

A rail (Aves, Rallidae) from the early Oligocene of Germany

Gerald Mayr¹

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A partial skeleton of a medium-sized fossil rail is described from the early Oligocene of Hofheim-Wallau in Germany and tentatively assigned to *Belgirallus oligocaenus* Mayr & Smith 2001. It is the earliest substantial fossil record of Rallidae and for the first time provides information on the limb proportions of Paleogene rails. Based on foot morphology, the fossil specimen can be assigned to the Rallinae, i.e. a clade including all Rallidae except the Nkulengu Rail *Himantornis haematopus*. Although it is not possible to further assign it to any subclade within Rallinae, the fossil provides an early Oligocene minimum age for the divergence between *H. haematopus* and Rallinae.

Key words: fossil birds, Oligocene, Rallidae, Germany

¹Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, D-60325 Frankfurt/M., Germany (Gerald.Mayr@senckenberg.de)

INTRODUCTION

The 133 extant species of rails (Rallidae) have a worldwide distribution and include ecologically diverse taxa, such as crakes (*Crex*, *Porzana*), water rails and true rails (*Rallus*), wood-rails (*Aramides*), gallinules (*Gallinula*), and coots (*Fulica*) (Taylor 1996). Recent phylogenetic studies have shown that the sister group of Rallidae are the sungebes (Heliornithidae) and that the clade (Rallidae + Heliornithidae) in turn is the sister taxon of the clade (Psophiidae [trumpeters] + Aramidae [limpkin] + Gruidae [cranes]) (Livezey 1998, Fain & Houde 2004, Cracraft *et al.* 2004). However, owing to the morphological homogeneity of the taxon and the lack of sufficiently comparative molecular studies, the phylogeny within Rallidae is still poorly resolved, although there is morphological evidence for sister group relationship between the Nkulengu Rail, *Himantornis haematopus*, and all other rails, the Rallinae (Olson 1973a, Livezey 1998).

Little is known about the osteology and phylogenetic relationships of early Paleogene Rallidae, as most pre-Miocene taxa are known from fragmentary bones only (Olson 1977, Mlíkovský 2002, Mayr 2005a). A number of Eocene species have been described on the basis of distal tibiotarsi (Olson 1977) and their identification as Rallidae needs to be substantiated by additional material. Two species of *Quercyrallus* Lambrecht 1933 are known from fragmentary humeri from the Middle Eocene to Upper Oligocene fissure fillings of the Quercy in France and their assignment to Rallidae also needs to be corroborated by additional bones (Cracraft 1973, Olson 1977, Mayr 2005a; see also Mourer-Chauviré 1992: p. 83). As indicated by Mayr (2000), *Ludiortyx hoffmanni* (Gervais 1852), known from a complete but poorly preserved skeleton from the Upper Eocene of France, may be a representative of the galliform Quercymegapodidae Mourer-Chauviré, 1992, whereas *L. adelus* (Oberholser 1917) from the same locality is probably too incompletely preserved for a phylogenetic

assignment. The earliest reliably identified fossil remain of a rail is thus an incomplete coracoideum from the Upper Eocene of England which was referred to *Ibidopsis* Lydekker 1891 by Harrison & Walker (1976). From the lowermost Oligocene of Belgium (MP 21, i.e. 33 million years ago), two species of *Belgirallus* Mayr & Smith 2001 are known from several postcranial bones.

Based on an incomplete left foot and without presenting a rationale for his identification, Martini (1967) described a putative rail from the early Oligocene of Germany; I concur with Olson (1977) that this specimen is too incompletely preserved for an assignment to the Rallidae.

Fischer (1997) further described a putative taxon of Rallidae from the early Oligocene of Germany. However, *Rupelrallus* Fischer 1997, which is based on associated incomplete bones of a single individual, is larger than any extant species of Rallidae, the carpometacarpus measuring more than 50 mm (Fischer 1997), and distinctly differs from Rallidae in the much wider scapi clavicularum and the shape of the extremitas sternalis of the coracoideum. In the preserved skeletal elements *Rupelrallus* closely resembles the contemporaneous *Parvigrus* Mayr 2005b, which is a stem lineage representative of Grues (Gruidae + Aramidae) (Mayr 2005b), and I consider it likely that *Rupelrallus* is more closely related to *Parvigrus* than to Rallidae (contra Mayr 2005a).

Here I report on a partial skeleton of a rail from the early Oligocene of Germany, which represents the most substantial fossil record of a Paleogene rail and for the first time provides information on limb proportions of a Paleogene representative of Rallidae.

METHODS

The fossil specimens are deposited in the Hessisches Landesmuseum Darmstadt, Germany (HLMD) and the Institut Royal des Sciences Naturelles de Bruxelles, Belgium (IRScNB). Osteological terminology follows Baumel and Witmer (1993), taxonomy of the extant taxa

Dickinson (2003); measurements are in millimeters.

Osteological comparisons were made with the following extant taxa of Rallidae (all skeletons in the collection of Forschungsinstitut Senckenberg): *Amaurornis* (*phoenicurus*, *flavirostra*), *Aramides* (*cajanea*, *saracura*, *ypecaha*), *Crex crex*, *Fulica* (*americana*, *atra*), *Gallinula* (*chloropus*, *melanops*), *Gallirallus australis*, *Himantornis haematopus* [limb elements], *Laterallus melanophaius*, *Pardirallus maculatus*, *Porphyrio* (*martinica*, *poliocephalus*, *porphyrio*), *Porzana* (*flaviventer*, *porzana*), *Rallus* (*aquaticus*, *longirostris*).

Systematic paleontology

Rallidae Vigors 1825

Rallinae sensu Olson (1973a)

?*Belgirallus* Mayr & Smith 2001

cf. *Belgirallus oligocaenus* Mayr & Smith 2001

RESULTS

Referred specimen

HLMD-WT 238 a–e, dissociated postcranial skeleton on two slabs lacking the skull, most of the left wing, and the left leg (Fig. 1); the extremitas omalis of the left coracoideum, the extremitas cranialis of the right scapula, and the right caput humeri are preserved as isolated skeletal elements (Fig. 2).

Locality and horizon

Hofheim-Wallau, Hessen, Germany; early Oligocene (Rupelian, i.e. 30–33 million years ago; see Legendre & Lévêque 1997); discovered during railway construction work for the Intercity Express train (ICE).

Measurements

See Table 1 for the dimensions of the major limb elements. Length of pedal phalanges: I1, 12.5; I2, 6.3; II1, 18.6; II2, 15.0; II3, 5.7; III1, 19.2; III2, 13.9; III3, 10.6; III4, 5.0; IV1, 13.7; IV2, 9.0; IV3, 7.6; IV4, 4.5. Some measurements in comparison to the Belgian specimens of *B. oligocaenus* (in brackets, after Mayr & Smith 2001): distance from

Table 1. Dimensions of the major limb bones (maximum length along longitudinal axis) and ratio ulna/tarsometatarsus (uln/tmt) of the new rail HLMD-WT 238 (cf. *Belgirallus oligocaenus*) in comparison with selected species of extant Rallidae. For the fossil the measurements of both sides (left/right) are given; a dash indicates that no measurements were available. The taxa are ordered according to increasing uln/tmt ratios.

	humerus	ulna	carpometacarpus	tibiotarsus	tarsometatarsus	ratio uln/tmt
<i>Gallirallus australis</i>	56.3	28.4	42.8	114.3	66.4	0.43
<i>Aramides saracura</i>	53.4	45.1	31.3	105.0	73.6	0.61
<i>Amaurornis flavirostra</i>	35.7	29.4	21.1	65.5	44.5	0.66
HLMD-WT 238	/40.4	/~31.7	22.6/22.9	/72.3	/47.5	0.67
<i>Laterallus melanophaius</i>	25.4	21.7	15.6	46.5	31.0	0.70
<i>Porphyrio martinica</i>	49.6	42.7	30.0	87.9	58.7	0.73
<i>Himantornis haematopus</i>	-	~58.5	35.5	-	80.4	0.73
<i>Aramides ypecaha</i>	67.1	61.2	42.1	122.0	81.8	0.75
<i>Porzana flaviventer</i>	23.1	18.7	13.3	40.9	24.8	0.75
<i>Porphyrio porphyrio</i>	72.0	64.6	44.3	125.3	85.4	0.76
<i>Rallus aquaticus</i>	42.8	34.6	23.6	70.2	45.7	0.76
<i>Gallinula melanops</i>	42.0	32.3	26.1	68.0	42.1	0.77
<i>Porphyrio poliocephalus</i>	63.6	60.5	40.9	117.9	74.4	0.81
<i>Gallinula chloropus</i>	52.3	42.2	32.6	83.5	51.1	0.83
<i>Amaurornis phoenicurus</i>	31.7	47.1	31.5	80.0	54.9	0.86
<i>Rallus longirostris</i>	52.5	42.9	27.5	-	48.6	0.88
<i>Porzana porzana</i>	34.4	29.2	20.0	53.0	32.9	0.89
<i>Pardirallus maculatus</i>	44.5	37.0	24.6	63.8	37.9	0.98
<i>Crex crex</i>	45.6	41.1	28.0	60.4	40.5	1.01
<i>Fulica americana</i>	72.9	62.5	41.6	100.9	59.2	1.05
<i>Fulica atra</i>	69.7	70.0	36.9	96.9	57.3	1.22

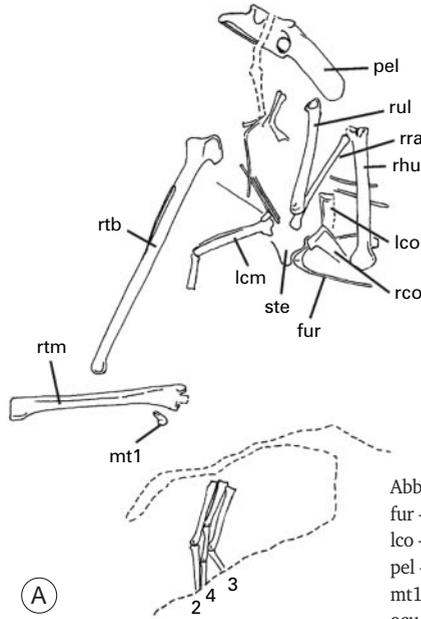
centre of cotyla scapularis to tip of processus acrocoracoideus of coracoideum, 3.6 [3.7]; width of trochlea metatarsi III: 1.9 [~1.7]; length of trochlea metatarsi III: 3.3 [~3.0]; minimum width of shaft of tarsometatarsus: 2.5 [2.5].

Description and comparison

As in most extant Rallidae, the furcula (HLMD-WT 238b, Fig. 1) exhibits thin scapi clavicularem and a wide extremitas sternalis (among the examined taxa the extremitas sternalis is proportionally narrower in *Aramides*, *Crex*, and *Porzana flaviventer*). There is a low ridge along the midline of the caudal surface of the extremitas sternalis; a dorsally protruding projection is absent (this projection is very distinct in, e.g., *Rallus*, *Pardirallus*, and *Fulica*). The scapi clavicularem are diverging towards the extremitates omale as in, e.g.,

Aramides and *Gallinula*, whereas they are more parallel in *Rallus* and *Pardirallus*, i.e. taxa with a slim body.

Both coracoidea are preserved; the extremitas omalis of the right coracoideum is visible in ventral view (HLMD-WT 238a, Fig. 1) whereas the extremitas omalis of the left coracoideum is preserved as an isolated bone, its processus procoracoideus being broken. The bone corresponds well with the coracoideum of the Belgian specimens of *Belgirallus oligocaenus* (Fig. 2). On the proximal end, the processus procoracoideus is not as expanded as in *Aramides* and *Canirallus* (Olson 1973a), and the facies articularis clavicularis is small as in, e.g., *Gallinula*, whereas it forms a ventrally protruding projection in *Rallus*, *Pardirallus*, and *Amaurornis flavirostra*. The extremitates sternaes of both coracoidea expose their dorsal surfaces



Abbreviations:
 fur – furcula
 lco – left coracoideum
 pel – pelvis
 mt1 – os metatarsale I
 ocu – os carpi ulnare
 ote – ossified tendon
 rcm – right carpometacarpus
 rco – right coracoideum
 rfe – right femur
 rhu – right humerus
 rra – right radius
 rtb – right tibiotarsus
 rtm – right tarsometatarsus
 rul – right ulna
 ste – sternum.

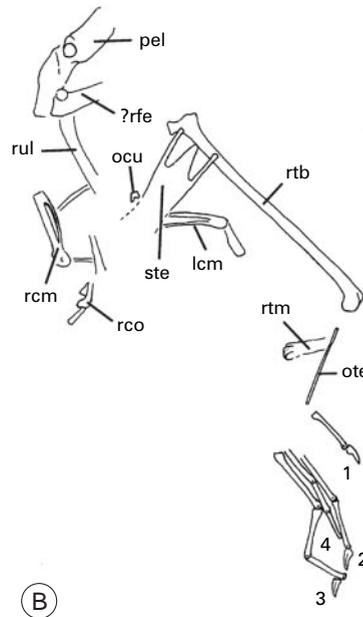


Figure 1. The newly described rail cf. *Belgirallus oligocaenus* from the early Oligocene (Rupelian) of Hofheim-Wallau, (A) specimen HLMD-WT 238b with interpretative drawing, (B) specimen HLMD-WT 238a with interpretative drawing. The toes are numbered. The specimens are coated with ammonium chloride to enhance contrast. Scale bars equal 10 mm.

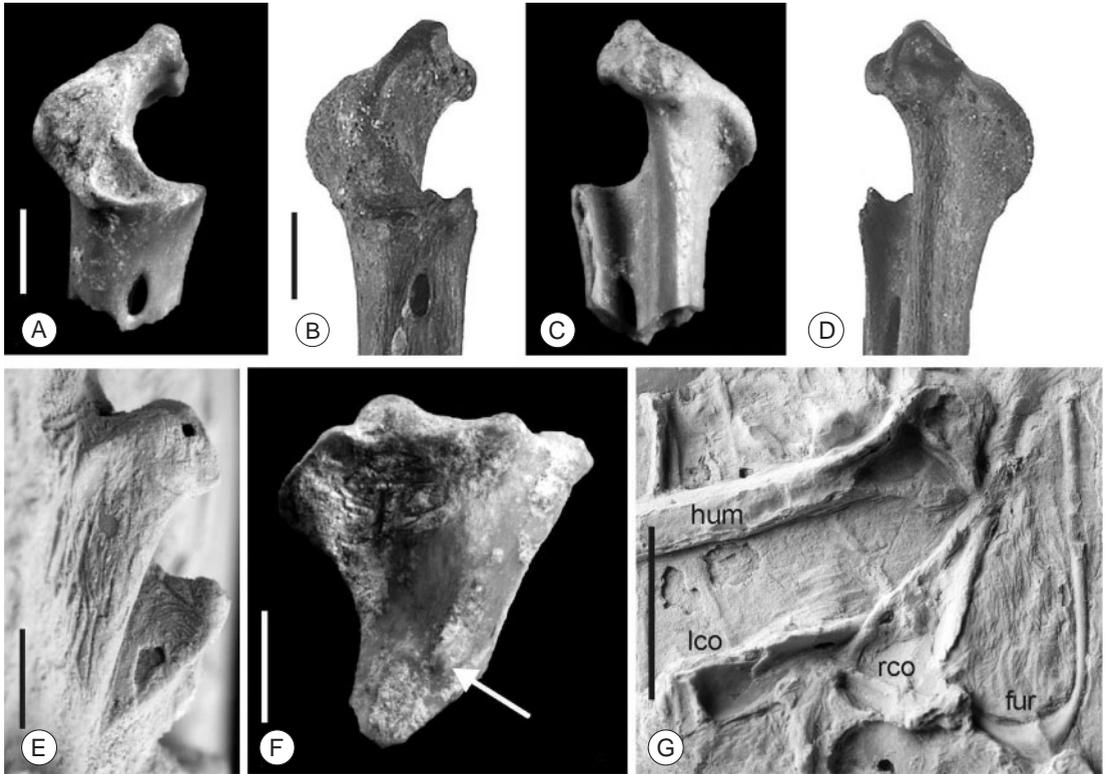


Figure 2. The newly described rail cf. *Belgirallus oligocaenus* from the early Oligocene (Rupelian) of Hofheim-Wallau, isolated extremitas omalis of the left coracoideum in dorsal (A) and ventral (C) view (HLMD-WT 238c), in comparison to the dorsal (B) and ventral (D) aspect of the left coracoideum of *Belgirallus oligocaenus* Mayr & Smith 2001 from the early Oligocene of Belgium (IRScNB Av 57); (E) extremitas omalis of the right coracoideum in ventral view (HLMD-WT 238a); (F) isolated extremitas cranialis of the right scapula, facies medialis (HLMD-WT 238d); (G) furcula in caudal view and extremitates sternales of left and right coracoideum in dorsal view (HLMD-WT 238b). Abbreviations: fur – furcula; hum – right humerus; lco – extremitas sternalis of left coracoideum; rco – extremitas sternalis of right coracoideum. The white arrow in F points to a tubercle which is an apomorphy of Rallidae. Specimens in E and G were coated with ammonium chloride; scale bars equal 2 mm.

(HLMD-WT 238b, Fig. 2). In concordance with other Rallinae but contrary to *Himantornis* (Olson 1973a), there are no pneumatic foramina on the dorsal surface of the extremitas sternalis.

The extremitas cranialis of the right scapula is preserved as an isolated bone. It bears a tubercle on its costal surface which is an apomorphy of Rallidae (Fig. 2); in the fossil this tubercle is small as in *Aramides* and *Gallinula*, whereas it is very prominent in, e.g., *Rallus*, *Laterallus*, and *Pardirallus*. As in extant Rallidae and Heliornithidae, the acromion slants towards the lateral surface of the

bone. As in most other rails but contrary to *Pardirallus maculatus*, there is no fossa on the costal surface of the acromion. The tubercle between the acromion and the tuberculum coracoideum is small (larger in *P. maculatus*).

The caudal two thirds of the sternum are visible in ventral view in HLMD-WT 238a (Fig. 1B), the right portion of the cranial end is preserved in HLMD-WT 238b (Fig. 1A). As in extant Rallidae, the corpus sterni is elongate and narrow, with two incisions in its caudal margin, and the trabecula mediana is of triangular shape (Fig. 3). The distal

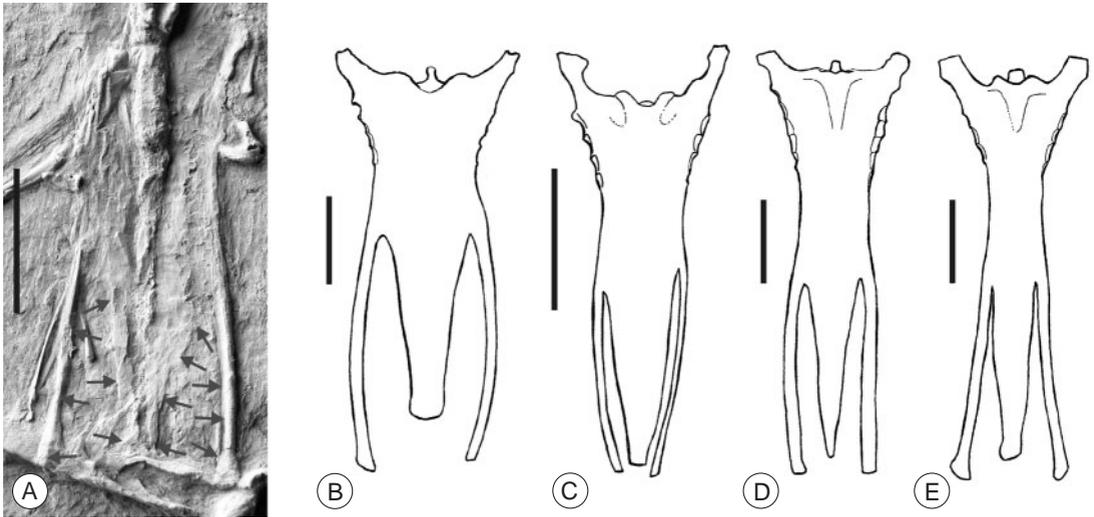


Figure 3. The newly described rail cf. *Belgirallus oligocaenus* from the early Oligocene (Rupelian) of Hofheim-Wallau (HLMD-WT 238a), sternum (A) in comparison to the ventral view of the sterna of (B) Spot-flanked Gallinule *Gallinula melanops*, (C) Spotted Rail *Pardirallus maculatus*, (D) Rufous-sided Rail *Laterallus melanophaius*, and (E) Water Rail *Rallus aquaticus*. The black arrows indicate the incisurae laterales. Specimen in A is coated with ammonium chloride. Scale bars equal 10 mm.

end of the trabeculae laterales forms a small, knob-like broadening. The corpus sterni is similar in its proportions to that of *Gallinula chloropus*, although the incisions are less deep, measuring only slightly more than one third of the length of the sternum (half of its length in *Gallinula chloropus*) (Fig. 3). The trabecula mediana reaches almost as far caudally as the trabeculae laterales.

As far as morphological details of these bones are visible, humerus, ulna, carpometacarpus, and the other wing elements closely resemble the corresponding bones of extant rails, which show little morphological variation. Unfortunately, the distal end of the humerus is too incompletely preserved for meaningful comparisons with the distal humerus of the Belgian specimens of *Belgirallus*. The ulna is much shorter than the tarsometatarsus, whereas it is as long as or longer than the tarsometatarsus in *Pardirallus*, *Crex*, and *Fulica* (Table 1).

On both slabs the pelvis is visible in lateral view. It exhibits a prominent laterally protruding flange in the midsection of the crista dorsolateralis ilii, which is an apomorphy of Rallidae (Fig. 4). The

morphology of the alae praeacetabulares ilii corresponds with that of terrestrial rails in which the crista iliaca dorsalis is complete and fuses with the crista spinosa synsacri. By contrast, in the aquatic *Gallinula* and *Fulica* (and also, as an exception, in the terrestrial *Porzana porzana*), the crista iliaca dorsalis is reduced and exhibits a concave margin.

The tibiotarsus is the longest limb element and, as in most extant Rallidae, measures about 1.5 times the length of the tarsometatarsus. Also as in extant Rallidae, the crista cnemialis cranialis is very large and strongly cranially protruding (Fig. 4). In its shape this crest resembles that of, e.g., *Aramides saracura*, whereas in *Fulica* and, to a lesser degree, *Gallinula*, which use the feet for propulsion, the crista cnemialis cranialis protrudes more strongly in proximal direction. There is no prominent tubercle latero-distal to the pons supratendineus (see Mayr & Clarke 2003: figure 9G), which occurs in *Aramides*, but, according to the figures in Milne-Edwards (1867–71) (see plate 104, figure 18) is absent in the early Miocene *Palaeoaramides* Lambrecht 1933.

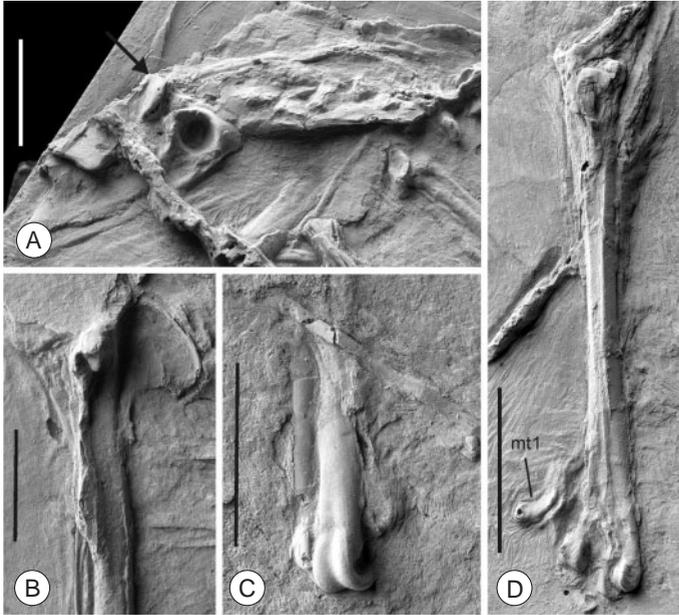


Figure 4. Selected skeletal elements of the new rail cf. *Belgirallus oligocaenus* from the early Oligocene (Rupelian) of Hofheim-Wallau: (A) pelvis in right lateral view (HLMD-WT 238b); (B) proximal end of right tibiotarsus in craniolateral view (HLMD-WT 238b); (C) distal end of right tarsometatarsus in dorsal view (HLMD-WT 238a); (D) right tarsometatarsus in plantar view (HLMD-WT 238b). Abbreviation: mt1 – os metatarsale I. The black arrow in A indicates the prominent laterally protruding flange in the midsection of the crista dorsolateralis ilii, which is an apomorphy of Rallidae. Specimens are coated with ammonium chloride. Scale bars equal 10 mm.

The tarsometatarsus (Fig. 4) is of similar proportions to that of *Gallinula chloropus*. It is less elongated than in, e.g., *Himantornis* and *Aramides* and stouter than in *Aramides flavirostra*. The bone does not exhibit the derived morphology of the tarsometatarsus of *Porphyrio* (e.g. Olson 1973b: p. 26), in which the shaft is more flattened dorsoventrally and the margo medialis very narrow. The hypotarsus exhibits the characteristic ‘rallid’ morphology in that there is a prominent crista lateralis, whereas the crista medialis is greatly reduced. As in other Rallinae but contrary to *Himantornis*, the trochlea metatarsi II is much shorter than the trochlea metatarsi IV, its distal end reaching only slightly beyond the base of the latter.

In HLMD-WT 238a, an ossified tendon is preserved which may have ran along the dorsal side of the tarsometatarsus (Fig. 1B).

As in extant Rallinae, the three anterior toes and the hindtoe are very long (Fig. 5); the third toe measures about the length of the tarsometatarsus, the second and fourth toes are somewhat shorter and have about the same length. By contrast, the toes of *Himantornis* are considerably shorter (Fig. 5), a feature not mentioned by earlier

authors (Olson 1973a, Livezey 1998). The morphology of the phalanges unguales and os metatarsale I corresponds to that of extant Rallidae (e.g., *Aramides saracura*).

DISCUSSION

The fossil specimen closely corresponds to extant rails in its osteology. It is unequivocally identified as a rail by, e.g., its derived limb proportions (very long toes and short ulna), and the derived morphology of the sternum (very elongated and narrow with two deep incisions) and the pelvis (with prominent, laterally protruding flange in midsection of crista dorsolateralis ilii).

HLMD-WT 238 was a medium-sized species, about the size of the extant Spot-flanked Gallinule, *Gallinula melanops*, or the Water Rail, *Rallus aquaticus* (Table 1). In size and morphology it corresponds well with *Belgirallus oligocaenus* Mayr & Smith 2001 (see measurements above). Assignment to *B. oligocaenus* is, however, tentative, as the preservation of the specimens does not allow detailed comparisons, and as only few skeletal

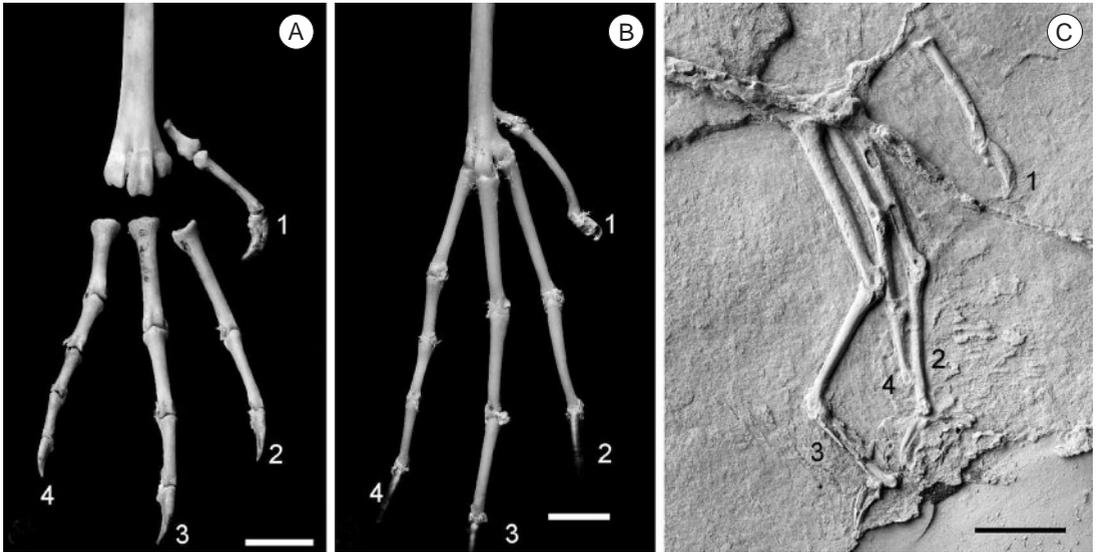


Figure 5. Right feet of selected species: (A) Nkulengu Rail *Himantornis haematopus* (Himantornithinae); (B) Common Moorhen *Gallinula chloropus* (Rallinae); (C) the new rail cf. *Belgirallus oligocaenus* from the early Oligocene (Rupelian) of Hofheim-Wallau (HLMD-WT 238a). The toes are numbered. Specimen in C is coated with ammonium chloride. Scale bars equal 10 mm.

elements are known from the Belgian specimens of *B. oligocaenus* (Mayr & Smith 2001).

Based on foot morphology, HLMD-WT 238 can be assigned to the Rallinae sensu Olson (1973a), as comparisons with Heliornithidae, Psophiidae, the extinct Parvigruidae (Mayr 2005b), Aramidae and Gruidae indicate that the short toes of *Himantornis* (Fig. 5) are plesiomorphic for rails. Owing to the great osteological similarity of rails and the poorly resolved relationships between the extant taxa, it is however not possible to further assign the fossil specimen to any subclade within Rallinae.

In limb proportions, the fossil species corresponds fairly well with the Black Crane, *Amaurornis flavirostra*. Judging from its wider sternum, the body of HLMD-WT 238 was not as strongly medio-laterally compressed as in the Water Rail *Rallus aquaticus*, which may indicate that the fossil species was not reed-dwelling. As exemplified by the morphology of the pelvis and proximal tibio-tarsus, HLMD-WT 238 lacks adaptations for an aquatic way of living, such as found in coots and gallinules. However, although the fossil species is

clearly distinguished from any extant European rallid taxon, it may well be on the stem lineage of a clade including one or more of these.

HLMD-WT 238 provides an early Oligocene minimum age for the divergence between *Himantornis* and Rallinae. The presence of rails in the early Oligocene further implies the existence of their sister group, the Heliornithidae, by that time, although the earliest known fossil record of sun-grebes is from the middle Miocene (Olson 2003). As noted above, stem lineage representatives of the taxon (Aramidae + Gruidae) are also known from the early Oligocene (Mayr 2005b).

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SAMENVATTING

Fossiele vondsten van rallen (Rallidae) zijn schaars, en gebaseerd op incomplete of slecht gefossiliseerde resten. Dit stuk beschrijft de vondst van een ral gedaan tijdens de aanleg van een nieuwe treinverbinding bij Hofheim-Wallau, Hessen, Duitsland. Het fossiele skelet is compleet op de schedel na, en zeer goed geconserveerd. De ral leefde tijdens het vroege Oligoceen (30–33 miljoen jaar geleden). De goede conservatie laat een eenduidige plaatsing binnen de ralachtigen (Rallinae) toe, o.a. zichtbaar in de typische morfologie van de poten (lange tenen met korte ulna). Het ontbreken van morfologische aanpassingen aan een meer aquatische levenswijze, zoals bij meerkoeten *Fulica* spp. en waterhoentjes *Gallinula* spp., duidt op een levenswijze aan de waterrand. Deze ral was ongeveer zo groot als een Waterral *Rallus aquaticus*, maar had een duidelijk bredere bouw (zichtbaar in het bredere sternum). Er zijn een paar overeenkomsten met een Oligoceen fossiel skelet van een ral gevonden in België (*Belgirallus oligocaenus*). Maar omdat deze laatste vondst zeer incompleet is, kan slechts geconcludeerd worden dat de hier beschreven soort identiek of nauw verwant is aan de soort gevonden in België. (DH)

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