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New records of buttonquails (Aves, Charadriiformes, Turnicidae) from the Oligocene and Miocene of Europe

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ABSTRACT
Buttonquails (Turnicidae) are morphologically derived, quail-like members of the avian order Charadriiformes (shorebirds) that live in Old World dry tropical and subtropical open habitats. The morphological disparity between modern buttonquails and other shorebirds is bridged by Paleogene stem-group turnicids, which have a less specialised morphology. However, there is currently a large temporal gap in the fossil record between the earliest European buttonquails (early Oligocene) and the youngest pre-Quaternary records (late Miocene). Here we describe two new taxa from France, based on partial humeri, which we refer to Turnicidae gen. et sp. indet. The oldest record stems from deposits from the latest Oligocene, which are part of the Saint-Gérand-le-Puy fossil sites. The younger record is from the early-middle Miocene fissure filling of Vieux-Collonges. In morphology, both taxa are more similar to early Oligocene species of *Turnipax* Mayr, 2000 than to crown-group turnicids.

KEY WORDS
Fossil birds,
shorebird evolution,
Miocene aridification,
French fossil sites,
palaeobiology.

Although the fossils are too fragmentary to allow ecomorphological interpretations, paleoenvironmental data suggest that, like Paleogene buttonquails, these taxa departed from the adaptations to open arid environments by modern-type turnicids. Our assessments therefore reinforce previous hypotheses that crown-group turnicids probably did not diversify before the late Miocene, and argue in favour of broader ecological preferences in stem-group turnicids.

RÉSUMÉ
Nouveaux spécimens de turnicidés (Aves, Charadriiformes, Turnicidae) de l'Oligocène et du Miocène d'Europe.
Les turnicidés (Turnicidae) sont des oiseaux morphologiquement dérivés, ressemblant quelque peu à des cailles, mais appartenant à l'ordre Charadriiformes (limicoles et alliés) et habitant actuellement les zones tropicales et subtropicales ouvertes de l'ancien monde. La disparité morphologique entre les turnicidés modernes et les autres Charadriiformes est complétée par le groupe tronc des Turnicidae du Paléogène, qui montrent une morphologie générale moins spécialisée. Cependant, il existe actuellement un fossé temporel important dans l'enregistrement fossile entre les premiers turnicidés européens (Oligocène inférieur) et les fossiles les plus récents connus avant le Quaternaire (Miocène supérieur). Nous décrivons ici deux nouveaux taxons de France, attestés par la présence d'humérus partiels, que nous attribuons à des Turnicidae gen. et sp. indet. Le plus ancien de ces spécimens provient de dépôts de l'Oligocène terminal appartenant au complexe de sites de la région de Saint-Gérand-le-Puy. Le plus récent provient du remplissage karstique de la fin du Miocène inférieur-début du Miocène moyen de Vieux-Collonges. En terme de morphologie, les deux taxons sont plus proches des espèces du début de l'Oligocène du genre *Turnipax* Mayr, 2000 que des Turnicidae du groupe couronne. Bien que les fossiles soient trop fragmentaires pour permettre des interprétations éco-morphologiques, les données paléoenvironnementales suggèrent, tout comme pour les Turnicidae paléogènes, que ces animaux différaient des turinicidés actuels, plus adaptés aux environnements ouverts. Notre étude renforce donc l'hypothèse selon laquelle les Turnicidae du groupe couronne ne se sont probablement pas diversifiés avant la fin du Miocène, et propose des préférences écologiques plus larges chez les Turnicidae du groupe tronc.

MOTS CLÉS
Oiseaux fossiles,
évolution des limicoles,
aridification Miocène,
sites fossilifères français,
paléobiologie.

INTRODUCTION

Buttonquails (Turnicidae) are one of the most unusual charadriiform birds – unlike their shorebird relatives they are small quail-like birds that live in Old World dry tropical and subtropical habitats and are widely distributed from sub-Saharan Africa and small areas of the southwestern Palearctic to Southern East Asia and Australia (Mayr 2017; Winkler *et al.* 2020). Until recently, populations of the Common Buttonquail *Turnix sylvaticus* Desfontaines, 1789 were distributed across southern Europe (Ministerio para la Transición Ecológica 2018; Gutiérrez-Expósito *et al.* 2019, 2020). Fifteen extant species are placed in the genus *Turnix* Bonnaterre, 1791, whereas the Quail-plover *Ortyxelos meiffrenii* (Vieillot, 1819) (Vieillot 1819, 1925) is the only extant species in the genus *Ortyxelos* Vieillot, 1825. The adaptation of modern turnicids to open habitats like grassland, scrubland, and open woodlands is reflected in their skeletal and overall morphology, which strongly departs from that of other charadriiform birds and has confounded their phylogenetic affinities in the past (e.g. Gadow 1891, 1893; Lowe 1923; Bock & McEvey 1969; Olson & Steadman 1981; Livezey 2010; Mayr 2011). This morphological disparity is somewhat bridged by Paleogene turnicids, which have a less specialised morphology, and are therefore more charadriiform-like than crown-group Turnicidae (Mayr 2000, 2017; Mayr & Knopf 2007).

The oldest taxon that can be considered a stem-group turnicid is *Eocliffia primaeva* Mourer-Chauviré, Pickford & Senut, 2017, from the Bartonian (late middle Eocene) of southern Namibia, which was referred to a family incertae sedis but related to the Turnicidae (Mourer-Chauviré *et al.* 2017). This bird is known from a few wing bones and a tarsometatarsus which, like younger stem-group turnicids, possesses a fossa metatarsi I, indicating the presence of a hallux, unlike in extant Turnicidae (Mourer-Chauviré *et al.* 2017). All other Paleogene turnicids stem from early Oligocene deposits of Europe and are placed in the taxon *Turnipax* Mayr, 2000, which includes *T. dissipata* Mayr, 2000, from France, and *T. oechslerorum* Mayr & Knopf, 2007, from Germany. The putative turnicid *Cerestenia pulchrapenna* Mayr, 2000 from the early Oligocene of France resembles species of *Turnipax* in the morphology of some of its wing bones but the holotype specimen is too poorly preserved to confidently refer it to the Turnicidae (Mayr & Knopf 2007).

The spread of grasslands and open habitats towards the Neogene is thought to have influenced the diversification of crown-group Turnicidae (Mayr & Knopf 2007; Zelenkov *et al.* 2016; Mayr 2017), whose members differ morphologically from Paleogene buttonquails, likely indicating differences in habitat preference and way of life (Mayr & Knopf 2007; Mayr 2017). The earliest records of modern-type buttonquails stem from late Miocene deposits in Hungary, southern Ukraine,

and northern Kazakhstan (Zelenkov *et al.* 2016). Of these, one species based on a coracoid was referred to the genus *Ortyxelos* whereas a closer resemblance to *O. meiffrenii* than to species of *Turnix* was noted for other specimens (Zelenkov *et al.* 2016). The morphological distinctiveness of *O. meiffrenii* has warranted generic separation from *Turnix* (Vieillot 1825; Lowe 1923; Bock & McEvey 1969) and some bones, particularly those of the pectoral girdle (see Bock & McEvey 1969) bear more of a resemblance to those of other Charadriiformes (Zelenkov *et al.* 2016). That *Ortyxelos* displays skeletal features that may be plesiomorphic for Turnicidae is also supported by some of the oldest fossil taxa being more similar to *O. meiffrenii* than to species of *Turnix* (Mayr 2000; Mayr & Knopf 2007; Zelenkov *et al.* 2016). A further, pre-Quaternary, record of modern-type buttonquails stems from the early Pliocene of South Africa and is based on a distal humerus that was referred to the genus *Turnix* and was tentatively associated with the extant Hottentot Buttonquail *T. hottentottus* Temminck, 1815 (Olson 1994).

Here we describe two new records of buttonquails from Europe, based on partial humeri, which bridge the large temporal gap in their evolutionary history from the early Oligocene (Mayr & Knopf 2007) to the late Miocene (Zelenkov *et al.* 2016). The earlier of these two new records comprises two specimens from the latest Oligocene of central France, and represents the first record of these charadriiform birds in the fluvio-lacustrine late Oligocene-early Miocene fossiliferous deposits of the Saint-Gérand-le-Puy area (see e.g. Hugueney *et al.* 2006) in the Département of Allier, central France. The second record comprises a further two specimens from the late early-middle Miocene fossiliferous fissure filling of Vieux-Collonges in France, which is located *c.* 175 km SE of the Saint-Gérand-le-Puy fossil sites. To inform the early evolutionary history of turnicids, we assess the significance of these fossils in a palaeoenvironmental context and relative to other known buttonquail fossils.

MATERIAL AND METHODS

Osteological nomenclature follows Nomina Anatomica Avium (Baumel & Witmer 1993) and taxonomic nomenclature follows Dickinson & Remsen (2013). The following extant turnicids were examined as comparative material: SMF 8760 *Turnix hottentottus*; SMF 19452 *T. sylvaticus*; SMF 575 *T. tanki* Blyth, 1843; SMF 7267 *T. varius* (Latham, 1801); SAMA B46502 *T. velox* (Gould, 1841); NHMUK S/1952.2.71, S/1965.22.1 *Ortyxelos meiffrenii*. Other Charadriiformes mentioned in the descriptions are: SMF 9609 *Nycticryphes semicollaris* (Vieillot, 1816); SMF 16060 *Rostratula benghalensis* (Linnaeus, 1758); SMF 7874 *Pluvianus aegyptius* (Linnaeus, 1758). The osteology of *Ortyxelos meiffrenii* and other species of *Turnix* was further assessed based on Bock & McEvey (1969).

Institutional abbreviations

NHMUK Natural History Museum, Tring;
NMB Naturhistorisches Museum Basel, Basel;
NMNHU National Museum of Natural History of the National Academy of Science of Ukraine, Kyiv;
SAMA South Australian Museum, Adelaide;
SMF Forschungsinstitut Senckenberg, Frankfurt-am-Main.

SYSTEMATIC PALAEONTOLOGY

Class AVES Linnaeus, 1758
Order CHARADRIIFORMES Huxley, 1867

Family Turnicidae Gray, 1840

Remarks

The following combination of characters of the distal humerus, present in both stem and crown-group turnicids, supports, within Charadriiformes, referral to the Turnicidae: fossa musculi brachialis well defined and situated on the ventral portion of the distal end, close to the margo ventralis; processus supracondylaris dorsalis present but small; distal end ventrally expanded at level of fossa musculi brachialis; wide but shallow sulcus humerotricipitalis and fossa olecrani. The proximal end of the humerus is highly derived for crown-group Turnicidae (e.g. Bock & McEvey 1969), especially in species of *Turnix,* and other than for specimens of the genus *Turnipax* showing partial views, it is essentially unknown for other pre-Quaternary specimens. Nevertheless, we refer the proximal humeri described below to the Turnicidae based on a combination of features present in *Ortyxelos meiffrenii* and/or *Turnipax* (e.g. transverse ridge across a very deep incisura capitis; shallow depression in lieu of dorsal fossa pneumotricipitalis in *Turnipax*) and in crown-group Turnicidae (e.g. poorly marked/defined sulcus transversus and impressio coracobrachialis; tuberculum dorsale not raised).

These features of the proximal and distal humerus are easily distinguished from the condition in most other charadriiform family-level taxa and have been assessed by many authors (e.g. Bock & McEvey 1969; Strauch 1978; Mayr 2000; De Pietri *et al.* 2011, 2016a, b, 2020a, b; De Pietri & Mayr 2012; Zelenkov *et al.* 2016). However, due to the fragmentary nature of the fossils we describe, below we provide more detailed comparisons with some other charadriiforms, where appropriate. For example, Rostratulidae have been recorded in the early Miocene of Europe (Mlíkovský 1999) and some authors have noted similarities between the humerus of stem-group turnicids and rostratulids (Mayr 2000; Mayr & Knopf 2007).

Gen. et sp. indet. A
(Fig. 1A, E, F)

Material. — NMB Bst 2550, distal left humerus (Fig. 1A, F).

Tentatively referred material. — NMB Bst 3663, distal right humerus (Fig. 1E).

MEASUREMENTS. — NMB Bst 2550, distal width: 3.9; minimum shaft width: 1.7; NMB Bst 3663, distal width: 3.4 (broken), minimum shaft width: 1.9.

LOCALITY AND AGE. — Coderet-Bransat (Commune de Bransat, Département of Allier), Massif Central, France; NW part of the Limagne Rift Basin; late Oligocene (MP 30), *c.* 23.03 Ma (see e.g. Pickford & Hugueney 2018 and references in De Pietri & Scofield 2014). The fossiliferous layer is a marly lens located in fluvio-lacustrine limestones. The site was found and excavated by Jean Viret from Lyon and Johannes Hürzeler from Basel in 1925 and later Marguerite Hugueney from Lyon undertook a new excavation in the 1960's (Hugueney 1969).

REMARKS

We abstain from naming this species because of the fragmentary nature of the material. NMB Bst 3663 is only tentatively allied with NMB Bst 2550 as the ventral side of the specimen is missing. The dorsal portion of this bone, however, agrees with NMB Bst 2550 but we cannot confidently ascertain whether they represent the same species as most diagnostic features are present on the ventral side of the distal humerus (see below).

We also note that, although most material recovered from Coderet-Bransat was usually found disarticulated, articulated (mammalian) specimens are not uncommon (Pickford & Hugueney 2018). For example, it is therefore likely that, given the preservation of the bones, the burhinid from this locality described by De Pietri & Scofield (2014) represents one individual. Similarly, if both NMB Bst 3663 and 2550 do represent the same species, preservation might indicate they also belong to the same individual, although it would be difficult to explain why only distal humeri were preserved. Both bones were field collected by Herrmann Helbing and were catalogued at NMB as "bird bones"in 1925.

DESCRIPTIONS AND COMPARISONS

In NMB Bst 2550, the fossa musculi brachialis is distinct but shallow, proximodistally elongated and restricted to the ventral side of the distal end, situated very close to the margo ventralis distally, as in all turnicids (Fig. 1A-E). It differs from *Turnipax oechslerorum* (Fig. 1B) in that the fossa musculi brachialis is not subdivided into two depressions by a transverse embossment. The distal end of the humerus is ventrally expanded compared to that of other charadriiforms, and although a ventral expansion is also present in the humerus of the Egyptian Plover *Pluvianus aegyptius*, in the latter, it is primarily a salient epicondylus ventralis that is responsible for that expansion. The tuberculum supracondylare ventrale bears a large facet for attachment of the ligamentum collaterale ventrale, which is similarly well developed in species of *Turnipax* and within crown-group Turnicidae in *O. meiffrenii,* although it is also distinct in species of *Turnix* (Bock & McEvey 1969).

The processus flexorius (Fig. 1F) shows some minimal damage to its surface, which does not affect its assessment. It is not as ventrodistally prominent as in crown-group turnicids, ending proximally of the distal end of the condylus ventralis and resembling the condition in *Turnipax*. In species of *Turnix,* the flexor process projects distinctly ventrally past the attachment facet for the articular ligament, whereas it is less distally projecting in *Ortyxelos meiffrenii*. In caudal view (Fig. 1F-H), the processus flexorius is not as dorsoventrally compressed as in species of *Turnix*, resembling the condition in *O. meiffrenii*. As in other Turnicidae, both the sulcus humerotricipitalis and the fossa olecrani are very wide but shallow.

The processus supracondylaris dorsalis is damaged in NMB Bst 2550 (Fig. 1A) but the small size of its base is consistent with the condition in crown-group Turnicidae. The process is intact in NMB Bst 3663 (Fig. 1E) and it matches species of *Turnix* and *Turnipax* in shape and size, but it is not as proximally situated as in extant turnicids although its position is more proximal than in *Turnipax*. However, because there is extensive damage to the ventral side of this specimen, we can only tentatively refer it to this turnicid taxon. A small, more proximally situated processus supracondylaris dorsalis is also present in Rostratulidae but in members of this family group the fossa musculi brachialis does not reach as close to the margo ventralis and the distinct ventral expansion of the distal end is not present. The processus supracondylaris dorsalis is also small in *P. aegyptius*, but is more distally situated and projects dorsally rather than cranio-dorsally. The condylus ventralis (Fig. 1A) is similar in size and shape to that of species of *Turnipax*, but it appears to be more rounded proximally. In crown-group turnicids, the condylus ventralis is more prominent, projecting distinctly distally.

NMB Bst 2550 is also overall similar to a late Miocene specimen (NMNHU-P Eg-1-20) from Ukraine (Zelenkov *et al.* 2016). This fragmentary specimen was described as a turnicid and a closer resemblance to *O. meiffrenii* was noted (Zelenkov *et al.* 2016). NMNHU-P Eg-1-20 is slightly larger than both NMB Bst 2550 and NMB Bst 3663 but there are some ascertainable differences between the two taxa: in the Ukrainian specimen, the processus flexorius appears to be slightly better developed distally, and the processus supracondylaris dorsalis is narrower at its base and more proximally situated, indeed approaching the condition in *O. meiffrenii*. A distal humerus from the early Pliocene South African Langebaanweg fossil site was referred to an indeterminate species of *Turnix* tentatively associated with the extant *T. hottentottus* by Olson (1994). The shape and size of the processus flexorius, epicondylus ventralis, and the condylus ventralis, as seen in Olson (1994: fig. 3), however, are very different from those of crown-group turnicids, and although they might resemble species of *Turnipax* and NMB Bst 2550 in these features, detailed comparisons are currently not possible.

Gen. et sp. indet. B
(Fig. 1J, K, N, O)

MATERIAL. — NMB V.C. 61 (proximal right humerus; Fig. 1K, O); NMB V.C. 4258 (proximal right humerus; Fig. 1J, N).

MEASUREMENTS. — NMB Vc 61: proximal width, 6.8, minimum shaft width, 2.2; NMB V.C. 4258: proximal width, 7.1.

LOCALITY AND AGE. — Vieux-Collonges, Central-Eastern France; MN5, 17-15 Ma, late early to middle Miocene (Mein 1958, 1975).

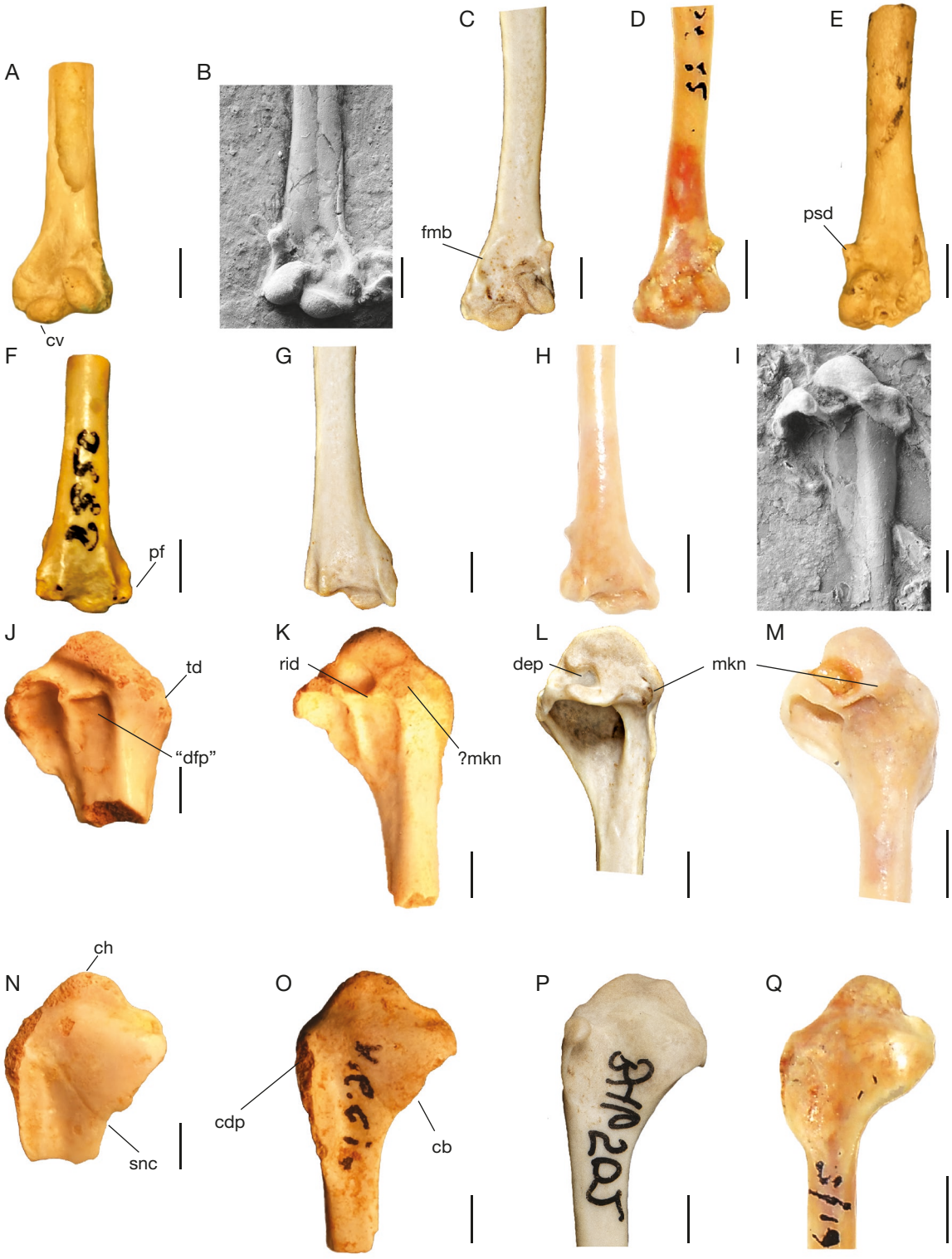

FIG. 1. — Turnicidae gen. et sp. indet. A (**A**, **E**, **F**) from Coderet-Bransat and Turnicidae gen. et sp. indet. B (**J**, **K**, **N**, **O**) from Vieux-Collonges, France, in comparison to *Turnipax oechslerorum* Mayr & Knopf, 2007 (**B**, **I**) from the early Oligocene of Germany and extant Turnicidae. Distal left humerus of: **A**, **F**, NMB Bst 2550 Turnicidae gen. et sp. A in cranial (**A**) and caudal (**F**) views; **C**, **G**, *Turnix velox* (Gould, 1841) SAMA B46502 in cranial (**C**) and caudal (**G**) views. Distal right humerus of: **B**, *Turnipax oechslerorum* in cranial view; **D**, **H**, *Ortyxelos meiffrenii* (Vieillot, 1819) NHMUK S/1952.2.71 in cranial (**D**) and caudal (**H**) views (mirrored to facilitate comparisons); **E**, NMB Bst 3663 in cranial view. Proximal right humerus of: **I**, *Turnipax oechslerorum* in caudal view; **J**, **N**, NMB V.C. 4258 in caudal (**J**) and cranial (**N**) views; **K**, **O**, NMB V.C. 61 in caudal (**K**) and cranial (**O**) views; **L**, **P**, *Turnix velox* SAM B46502 in caudal (**L**) and cranial (**P**) views; **M**, **Q**, *Ortyxelos meiffrenii* NHMUK S/1952.2.71 in caudal (**M**) and cranial (**Q**) views. Abbreviations: **cb**, crista bicipitalis; **cdp**, crista deltopectoralis; **ch**, caput humeri; **cv**, condylus ventralis; **dep**, depression of incisura capitis; **dfp**, dorsal fossa pneumotricipitalis; **fmb**, fossa musculi brachialis; **mkn**, "medial knob" *sensu* Bock & McEvey (1969); **pf**, processus flexorius; **psd**, processus supracondylaris dorsalis; **snc**, sulcus nervi coracobrachialis; **td**, tuberculum dorsale. Scale bars: 2 mm.

The site is a now empty fissure filling within Aalenian marine limestones, which was filled with siderothithic red clay. It is located in a former quarry in the village of Saint-Cyr north to the city of Lyon. It was discovered as early as 1875 by an amateur palaeontologist and subsequently visited by various palaeontologists from Basel in the 1930's (Johannes Hürzeler and Charles Immanuel Forsyth-Major) and Lyon (Pierre Mein) in the late 1940's to late 1950's (Mein 1958).

Remarks

Although direct comparisons of the proximal humerus with other turnicids are, for the most part, not straightforward because the proximal humerus of stem-group turnicids is only partially known and the morphology in species of *Turnix* is very derived, some features, particularly similarities with *Ortyxelos meiffrenii* (Fig. 1M, Q) and species of *Turnipax* (Fig. 1I), do support this attribution.

Description and comparisons

The humerus of this species is proportionally larger than that of gen. et sp. indet. A. As in *Ortyxelos meiffrenii* (Fig. 1M, Q) but contrary to the condition in species of *Turnix* (Fig. 1L, P), the caput humeri (Fig. 1N, O) is high and well-defined, which is also the condition in species of *Turnipax*; it differs from *O. meiffrenii*, however, in that in the latter the caput humeri is dorsoventrally narrower. Unlike in crown-group Turnicidae, the sulcus nervi coracobrachialis is present and is well marked (Fig. 1N); this feature is present at least in *Turnipax dissipata*. Unlike in most charadriiforms, the sulcus transversus and the impressio bicipitalis are poorly marked, being only slightly more noticeable than in crown-group Turnicidae (Fig. 1N-Q). In cranial view, the crista deltopectoralis (Fig. 1O) differs from that of *O. meiffrenii* and species of *Turnix* in being slightly more elongated ending, farther distally. In this condition, it is more similar to species of *Turnipax.* The crista deltopectoralis also does not appear to have a cranial overhang, as crown-group turnicids do, but the cranial rim of the crest is slightly damaged in both specimens. Like in species of *Turnipax* (and many other charadriiforms), the ventral rim of the crista bicipitalis is more rounded (Fig. 1O), differing from the low, straight margin in species of *Turnix* (Fig. 1P) and the proximodistally compressed shape of the crista bicipitalis of *O. meiffrenii* (Fig. 1Q). In caudal view, the tuberculum dorsale (Fig. 1J) resembles that of *Turnipax oechslerorum* in shape but it is not as salient or well defined, being low as in crown-group Turnicidae. However, it differs from species of *Turnix* in that it does not border proximally a sulcus or groove for "the pectoral attachment" *sensu* Bock & McEvey (1969) – this is presumably an attachment area for the musculus supracoracoideus (see Watanabe *et al.* 2020). In crown-group Turnicidae this attachment area is bordered by a pronounced tubercle ("medial knob" in Bock & McEvey 1969), the position of which differs between species of *Turnix* and *O. meiffrenii* (Fig. 1L, M). A similar feature, as seen in *O. meiffrenii* (Fig. 1M), is visible in NMB V.C. 61 (Fig. 1K), but the area is slightly worn in NMB V.C. 4258. This tubercle is likely absent in species of *Turnipax*, as the whole area is part of the raised tuberculum dorsale (Fig. 1L). The fossa pneumotricipitalis is distinctly different from that of species of *Turnix*, in which it occupies most of the caudal surface of the proximal end of the humerus and penetrates deeply into the caput humeri. In NMB V.C. 61 and V.C. 4258, the fossa is smaller, resembling the condition in *Ortyxelos* and species of *Turnipax*. There is a very shallow impression in lieu of a deep and well-marked dorsal fossa pneumotricipitalis (Fig. 1J). This condition is absent in crown-group Turnicidae but may be similar to that of some species of *Turnipax* (Fig. 1I; see also Mayr 2000; Mayr & Knopf 2007). As in *Turnipax* and crown-group turnicids, the incisura capitis is deeply excavated (Fig. 1I-M). A ridge across a deep incisura capitis, which in NMB V.C. 61 and V.C. 4258 is oriented nearly perpendicular to the longitudinal axis of the bone (Fig. 1I), is also present in *Turnipax oechslerorum* and *O. meiffrenii.* While a transverse ridge across the incisura capitis is a distinctive feature of the suborder Scolopaci (e.g. Strauch 1978; Mayr 2011; see also De Pietri *et al.* 2020a, b for variations of this feature in scolopacids), it is uncertain whether the ridge in turnicids is homologous to that of Scolopaci (Mayr 2011). We note, however, that a similar feature is present in some glareolids (De Pietri *et al.* 2020a). *Ortyxelos meiffrenii* (Fig. 1M) resembles NMB V.C. 61 and V.C. 4258 (and species of *Turnipax*) but the ridge is more obliquely oriented rather than perpendicular to the longitudinal axis of the humerus. In fossil turnicids, the area is thus only superficially similar to that of *Rostratula benghalensis,* in which the incisura capitis is rather deeply excavated proximal to the ridge but, like in other Scolopaci, the ridge is transverse across the incisura capitis. A deep incisura capitis is not present in other examined rostratulids (i.e., *Nycticryphes semicollaris*).

DISCUSSION

The partial humeri we here describe support the presence of two previously unrecognised species of buttonquail (Turnicidae), one from the latest Oligocene (gen. et sp. indet. A) and one from the early-middle Miocene (gen. et sp. indet. B) of France. The latter is the larger of the two, but further comparisons between them are not possible because each species is known from a different end of the humerus. Nevertheless, comparisons with other fossil and extant turnicids indicate that these taxa, in many features, were closer in morphology to the early Oligocene members of the genus *Turnipax* (Mayr 2000; Mayr & Knopf 2007) than to modern-type turnicids, and are therefore unlikely to have belonged to crown-group Turnicidae. Gen. et sp. indet. A differs from members of the crown-group, and is similar to *Turnipax*, in the morphology of the processus flexorius and the condylus ventralis, whereas gen. et sp. indet. B, contrary to crown-group Turnicidae, bears a sulcus nervi coracobrachialis and has a proportionally longer crista deltopectoralis. The cranial surface of the humerus of gen. et sp. indet. B closely matches that of *Turnipax dissipata* (Mayr & Knopf 2007: fig. 4C) in overall morphology.

The late Oligocene-early Miocene fluvio-lacustrine deposits of the Limagne Basin (Massif Central) in France have yielded a diverse fauna of charadriiform birds (Milne-Edwards 1867-1871), including larids (De Pietri *et al.* 2011), glareolids (De Pietri *et al.* 2020a), scolopacids (De Pietri & Mayr 2012), burhinids (De Pietri & Scofield 2014), and charadriids (De Pietri *et al.* 2013). Many of these family groups are known from the early Oligocene of Europe (e.g. Bessonat & Michaut 1973; Mayr & Smith 2001; Roux 2002; Mlíkovský 2002; Mourer-Chauviré *et al.* 2004; Mayr 2009) and continued to be present through to the middle (e.g. Ballmann 1972, 1979, 2004; Cheneval 2000; Mlíkovský 2002) and late (e.g. Mlíkovský 2002; Zelenkov & Panteleyev 2015; Bocheński *et al.* 2019) Miocene. Similarly for turnicids, the 23 Ma and 16 Ma records here discussed likely attest to a continuous presence of this charadriiform lineage in Europe, from the early Oligocene (Mayr 2000; Mayr & Knopf 2007) through to the late Miocene (Zelenkov *et al.* 2016).

The morphological differences between fossil representatives of the Turnicidae and crown-group turnicids indicate, however, that the ecological preferences of these birds are unlikely to have remained static (Mayr & Knopf 2007; Zelenkov *et al.* 2016). Today turnicids predominantly inhabit grassy or low brushy habitats (Debus 1996; Winkler *et al.* 2020); open grasslands are not thought to have been widespread in Western Eurasia until the middle or late Miocene (Jacobs *et al.* 1999; Strömberg 2011), and even then faunas may have occupied a mix of grass-dominated and woodland habitats (Strömberg 2011). The adaptations of crown-group turnicids to arid, open, environments include the absence of a hallux, which permits better movement through scrub, and a derived morphology of bones of the wing and pectoral girdle, which likely facilitates a quick take-off (Stegmann 1978; Debus 1996; Mayr & Knopf 2007). Although the late Oligocene and early-middle Miocene specimens we here describe are too fragmentary to allow ecomorphological assessments, both species more closely resemble the early Oligocene species of *Turnipax* in features of the humerus (see descriptions for details). Morphological similarities to these less derived turnicids (Mayr & Knopf 2007; Zelenkov *et al.* 2016) indicate that the two species here described also differed in their ecological preferences from extant buttonquails, which is further supported by palaeoenvironmental assessments of the deposits these fossils were recovered from.

The late Oligocene turnicid (gen. et sp. indet. A) from the fluvio-lacustrine locality of Coderet-Bransat demonstrates that, unlike most of its modern counterparts that are found in arid environments, these turnicids were found close to water sources. However, so far turnicids have not been recovered from the Aquitanian (MN1-MN2, early Miocene) fluvio-lacustrine fossiliferous deposits of the Saint-Gérand-le-Puy area (see e.g. Hugueney *et al.* 2006; De Pietri *et al.* 2011), despite thousands of bird fossils belonging to primarily aquatic and semi-aquatic taxa, but also to terrestrial and arboreal taxa, being known (e.g. Milne-Edwards 1867-1871; Mlíkovský 2002). Although bird remains from Coderet-Bransat have only more recently been published on (De Pietri & Scofield 2014) and are rare by comparison to fossils yielded from Aquitanian deposits, mammalian faunas do show a different composition compared to younger localities in the area (Pickford & Hugueney 2018). One other charadriiform bird has been described from Coderet-Bransat (De Pietri & Scofield 2014), namely a burhinid (stone-curlew), which, so far, has also not been recovered from the early Miocene deposits of the area. Like buttonquails, most (but not all) extant burhinids prefer arid to semi-arid habitats (Hume 1996). Although the avian fossils known from Coderet-Bransat are not nearly as numerous as those from other localities from the Saint-Gérand-le-Puy area, these early findings may indicate avifaunal differences (and therefore environmental differences) between the younger and older deposits, similar to those observed for some mammals (Costeur & Legendre 2008; Costeur *et al.* 2012; Hugueney *et al.* 2012; Pickford & Hugueney 2018). The environment associated with the MN2 localities of the Saint-Gérand-le-Puy fossil localities is an open lacustrine landscape in a warm temperate climate (Hugueney 1984; Mosbrugger *et al.* 2005; Costeur *et al.* 2012; Pickford & Hugueney 2018), whereas the faunal community of Coderet-Bransat (MP 30) corresponds to relatively humid, warm, and forested conditions under a humid subtropical climate (Mosbrugger *et al.* 2005; Pickford & Hugueney 2018; Li *et al.* 2018), which may explain these faunal differences (Pickford & Hugueney 2018). It is also therefore likely that the turnicids and burhinids that inhabited the Coderet-Bransat area in the late Oligocene, unlike their modern counterparts, were not adapted to dry, open environments.

The French locality of Vieux-Collonges, from where the two proximal humeri representing gen. et sp. indet. B are from, is a fissure-filling in a limestone quarry and documents the transition between the early and middle Miocene (Mein 1958, 1975; Hugueney *et al.* 2012; see Ballmann 1972 for records of birds). Similarly, the faunal assemblage from Vieux-Collonges points to warm and humid conditions [Middle Miocene Climatic Optimum] (Hugueney *et al.* 2012). Although *Turnipax oechslerorum* was recovered from early Oligocene (MP 22) marine (coastal) deposits from Germany (Frauenweiler), small, non-marine birds, are not uncommon in the type locality (e.g. Mayr & Micklich 2010). Faunal and floral studies have shown that the terrestrial environment around these early Oligocene deposits was forested, with a warm-temperate climate (Maxwell *et al.* 2016). Therefore, the early and late Oligocene records of buttonquails and the late early Miocene record here described, suggest that these early turnicids did not inhabit arid, open landscapes, like their modern counterparts.

However, palaeoenvironmental studies from the limestone deposits of Eocliff, Namibia, which yielded *Eocliffia primaeva*, have shown that during the (Bartonian) Eocene, conditions were semi-arid to sub-humid (Pickford *et al.* 2014; Mourer-Chauviré *et al.* 2017). As exemplified above, this type of environment differs from those inferred for European fossil buttonquails from the Oligocene and Miocene, and it is also different from the arid habitats primarily preferred by modern buttonquails. There are notable morphological differences

between species of *Turnipax* and *Eocliffia primaeva*, such as a longer tarsometatarsus and more robust wing elements in the latter (Mourer-Chauviré *et al.* 2017), which again would indicate adaptations to different environments. Nevertheless, the presence of a hallux, as in species of *Turnipax*, suggests that *E. primaeva* and species of *Turnipax* were stem-group representatives of the Turnicidae, which by the early Oligocene may have diversified several times to occupy different environments, considering the lineage likely split from other Lari (i.e., gulls, terns, auks, pratincoles, and allies) around the late Paleocene or early Eocene (De Pietri *et al.* 2020b).

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