diversité éocène des galliformes en Asie, bien que ce vaste continent, avec une grande variété d'habitats, puisse avoir joué un rôle significatif dans leur évolution précoce. Dans cet article est décrit un coracoïde partiel du Lutétien–Bartonien d'Ouzbékistan, qui est le plus ancien oiseau de type galliforme qu'on puisse diagnostiquer

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et, en outre, le premier qui soit connu dans cette zone géographique. Le spécimen présente une morphologie unique, avec plusieurs autapomorphies et une combinaison inattendue de similarités avec les genres africain *Scopelortyx* et eurasien *Paraortyx*, d'où sa description en tant que *Xorasmortyx turkestanensis* gen. et sp. nov. au sein de la famille éteinte des Paraortygidae, tout en étant le premier représentant asiatique de ce clade. Des similarités avec le genre africain *Scpelortyx* et eurasien *Paraortyx* indiquent une connexion de faunes d'oiseaux entre l'Afrique du Nord/Arabie et l'Asie à l'Éocène moyen. De meilleures aptitudes à la dispersion des galliformes précoces Paraortyugidae sont déduites de l'ostéologie de leur ceinture pectorale et de l'humérus, qui ne montrent pas d'adaptation à un puissant élan d'envol (vol de fuite), caractéristique des Phasianidae les plus modernes.

1. Introduction

The modern landfowl (order Galliformes) is an old lineage of the living birds (Neornithes), which might have diverged from its sister clade, Anseriformes, as early as the Late Cretaceous (Stein et al., 2015; Wang et al., 2017; Worthy et al., 2017; but see Jarvis et al., 2014). However, the oldest undoubtable galliforms in the fossil record (extinct family Gallinuloididae) first appear only in the early Eocene of Europe and North America and they still bear a significant morphological resemblance to Anseriformes (Mayr, 2000, 2006, 2009, 2017, and references therein). The morphologically more derived extinct family Paraortygidae is known since the middle Eocene (Bartonian) of Namibia (genus *Scopelortyx;* Mourer-Chauviré et al., 2015, 2017). The other African Eocene galliforms are *Namortyx* from the middle Eocene (probably Lutetian) of Namibia (Mourer-Chauviré et al., 2011) and *Chambiortyx* from the late early–early middle Eocene (late Ypresian–early Lutetian) of Tunisia (Mourer-Chauviré et al., 2013), whose affinities are unclear. By the late Eocene, Paraortygidae have reached western Europe, where they are recorded at the "Phosphorites du Quercy" in France together with late Gallinuloididae and yet another extinct family Quercymegapodiidae (Mourer-Chauviré, 1992). Several late Eocene galliforms from North America may further represent Paraortygidae (Mayr, 2009). The earliest proposed member of the living family Numididae, and the crown-group Galliformes in general, is *Telecrex grangeri* Wetmore, 1934 from the late Eocene of China (Olson, 1974), but the systematic affinities of this form must be considered with caution (Mourer-Chauviré, 1992).

It is thus apparent that significant morphological evolution within Galliformes took place during the Eocene, and the huge Asian continent with diverse habitats might have played a significant role in this evolution. In particular, it was suggested (Mayr, 2009), that at least some of the avian families, which first appear in Europe in the late Eocene, may have an Asian origin. However, almost nothing is known about the Eocene diversity of galliforms in Asia. In addition to the previously mentioned *Telecrex grangeri*, the only other find is represented by a proximal humerus from the late Paleocene–early Eocene of Mongolia, which belonged to a stem-galliform bird of unclear affinities (Hwang et al., 2010). Here we describe a partial coracoid of a small galliform bird from the middle Eocene (Bartonian) of Uzbekistan, which shows similarity with Paraortygidae, and especially the African genus *Scopelortyx*, but clearly belongs to a distinct genus. This is the first indication of the presence of Paraortygidae in Asia, and is further the first landbird from the Paleogene of this geographical area, which bears importance on the past biogeography of Galliformes and possibly other land birds as well.

2. Material and methods

The specimen comes from the Dzheroy Sand Member (see Malyshkina and Ward, 2016) of the Dzheroy-II locality (N41°38'59"; E064°41'30"), some 20 km to the north of the village of Muruntau in Uzbekistan (Navoiy viloyati; Central Kyzyl-Kum; Fig. 1). The member represents shallow marine deposits that were accumulated in close proximity to the shoreline (Malyshkina and Ward, 2016). The age of the locality, inferred from the assemblage of fossil sharks, is latest Lutetian–Bartonian (Case et al., 1996; Malyshkina and Ward, 2016). The vertebrate fauna includes a number of sharks, rays, and turtles (Averianov, 2002, 2005; Case et al., 1996; Malyshkina and Ward, 2016). Bird remains are represented by Pelagornithidae, procellariform *Murunkus subitus* Panteleyev et Nessov, 1993, as well as a waterbird of unclear affinities *Zheroia kurochkini* Nessov, 1988 (Averianov et al., 1991; Nessov, 1992; Panteleyev and Nessov, 1993; Zelenkov and Kurochkin, 2015).

Comparative materials of Paleogene galliforms were examined at the "Muséum national d'histoire naturelle" (Paris, France), University Claude-Bernard (Lyon, France), the University of Montpellier (hereafter USTL, France), the Senckenberg Research Institute and Natural History Museum (Frankfurt, Germany), and the "Naturhistorisches Museum Wien" (Vienna, Austria). Fossils from the Bavarian Natural History Collections (hereafter SNSB) were also consulted.

The osteological nomenclature generally follows Baumel and Witmer (1993), if not indicated otherwise. We use the traditional term facies articularis clavicularis for the medial surface of the processus acrocoracoideus, although the articular facet for furcula is not developed on the coracoid in Galliformes. In the description and comparison section below, we use genus names when a discussed feature is common for all examined species, and a particular species, when it applies to one of them.

Fig. 1. General outline map of Asia and Uzbekistan showing the geographical position of Dzheroy-II locality.

Fig. 1. Grandes lignes de la carte d'Asie et d'Ouzbékistan montrant la position géographique de la localité Dzehroy-II.

3. Systematic paleontology

Class AVES Linnaeus, 1758
Order GALLIFORMES Temminck, 1820
Family PARAORTYGIDAE Mourer-Chauviré, 1992

The new taxon represents stem-galliforms because it has a concave cotyla scapularis (Mourer-Chauviré, 1992; Mayr, 2000). It may be referred to Paraortygidae because it displays a number of morphological characters that, among stem-galliforms, are present in various taxa belonging to this family. The limited medial projection of the processus acrocoracoideus is known only in *Scopelortyx*, and the narrow shaft ventromedial to the facies articularis humeralis and forming the wall of the sulcus supracoracoideus is present in *Paraortyx*. The broad and craniocaudally short facies articularis humeralis is present in *Paraortyx brancoi*, but not in other species of Paraortygidae. Two features, distinguishing the coracoid of Paraortygidae from that of Quercymegapodiidae (Mourer-Chauviré, 1992), are observable in the new taxon: the obliquely oriented cotyla scapularis and sharp and not fully reduced processus procoracoideus.

XORAZMORTYX n. gen.

Type species. Xorazmortyx turkestanensis n. sp.

Derivation of name. After ancient region and country Xorazm (Uzbek spelling; "Khwarazm" in English) and Ortyx, a commonly used name for fossil small galliforms. The gender is masculine.

Diagnosis. Monotypic genus, as for the only species.

Xorazmortyx turkestanensis n. sp.
(Fig. 2)

Derivation of name. "turkestanensis" refers to the geographical region Turkestan.

Holotype. Zoological institute of RAS (ZIN PO 4991), cranial half of the right coracoid.

Diagnosis. In dorsal aspect, processus acrocoracoideus largely aligned with longitudinal axis of bone (not bent or expanded medially); processus acrocoracoideus not hooked over sulcus supracoracoideus either ventrally and dorsally; ventral facies of shaft straight and narrow adjacent to the facies articularis humeralis; crista acrocoracoidea (sensu Elzanowski et al., 2012) very short and obliquely (not transversally) oriented (Fig. 2, cac); impressio bicipitalis prominent; medial margin of the shaft bifurcates cranially and encloses distinct pit (Fig. 2, p), undercutting ventral part of facies articularis clavicularis; facies articularis clavicularis craniocaudally high; facies articularis humeralis is craniocaudally short; processus procoracoideus is strongly reduced; cotyla scapularis

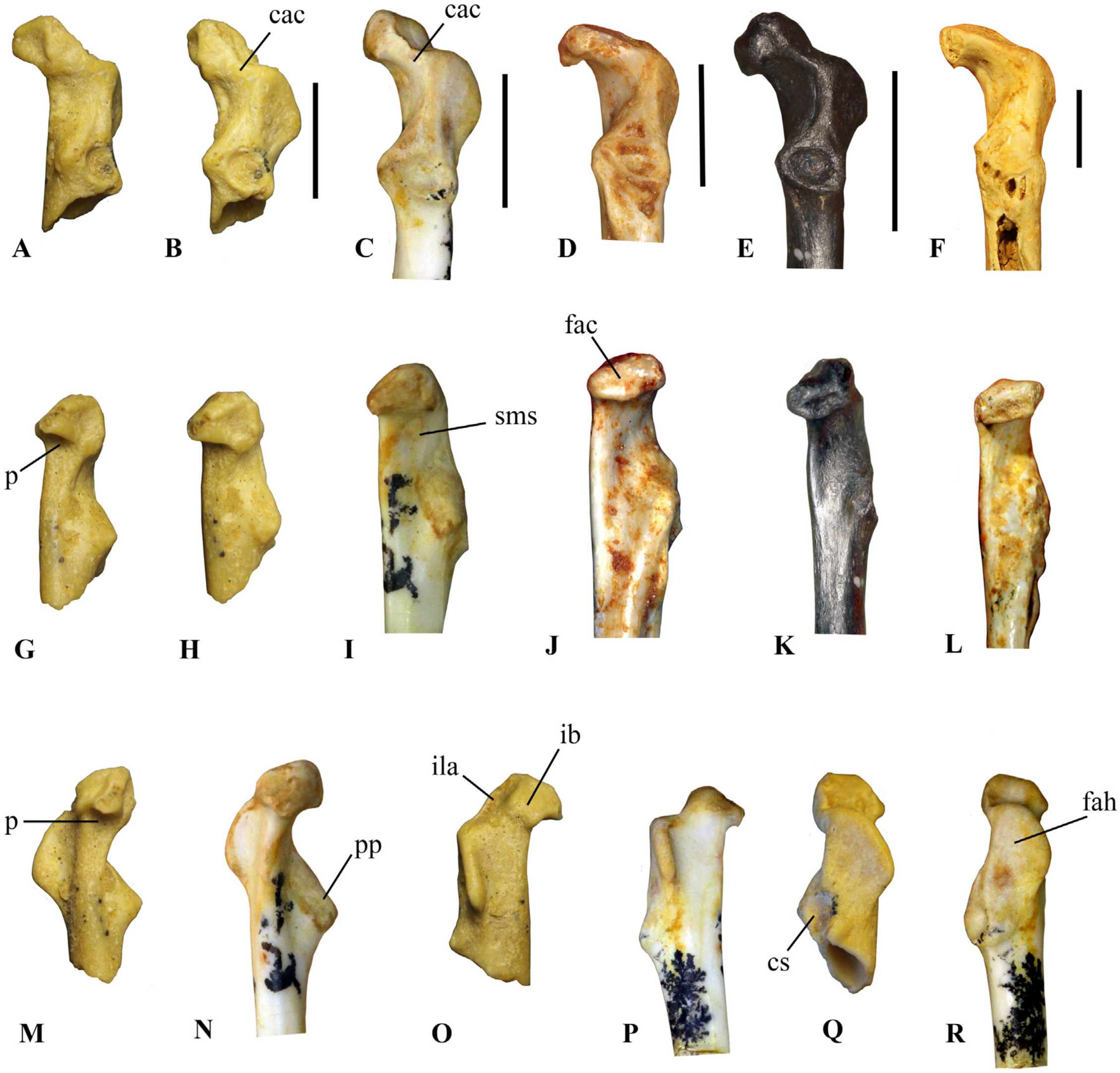

Fig. 2. Coracoids of fossil Galliformes. A, B, G, H, M, O, Q. *Xorazmortyx turkestanensis* n. gen. et n. sp., holotype ZIN 4991, middle Eocene of Dzheroy II, Uzbekistan. C, I, N, P, R. *Scopelortyx klinghardtensis*, holotype GSN EC 6-01′13, middle Eocene of Eocliff, Namibia. D, J. *Paraortyx lorteti*, specimen USTL ITD 530, early Oligocene of Itardies, France. E, K. *Quercymegapodius brodkorbi*, specimen USTL BFI 1849, late Eocene of la Bouffie, France; reversed to facilitate comparisons. F, L. *Palaeortyx intermedia*, specimen SNSB 18097, early Miocene of Wintershof-West, Germany. A: dorsomedial view; B–F: dorsal view; G: ventromedial view; H–L: medial view; M, N: ventral view; O, P: ventrolateral view; Q, R: lateral view. Abbreviations: cac: crista acrocoracoidea; cs: cotyla scapularis; fac: facies articularis clavicularis; fah: facies articularis humeralis; ib: impressio bicipitalis; ila: impressio lig. acrocoracohumeralis; p: autapomorphic pit; pp: processus procoracoideus; sms: sulcus m. supracoracoidei. The scale bars equal 0.5 cm.

Fig. 2. Coracoïdes de Galliformes fossiles. A, B, G, H, M, O, Q. *Xorazmortyx tutkestanensis* n. gen. et n. sp. holotype ZIN 4991, Éocène moyen de Dzehroy II, Ouzbékistan. C, I, N, P, R. *Scopelortyx klinghardtensis*, holoptye GSN EC–01′13, Éocène moyen d'Eocliff, Namibie. D, J. *Paraortyx lorteti*, spécimen USTL ITD 530, Oligocène précoce d'Itardies, France. E, K. *Quercymegapodius brodkorbi*, spécimen USTL BFI 1849, Éocène final de la Bouffe, France ; retournés pour faciliter les comparaisons. F, L. *Palaeortyx intermedia*, spécimen SNSB18097, Miocène inférieur de Wintershof-West, Allemagne. A : vue dorsomédiale; B, F : vue dorsale; G : vue ventromédiale; H–L : vue médiale; M, N : vue ventrale; O, P : vue ventrolatérale; Q, R : vue latérale. Abréviations: cac : crista acrocoracoidea; cs : cotyla scapularis; fah : facies articularis humeralis; fac: facies articularis clavicularis; ib : impressio bicipitalis; ila : impressio lig. acrocoracohumeralis; p : fosse autapomorphique; pp : processus procoracoideus; sms : sulcus m. supracoracoidei . Barres d'échelle = 0,5 cm.

concave and obliquely oriented. Size small, comparable with modern *Ammoperdix* spp.

Type locality and age. Dzheroy-II; Uzbekistan. Eocene (Lutetian–Bartonian).

Measurements, mm. Maximal length as preserved, 9.0; maximal (oblique) diameter of the cotyla scapularis, 2.5; dorsoventral shaft diameter at the level of the cotyla scapularis, 3.2; maximal width of the facies articularis humeralis, 3.3.

4. Description and comparisons

One of the most distinctive traits of *X. turkestanensis* is that the whole processus acrocoracoideus has little medial expansion and so it overhangs the sulcus supracoracoideus very slightly. This process is generally aligned with the longitudinal axis of the shaft, as in *Scopelortyx*, but in contrast to other Paleogene galliforms. When compared with *Scopelortyx*, *X. turkestanensis* has an even less medially shifted processus acrocoracoideus: in ventral view, the process does not protrude medially beyond the tip of the processus procoracoideus. The omal portion of the shaft, which normally broadens to more or less degree medially in most Galliformes, is distinctly straight in *X. turkestanensis*, and the medial margin of the shaft is thus roughly parallel to the articular surface of the facies articularis humeralis, as in *Paraortyx lorteti*. The ventral surface of the shaft is thus compressed at the level of the facies. The processus acrocoracoideus further does not form a distinct hook (although the dorsal angle of the facies articularis clavicularis slightly projects caudally), again as in *Scopelortyx*, but in contrast to the condition in *Paraortyx*. The crista acrocoracoidea (sensu Elzanowski et al., 2012) is very short, and it is shorter than in *Paraortyx*, *Scopelortyx* and *Quercymegapodius,* and is notably shorter than in *Paraortygoides*. This crest is obliquely oriented, as in *Scopelortyx*, but in contrast to the condition in *Paraortyx*, where it has a notably more transverse (i.e. mediolateral) orientation.

The impressio lig. acrocoracohumeralis is almost straight and is somewhat broadened cranially. The impressio bicipitalis is pentagonal and prominent, i.e. it distinctly protrudes ventrally relative to the adjacent portion of the shaft, as in *Scopelortyx*, *Quercymegapodius* and *Paraortygoides* (see Mayr and Weidig, 2004, Fig. 4). The caudal margin of the impressio protrudes ventromedially beyond the adjacent portion of the shaft. The medial margin of the shaft autapomorphically bifurcates approximately at the mid-level of the facies articularis humeralis, sending a branch dorsally, toward the dorsocaudal angle of the facies articularis clavicularis. Between the two branches there is a distinct deep concavity (autapomorphy) undercutting the ventral part of the facies articularis clavicularis (Fig. 2, p). The facies articularis clavicularis is craniocaudally high, as in *Quercymegapodius*, but in contrast to the narrow one in *Scopelortyx* and *Paraortyx*. The caudal margin of the facies articularis clavicularis is distinctly concave, in contrast to *Quercymegapodius*, where it is distinctly convex. Other Paraortygidae have a straight or slightly convex caudal margin of the facies. The medial surface of the facies contains a shallow but distinct concavity, not evident in other examined stem-galliforms (not visible in Gallinuliodidae).

The facies articularis humeralis is craniocaudally short, as in *Quercymegapodius* and *Paraortyx brancoi*, but in contrast to the markedly elongate facies in *Scopelortyx* and *Paraortyx lorteti*. The facies narrows cranially as in *Quercymegapodius*, whereas it is cranially wide in *Scopelortyx*. In lateral view, the dorsal margin of the facies articularis humeralis is almost straight as in *Quercymegapodius* (concave in *Scopelortyx* and *Paraortyx lorteti;* less so in *P. brancoi*). There are, however, differences in the morphology of the facies between *Xorazmortyx* and *Quercymegapodius*. In the same lateral view, the apex of the facies articularis humeralis (the most ventrally protruding point of its ventral margin) is positioned level with the cranial margin of the cotyla scapularis, whereas in *Quercymegapodius* this point is shifted much more cranially and is level with the sulcus m. supracoracoidei. The latter sulcus is shallow and is bordered ventrally by the abovementioned dorsal branch of the medial margin of the shaft.

The processus procoracoideus is strongly reduced as in *Gallinuloides wyomingensis* and *Quercymegapodius,* whereas it is notably larger in *Scopelortyx*. *Paraortyx* has a larger processus procoracoideus than it is in *Xorazmortyx*. The cotyla scapularis is concave as in all stem-galliforms (Mayr, 2000; Mourer-Chauviré, 1992) and is slightly ellipsoid in its shape, with the longer axis more obliquely oriented than in *Quercymegapodius brodkorbi,* where it is oriented more transversely. The transverse diameter of the cotyla is notably smaller than the shaft width, as in *Scopelortyx* and *Paraortyx brancoi*, but in contrast to *Paraortyx lorteti*, *Paraortygoides*, and *Quercymegapodius*, which all have very large cotyla scapularis.

Gallinuloididae have a general more anatid-like omal extremity of the coracoid (see Mayr, 2006), as can be seen in the European representative *Paraortygoides messelensis*. In dorsal view, the whole processus acrocoracoideus is more elongate and directed medially in *P. messelensis*, whereas in *Xorazmortyx* it is hardly protruding medially beyond the level of the processus procoracoideus. The crista acrocoracoidea (sensu Elzanowski et al., 2012) in *P. messelensis* is thick, elongate and cylinder-like, whereas in *Xorazmortyx* it is very short and indistinct. The ridge, running caudally and ventrally from the dorsal part of the facies articularis clavicularis, and the distinct large pit located ventrally to this ridge are absent in *P. messelensis*.

5. Discussion

The Paleogene fossil record of Asian land birds is scarce, and hence the discovery of the new stem-galliform adds significantly to our understanding of the Eocene avian diversity in Asia. The new find is further the first landbird known from this geographical area, from where only seabirds were previously known (see above). The distinct morphology of the coracoid from the Dzheroy II indicates that it belongs to a separate genus of stem-galliform birds, which can be attributed to the extinct family Paraortygidae (see above). This is only the third record of Eocene galliforms in Asia and the first find of Paraortygidae in this continent. It further may be the oldest one for this clade, because deposits of Dzheroy II locality may be late Lutetian in age (Malyshkina and Ward, 2016), whereas the Namibian taxon *Scopelortyx* is Bartonian. However, the general similarity between *Scopelortyx* and *Xorazmortyx* (when compared with other stem-galliforms) likely indicates an important biogeographical connection between the landbird faunas of Africa and Asia in the middle Eocene. Larger Tethys seaway, which separated Afro-Arabia and Asia in the late Cretaceous and earliest Paleogene, became much narrower in the Lutetian (Golonka, 2000) because of the uplift of the Arabian platform (Meulenkamp and Sissingh, 2003). The region of modern Turkestan experienced a retreat of sea basins in the second half of the Eocene (Golonka, 2000) and hence large islands could have been present here where an evolution of Galliformes might have taken place.

The finds of Lutetian–Bartonian paraortygids in both southwestern Asia and Africa indicate good dispersal abilities of these birds, which contrast with the very limited abilities to disperse over large water bodies in modern Galliformes (with some exceptions, e.g., basal Megapodiidae).

Modern galliforms are incapable of prolonged sustained flight, but in contrast are well adapted to a very powerful vertical take-off, the so-called escape flight (Askew and Marsh, 2002; Stegmann, 1950, 1953; Sych, 1985). It is this adaptation to vertical flight that limits the ability of sustained flight, as it requires a modification of the glenoid joint allowing rotation (pronating or supinating) of an adducted (attached close to the body) humerus, which is practically impossible in most birds except colibris, galliforms and partly tinamous (Karhu, 2001; Stegmann, 1950, 1953). The structure of the glenoid joint thus may serve as some kind of a proxy of dispersal abilities in modern and fossil galliforms. The main morphological indications of ability to rotate humerus in colibris and galliforms are the development of the caudal extension of the caput humeri (eminentia capitis humeri) and the presence of a shallow glenoid cavity, which is formed by the humeral articular surfaces on the coracoid and the scapula (Karhu, 2001; Stolpe and Zimmer, 1939). Mayr (2017) further notes a robust humerus as a morphological correlation of such flight adaptations in Phasianoidea, and Karhu (2001) observes a strongly convex ventral part of the humeral head in these birds (the head is thus asymmetrical), which allows contact between the humerus and the glenoid cavity when the humerus is attached to the body (adducted). Stem galliforms (especially Gallinuloididae; Mayr, 2000, 2006) had proportionally notably longer forelimbs, and thus were definitively capable of a more sustained active flight than modern Phasianidae. Importantly, all Paraortygidae lack the eminentia capitis humeri ("ridge connecting the humeral head with the internal tuberosity" of Mourer-Chauviré, 1992), and *Scopelortyx* has less ventrally convex humeral head (Mourer-Chauviré et al., 2017), as compared with modern phasianids. The humerus of Paraortygidae is markedly less robust than that of Phasianidae (see figs. 2, 5 in Mourer-Chauviré, 1992, and also Fig. 4 in Mourer-Chauviré et al., 2017). The scapula of *Scopelortyx* is more duck-like in its appearance than that of *Paraortyx* and Phasianidae. The glenoid surface of the coracoid is dorsoventrally wide and prominent in *Xorazmortyx* and *Paraortyx brancoi*, which indicates a less open glenoid cavity, as in Megapodiidae that are capable of oversee dispersal. These observations jointly strongly suggest that early Paraortygidae (*Xorazmortyx* and *Scopelortyx*) had a different wing kinematics as compared with Phasianidae, which likely explains their presence on both sides of the Mesopotamian Basin, which separated Arabia and southwestern Asia in the Eocene.

The coracoid is probably one of the most diagnostic bones in Galliformes, as it allows identification of families and even many genera (e.g., Mourer-Chauviré, 1992; Zelenkov and Kurochkin, 2009; Zelenkov and Panteleyev, 2015). Many fossil galliform taxa have been established based on humeri (see, for example Göhlich and Mourer-Chauviré, 2004), which appears to be an evolutionary much more stable skeletal element (although some taxa still have modified humeri). In particular, the humerus of *Paraortyx* from the late Eocene–Oligocene of Quercy is rather similar to that of the oldest phasianids *Palaeortyx* from the same localities (see Mourer-Chauviré, 1992). It is thus notable that the coracoid of *Paraortyx* from Quercy differs insignificantly from that of *Palaeortyx*– the only reliable difference is the presence of concave cotyla scapularis, which in addition is less concave in *Paraortyx* than in other stem galliforms. The general geometry of the omal part is very similar in *Paraortyx* and *Palaeortyx*, which may indicate close relationships between late Paraortygidae and early Phasianidae. It was previously suggested that Phasianidae, which first appear in Europe in the early Oligocene, might have dispersed to Europe from Asia (Mayr, 2009), but the poor fossil record of Eocene birds in Asia has not yet provided support for this hypothesis.

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