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Phylogenetic relationships of the early Tertiary Messel rails (Aves, Messelornithidae)

With 5 Text-figures

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Abstract

Messel rails (Messelornithidae) are among the best represented fossil birds and are considered to be the sister taxon of the extant South American sunbittern (Eurypygidae). However, it is shown that the original description of these birds contains several misinterpretations and that the presumed synapomorphies of the taxon (Messelornithidae + Eurypygidae) are not present in Messel rails. Moreover, it is generally assumed that the closest extant relative of sunbitterns is the New Caledonian kagu (Rhynochetidae), and Messel rails lack significant derived characters supporting monophyly of the taxon (Rhynochetidae + Eurypygidae). Derived characters are presented which support sister group relationship between Messelornithidae and the taxon (Rallidae + Heliornithidae).

Key words: Aves, Eocene, Messelornithidae, phylogenetic relationships

Kurzfassung

Messelrallen (Messelornithidae) zählen zu den häufigsten fossilen Vögeln und werden für das Schwestertaxon der rezenten Sonnenrallen (Eurypygidae) gehalten. Die Originalbeschreibung dieser Vögel enthält allerdings einige Fehlinterpretationen und die mutmaßlichen Synapomorphien des Taxons (Messelornithidae + Eurypygidae) konnten für die Messelrallen nicht bestätigt werden. Es wird darüber hinaus im allgemeinen angenommen, daß der nächste lebende Verwandte der Sonnenrallen der neukaledonische Kagu (Rhynochetidae) ist und Messelrallen fehlen wichtige Synapomorphien des Taxon (Rhynochetidae + Eurypygidae). Abgeleitete Merkmale werden beschrieben, die eine Schwestergruppenbeziehung zwischen den Messelornithidae und dem Taxon (Rallidae + Heliornithidae) begründen.

Introduction

Messel rails (Messelornithidae) are by far the most abundant birds in the Middle Eocene fossil site Messel in Germany and are among the early Tertiary birds with the best fossil record in general. Based on several hundred articulated skeletons of *Messelornis cristata* from Messel and on a skeleton of *M. nearctica* from the Green River Formation (Wyoming, USA),

the osteology of these birds was studied in detail by HESSE (1988a, 1988b, 1990, 1992). MOURER-CHAUVIRÉ (1995) further described isolated, three-dimensionally preserved bones of the Messelornithidae from the early Tertiary of France which she assigned to two new taxa, *M. russelli* and *Itardiornis hessae*.

HESSE (1990) considered Messel rails to be the sister taxon of the modern sunbittern *Eurypyga helias* which today

only occurs in South America and constitutes the sole living representative of the "gruiform" taxon Eurypygidae. Sister group relationship between Messel rails and the sunbittern has subsequently been widely accepted (e.g., PETERS 1991, MOURER-CHAUVIRÉ 1995, FEDUCCIA 1996, CRACRAFT 2001) and also resulted from a cladistic analysis by LIVEZEY (1998), although MOURER-CHAUVIRÉ (1995: 101) noted a "certain amount of parallelism with the family Rallidae [rails]".

The phylogenetic relationships within the probably polyphyletic "gruiform" birds are poorly understood, but most authors consider the sunbittern to be the sister taxon of the New Caledonian kagu (Rhynochetidae) (e.g., CRACRAFT 1982, HESSE 1990, HOUDE et al. 1997, LIVEZEY 1998, MAYR & ERICSON in press; contra SIBLEY & AHLQUIST 1990, LIVEZEY & ZUSI 2001). As HOUDE et al. (1997: 141) noted, monophyly of the taxon (Messelornithidae + Eurypygidae) would "place peculiar Amazonian and New Caledonian distributions" of Eurypygidae and Rhynochetidae into perspective.

HESSE's (1990) study of the Messelornithidae is certainly one of the most detailed descriptions of the osteology of a Tertiary avian species, but there are some misinterpretations and inaccuracies in her descriptions (see below). Moreover, although she emphasized the differences between Messel rails and true rails, she did not make comparisons with finfoots (Heliornithidae) which are considered by many authors to be the sister taxon of the Rallidae (e.g., LIVEZEY 1998, MAYR & ERICSON in press; see also HOUDE 1994). Messel rails further lack significant derived characters shared by Eurypygidae and Rhynochetidae (see below).

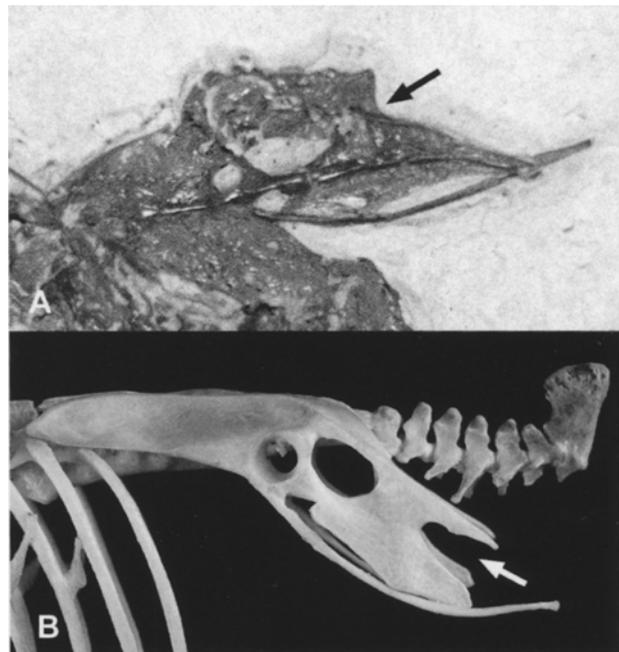
The phylogenetic affinities of the Messelornithidae are reevaluated in this study and evidence is presented that these birds are more closely related to rails and finfoots than to sunbittern and kagu.

The fossil specimens are deposited in Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF) and the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Anatomical terminology follows BAUMEL & WITMER (1993).

Evidence for monophyly of the taxon (Messelornithidae + Eurypygidae)

HESSE (1990: fig. 15) listed two characters as putative synapomorphies of the taxon (Rhynochetidae + (Eurypygidae + Messelornithidae)): (1) pelvis with deep incisura marginis caudalis and (2) crista nuchalis sagittalis of cranium reaching dorsally beyond crista nuchalis transversa, both cristae forming a platform-like triangular surface.

I could not confirm the presence of a deep incisura marginis caudalis in the specimens of *Messelornis cristata* available to me (e.g., SMF-ME 2380). Even if the structures HESSE (1990: pl. 6, fig. 18) identified in one, poorly preserved specimen of *M. cristata* as incisurae margines caudales were such incisions, these would be of quite different shape to the corresponding structures in modern Eurypygidae and Rhynochetidae in which, contrary to the specimen figured by HESSE, the spinae dorsolaterales ilii reach almost as far caudally as the processus terminalis ischii. A new and recently identified specimen of *Messelornis nearctica* (text-fig. 1) shows that the pelvis of this species also lacks deep incisurae margines caudales (the pelvis of the holotype which



Text-fig. 1. Pelvis in comparison. A) *Messelornis nearctica* HESSE 1992, newly identified specimen from the Green River Formation, Wyoming, USA (USNM 776273), B) *Eurypyga helias* (Eurypygidae). In contrast to modern Eurypygidae and Rhynochetidae, the caudal margin of the pelvis of *Messelornis nearctica* bears no deep incisura marginis caudalis (arrows). Not to scale.

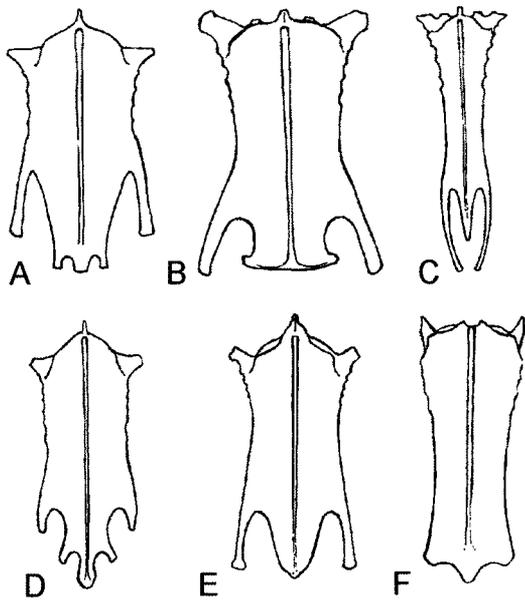
was figured by HESSE 1992: fig. 8 is too fragmentarily preserved to allow any detailed description).

I also cannot duplicate the second character which was not illustrated by HESSE (1990), and find the corresponding area of the skull of Eurypygidae and Rhynochetidae to be very different. Moreover, its presence in *Messelornis cristata* appears to have been based on the skull she figured on plate 5, figure 16 (SMF-ME 727) which actually is not from a Messel rail but from the stem group psittaciform *Pseudastur macrocephalus* (compare with MAYR 2002: fig. 1b).

Other characters HESSE (1990: fig. 15) listed in order to support monophyly of Rhynochetidae, Messelornithidae, and Eurypygidae were considered by her to be either of uncertain polarity (configuration of condyles of processus mandibularis of quadrate, relative length of pterygoids, and extent of caudoventral protrusion of condylus occipitalis) or plesiomorphic (absence of torsion of tarsometatarsus).

Monophyly of the taxon (Eurypygidae + Messelornithidae) was established with a single character of uncertain polarity, the shape of the sternum which HESSE (1990) considered to be short and wide in both taxa, not mediolaterally tapered, and with several caudal incisions and trabeculae in Messelornithidae and Eurypygidae. I cannot find any significant derived similarities shared by the sterna of Messelornithidae and Eurypygidae (text-fig. 2).

LIVEZEY (1998: tab. 2) listed eleven synapomorphies of his Eurypygae, i.e. the taxon (Rhynochetidae + (Eurypygidae + Messelornithidae)), five of which were coded as unknown for the Messelornithidae in the character matrix (LIVEZEY 1998: chs. 35, 38, 105, 297, 376). None of the remaining six characters convincingly supports a closer relationship be-

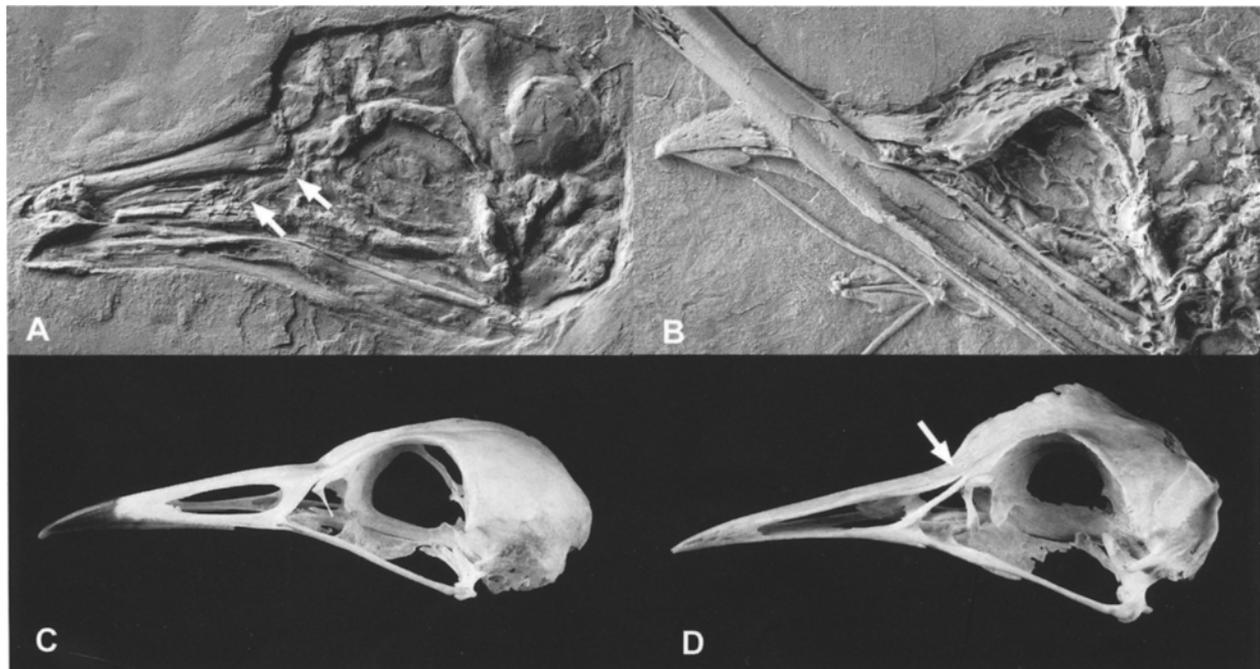


Text-fig. 2. Sternum in comparison. A) *Messelornis cristata* HESSE 1988 (“Gruiformes”, Messelornithidae, after specimens SMF-ME 1132a+b, SMF-ME 10942, SMF-ME 10958), B) *Heliornis fulica* (“Gruiformes”, Heliornithidae), C) *Aramides saracura* (“Gruiformes”, Rallidae), D) *Dromas ardeola* (Charadriiformes, Dromadidae), E) *Eurypyga helias* (“Gruiformes”, Eurypygidae), F) *Rhynochetos jubatus* (Rhynochetidae). Not to scale.

tween Messel-rails, kagu and sunbittern, so much the more since some were incorrectly coded in the character matrix. The “significant anterodorsal elongation and me-

diodorsal deflection” of the processus orbitalis of the quadrate (LIVEZEY 1998: character 50) cannot be verified in the Messelornithidae in which the rostral portion of the quadrate generally is very poorly preserved. Likewise, the “essentially flat” ventrocaudal surface of the os metacarpale majus of the carpometacarpus (LIVEZEY 1998: character 250) and the pronounced dorsoventral curvature of the corpus ilii (LIVEZEY 1998: character 271) cannot be seen in the flattened and crushed skeletons from Messel; at least the latter character is further absent in *Messelornis nearctica* (text-fig. 1). A deep fovea carpalis cranialis on the proximal end of the carpometacarpus (LIVEZEY 1998: character 240) is absent in both, Rhynochetidae and Messelornithidae (concerning the latter, see MOURER-CHAUVIRÉ 1995: pl.1, fig. 17). A pronounced dorsoventral curvature of the shaft of the humerus (LIVEZEY 1998: character 217) is also found in some Rallidae (e.g., *Aramides saracura*) and many other birds including the palaeognathous Lithornithidae (see HOUDE 1988) and might well be plesiomorphic within neornithine birds. The deep depressio ligamentosis on the distal half of the radius “extending almost to midpoint of corpus, producing a comparatively flattened facies ventralis” (LIVEZEY 1998: character 232) cannot be delimited against the very similar condition in some rails (e.g., *Aramides saracura*) and other birds (e.g., the charadriiform *Burhinus oedicnemus*).

The single character which LIVEZEY (1998: tab. 2) listed as a synapomorphy of his Eurypygoidea, i.e. the taxon (Messelornithidae + Eurypygidae) is absent in the Messelornithidae (“deep ovate depression” on the facies costalis of the acromion of the scapula – the absence of this character in *Messelornis cristata* is visible in specimen SMF-ME 10942).

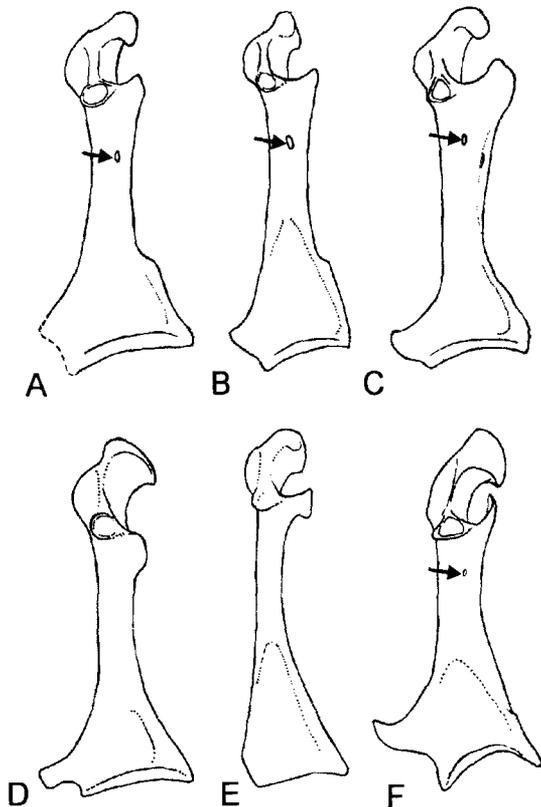


Text-fig. 3. Skull in comparison. A) *Messelornis cristata* HESSE 1988 (“Gruiformes”, Messelornithidae, after specimen SMF-ME 1766a), B) *Messelornis cristata* (SMF-ME 1132a), C) *Heliornis fulica* (“Gruiformes”, Heliornithidae), D) *Rhynochetos jubatus* (“Gruiformes”, Rhynochetidae). The arrows in A and D indicate the caudal end of the narial opening. Not to scale; the fossil specimens were coated with ammonium chloride.

Evidence for monophyly of the taxon (Eurypygidae + Rhynochetidae) to the exclusion of the Messelornithidae

Sister group relationship between Eurypygidae and Rhynochetidae, to the exclusion of the Messelornithidae, is supported by the following derived characters:

- (1) Nostrils schizorhinal. HESSE (1990) and LIVEZEY (1998) considered the nostrils of Messelornithidae to be schizorhinal but I cannot confirm this observation. Those specimens in which the nasofrontal hinge is well enough preserved show, that the caudal end of the narial opening of Messel rails does not extend behind this hinge (text-fig. 3) and is similar to that of *Rallus* spp. (Rallidae).
- (2) Coracoid without foramen nervi supracoracoidei (text-fig. 4). A foramen nervi supracoracoidei is present in most Mesozoic non-neornithine birds and its presence within Neornithes is plesiomorphic. Curiously, this clear-cut and phylogenetically important character was not included in the analysis of LIVEZEY (1998). HESSE (1990: 56) incorrectly considered a foramen nervi supracoracoidei to be present in extant Eurypygidae.



Text-fig. 4. Coracoid in comparison. A) *Messelornis cristata* HESSE 1988 ("Gruiformes", Messelornithidae, mainly reconstructed after specimen SMF-ME 10942), B) *Pardirallus maculatus* ("Gruiformes", Rallidae), C) *Heliornis fulica* ("Gruiformes", Heliornithidae), D) *Eurypyga helias* ("Gruiformes", Eurypygidae), E) *Rhynochetos jubatus* ("Gruiformes", Rhynochetidae), F) *Dromas ardeola* (Charadriiformes, Dromadidae). The arrows indicate the foramen nervi supracoracoidei. Not to scale.

- (3) Several thoracic vertebrae fused to a notarium. As also noted by HESSE (1990), the Messelornithidae lack a notarium, the presence of which unquestionably is derived within Neornithes.
- (4) Pelvis with very deep incisura marginis caudalis. See above, concerning the absence of this unquestionably derived feature in the Messelornithidae. The character was also considered a synapomorphy of the taxon (Eurypygidae + Rhynochetidae) by CRACRAFT (1982). Although LIVEZEY (1998: character 265) coded it as present in only Messelornithidae (incorrectly, see above), Eurypygidae, and Rhynochetidae, it was for some reason not listed as a diagnostic apomorphy of his Eurypygidae (LIVEZEY 1998: table 2).

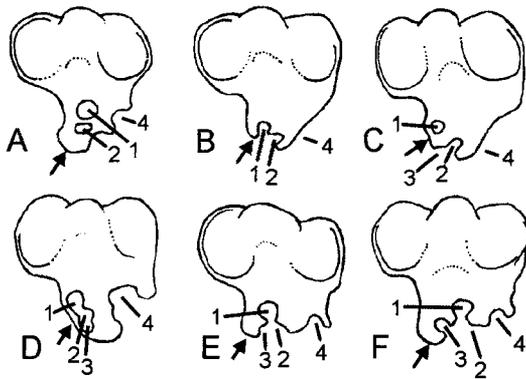
Evidence for monophyly of the taxon (Messelornithidae + (Rallidae + Heliornithidae))

Monophyly of a taxon including Messelornithidae, Heliornithidae, and Rallidae is supported by the following derived characters:

- (1) Coracoid, processus procoracoideus continuous with a sharp crest along medial margin of shaft. This unquestionably derived character occurs in few other taxa (e.g., Charadriiformes and Psophiidae) and is absent in Eurypygidae and Rhynochetidae. It corresponds to the crista procoracoidei of LIVEZEY (1998: character 189) which this author incorrectly considered to be absent in the Messelornithidae.
- (2) Humerus without foramina pneumatica at bottom of fossa pneumotricipitalis (contra HESSE 1990 and LIVEZEY 1998). The presence or absence of foramina pneumatica cannot be verified in the flattened skeletons of *M. cristata* and *M. nearctica* and according to my reinvestigation of the corresponding specimens, the structures figured by HESSE (1990: pl. 8, fig. 29) and HESSE (1992: fig. 4) do not represent such foramina. The absence of foramina pneumatica can be verified on the three-dimensionally preserved bones of the Messelornithidae from the Quercy fissure fillings (MOURER-CHAUVIRÉ 1995). The humerus lacks pneumatic foramina in few other avian taxa, most notably charadriiform birds and several diving birds (Gaviidae, Podicipedidae, some Anatidae).
- (3) Tarsometatarsus, hypotarsus, furrow/canal for tendon of musculus flexor perforatus digiti II (text-fig. 5, furrow/canal no. 2) marked and laterally bordered by a proximodistally long and plantarly protruding crista lateralis. The tendon of musculus flexor perforatus digiti II is situated in a marked furrow/canal in very few other avian taxa, e.g. parrots (Psittaciformes) and songbirds (Passeriformes), none of which appears to be closely related to the Messelornithidae.

Sister group relationship between Rallidae and Heliornithidae to the exclusion of the Messelornithidae is supported by:

- (1) Hypotarsus with crista medialis reduced to a proximodistally short osseous lamella. This character is unique to Rallidae and Heliornithidae.



Text-fig. 5. Hypotarsus of right tarsometatarsus in comparison. A) *Itardiornis hessae* MOURER-CHAUVIRÉ 1995 ("Gruiformes", Messelornithidae, after MOURER-CHAUVIRÉ 1995: pl. 2, fig. 31), B) *Himantornis haematopus*, ("Gruiformes", Rallidae), C) *Aramides saracura* ("Gruiformes", Rallidae), D) *Heliornis fulica* ("Gruiformes", Heliornithidae), E) *Eurypyga helias* ("Gruiformes", Eurypygidae), F) *Vanellus vanellus* (Charadriiformes, Charadriidae). The numerals indicate the furrows/canals for the tendons of: 1 – musculus flexor digitorum longus, 2 – musculus flexor perforatus digiti II, 3 – musculus flexor perforans et perforatus digiti II, 4 – musculus flexor hallucis longus. Homology of tendineal furrows/canals was verified against spirit specimens for Rallidae and Charadriidae (J. BOSCH, pers. comm.) and deduced from position of bony canals for the other taxa. Note that identification of tendineal furrows/canals in the Charadriidae strongly departs from STRAUCH (1978: fig. 29). The arrows point to the crista medialis hypotarsi. Not to scale.

Discussion

As has been detailed above, none of the characters listed by either HESSE (1990) or LIVEZEY (1998) convincingly supports a closer relationship between Messel rails and the sunbittern. Instead, previously unrecognized characters are presented which suggest a sister group relationship between Messel rails and the taxon (Heliornithidae + Rallidae).

As indicated by their common name, the skeleton of Messel rails shows some overall similarity to that of true rails. However, there are also significant osteological differences between Messelornithidae and Rallidae or Heliornithidae. Messel rails probably were rather unspecialized terrestrial birds with moderate flight capabilities (see HESSE 1990: 115). Probably as an adaptation to their habitat, mainly dense clutter of reed, rails have a much more mediolaterally compressed body, reflected osteologically by a much narrower sternum and pelvis, and much more elongated toes. The poorly known finfoots on the other hand are highly aquatic birds and distinctly differ from Messel rails in their apomorphic pelvis and hind limb morphology. Like the modern sungrebe, *Heliornis fulica*, Messel rails had a long tail (HESSE 1990: pl. 2, fig. 5) which differs from the short tail of true rails and the stiffened tail feathers of the heliornithid taxa *Heliopais* and *Podica*.

The early Tertiary fossil record of "gruiform" birds in general is still very scanty. There is no reliable record of true rails (Rallidae) from Eocene deposits (OLSON 1985) and the earliest European fossils of these birds are from the lowermost Oligocene (MAYR & SMITH 2001). The Heliornithidae have no Tertiary fossil record at all, and the same is true for Eurypygidae and Rhynochetidae. It is to be hoped that future findings will shed more light on the evolution of these and other "gruiform taxa".

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