



General palaeontology, systematics and evolution (Vertebrate palaeontology)

The Eocene *Juncitarsus* – its phylogenetic position and significance for the evolution and higher-level affinities of flamingos and grebes



Le Juncitarsus éocène – sa position phylogénétique et sa signification dans l'évolution et les affinités de niveau élevé des flamants et des grèbes

Gerald Mayr

Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

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ABSTRACT

The Early Eocene *Juncitarsus* was described as one of the earliest fossil flamingos, and played a critical role in the hypothesis of a charadriiform origin of Phoenicopteriformes. It has been noted that phoenicopteriform affinities of *Juncitarsus* conflict with the recently proposed sister group relationship between flamingos and the morphologically very divergent grebes (Podicipédiformes), but a detailed assessment of the evolutionary significance of *Juncitarsus* in light of this new hypothesis has not yet been performed. Here, the affinities of *Juncitarsus* are reviewed, and its position as sister group of the clade (Phoenicopteriformes + Podicipédiformes) is affirmed. The osteology of *Juncitarsus* suggests that swimming adaptations evolved in the stem lineage of this latter clade after the divergence of *Juncitarsus*. Charadriiformes remain among the candidate taxa for the closest extant relatives of flamingos and grebes, but more data are needed for well-supported phylogenetic hypotheses.

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R É S U M É

Le Juncitarsus de l'Éocène inférieur est l'un des flamants fossiles les plus précoces ; il a joué un rôle critique dans l'hypothèse de l'origine charadriiforme des Phœnicoptérimorphes. Il a été remarqué que les affinités phœnicoptérimorphes de *Juncitarsus* sont en désaccord avec la relation récemment proposée de groupe frère entre les flamants et les grèbes (Podicipédiformes), un groupe morphologiquement très différents. Néanmoins, une évaluation détaillée de la signification de *Juncitarsus* n'a pas encore été effectuée. Les affinités de *Juncitarsus* sont ici revues et sa position en tant que groupe frère du clade (Phœnicoptérimorphes + Podicipédiformes) est affirmée. L'ostéologie de *Juncitarsus* suggère que les adaptations à la natation ont évolué dans la lignée de ce clade après la divergence de *Juncitarsus*. Les Charadriiformes restent parmi les taxons candidats pour être considérés comme les plus proches apparentés vivants des flamants et grèbes, mais des données plus nombreuses sont nécessaires pour des hypothèses phylogénétiques mieux étayées.

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E-mail address: gerald.mayr@senckenberg.de

1. Introduction

Molecular analyses congruently and strongly support sister group relationship between the long-legged, filter-feeding flamingos (Phoenicopteriformes) and the morphologically very divergent grebes (Podicipediformes), which are foot-propelled diving birds (Fig. 1). A clade including these two taxa was first proposed based on analyses of sequence and DNA-DNA hybridization data (van Tuinen et al., 2001), and is now obtained from most phylogenetic studies of molecular data including the two groups. In addition to multigene analyses of nuclear sequences with comprehensive taxon samplings (Ericson et al., 2006; Hackett et al., 2008; Kimball et al., 2013; McCormack et al., 2013; Yuri et al., 2013), a flamingo/grebe clade resulted, with high support values, from analyses of complete mitochondrial genomes (Morgan-Richards et al., 2008; Pratt et al., 2009), individual nuclear genes such as ZENK (Chubb, 2004), RAG-1 (Ericson et al., 2006: Fig. ESM-2), and myoglobin intron-2 (Ericson et al., 2006: Fig. ESM-3), combined c-myc and RAG-2 sequences (Cracraft et al., 2004: Fig. 27.8), as well as nuclear gap characters (Yuri et al., 2013) and CR1 retroposon data (Suh et al., 2012). Analysis of nuclear β -fibrinogen sequences does not support sister group relationship between Phoenicopteriformes and Podicipediformes, but both taxa result in a “metavian”

clade, which is widely separated from taxa traditionally considered closely related to grebes and flamingos, such as loons (Gaviiformes) or storks (Ciconiidae; Ericson et al., 2006, Fig. ESM-4; Fain and Houde, 2004).

A flamingo/grebe clade was not assumed by early researchers studying the anatomy of these birds (see Olson and Feduccia, 1980; Sibley and Ahlquist, 1990), and is not recovered in numerical cladistic analyses of large morphological data sets with a taxon sampling comparable to that of the molecular studies, which consistently unite Podicipediformes with Gaviiformes and place Phoenicopteriformes within “ciconiiform” birds (Livezey and Zusi, 2007; Mayr and Clarke, 2003; Smith, 2010). However, these results are likely to be an artifact of convergence since morphological synapomorphies with a restricted distribution in birds were proposed in support of a flamingo/grebe clade (Manegold, 2006; Mayr, 2004), whereas no sequence data are in concordance with the traditional hypotheses on the affinities of flamingos and grebes. The high congruence of independent molecular data and the existence of morphological synapomorphies make sister group relationship between flamingos and grebes one of the best supported hypotheses concerning the higher-level affinities of neornithine birds, and the few critical nodes (Livezey, 2011; Storer, 2006) are not well founded (Mayr, 2007, 2011a). Sangster (2005: 612) proposed the name *Mirandornithes* for “the least inclusive clade comprising *Phoenicopterus ruber* Linnaeus, 1758 and *Podiceps cristatus* (Linnaeus, 1758)”.

The sister taxon of the flamingo/grebe clade remains elusive, and uncertainty also surrounds the morphology and ecology of the stem species of this clade. Because the extinct phoenicopteriform taxon *Palaelodus*, whose fossil remains are exceedingly abundant in the Early Miocene of Europe, exhibits swimming specializations, it has been assumed that the ancestor of grebes and flamingos was a swimming bird (Mayr, 2004). The skeletal bauplan of *Palaelodus* sharply contrasts, however, with that of *Juncitarsus*, another fossil taxon discussed as an early phoenicopteriform bird. *Juncitarsus* includes two species, *Juncitarsus gracillimus* Olson and Feduccia, 1980 from the Early and Middle Eocene of North America, and *Juncitarsus merkei* Peters, 1987 from the Middle Eocene of North America and Europe, which are known from various postcranial bones and, in the case of *J. merkei*, a largely complete skeleton on a slab (Ericson, 1999; Olson and Feduccia, 1980; Peters, 1987).

Juncitarsus was a very long-legged bird with an elongate and pointed beak unlike that of modern flamingos (Fig. 2), and its stilt-like morphology was considered evidence for an origin of flamingos from a charadriiform, i.e., shorebird-like, ancestor (Olson and Feduccia, 1980; Peters, 1987; see also Ericson, 1999). The taxon lacks, however, derived characters shared by flamingos and grebes, and phoenicopteriform affinities of *Juncitarsus* were first doubted by Cracraft (1981). More recently, it has been suggested that *Juncitarsus* is likely to be the sister taxon of the clade (Phoenicopteriformes + Podicipediformes) (Mayr, 2004, 2009). A detailed examination of the *Juncitarsus* fossils in light of the new hypothesis concerning the relationships of flamingos has, however, not yet been



Fig. 1. A: Black-necked Grebe, *Podiceps nigricollis* (Podicipedidae). B: Andean Flamingo, *Phoenicoparrus andinus* (Phoenicopteridae). Photos: J. Rathgeber.

Fig. 1. A: Grèbe à cou noir, *Podiceps nigricollis* (Podicipedidae). B: Flamant andin, *Phoenicoparrus andinus* (Phoenicopteridae). Photos: J. Rathgeber.



Fig. 2. *Juncitarsus merkei* from the Middle Eocene of Messel in Germany (cast of holotype in the collection of Senckenberg Research Institute Frankfurt, SMF A 295). Photo: A. Vogel.

Fig. 2. *Juncitarsus merkei* de l'Éocène moyen de Messel, Allemagne (moulage d'holotype de la collection du Senckenberg Research Institute, Francfort, SMF A 295). Photo: A. Vogel.

performed, and *Juncitarsus* continues to be assigned to Phoenicopteriformes in recent studies (Agnolin, 2009; Tambussi and DeGrange, 2013).

The affinities of *Juncitarsus* are reviewed in the present study, with the highly congruent and strongly supported molecular results taken as indicative of the correct phylogenetic affinities of flamingos and grebes, and the phylogenetic affinities of *Juncitarsus* being evaluated within that framework. Further evidence is presented for a position of this taxon outside *Mirandornithes* sensu Sangster (2005), and some implications of this phylogeny for the evolution of flamingos and grebes are discussed.

It has not been attempted to evaluate the position of *Juncitarsus* in a numerical cladistic context, as such would only be meaningful if a large number of potentially related taxa were included. The shortcomings of such large-scale

parsimony analyses of morphological data have been discussed elsewhere (Mayr, 2008), and parsimony analyses resulting in a flamingo/grebe clade are exposed to the suspicion of having been constructed in order to support the expected results (Livezey, 2011). Analyses of molecular data are certainly not per se superior to those based on morphological characters, and many of the well-supported avian higher-level clades were first suggested from studies of morphological data (Mayr, 2011a, b). If, however, the strong and highly congruent molecular evidence for a flamingo/grebe clade were to be called into question, one could, in fact, not trust any result of sequence-based analyses, as few other avian clades receive an equally high support in molecular studies.

2. The affinities of *Juncitarsus*

Apart from other derived anatomical features, such as the presence of eleven instead of ten primaries, an outer calcium phosphate layer of the eggshell, and a unique taxon of Cestodes, flamingos and grebes share a number of derived osteological characters. In addition to the characters optimized as synapomorphies of grebes and flamingos in the analysis of Mayr (2004) and those subsequently identified by Manegold (2006), there are previously unrecognized derived characters, which bear on the affinities of *Juncitarsus*. Four synapomorphies support a clade including *Juncitarsus*, Phoenicopteriformes, and Podicipediformes:

- cervical vertebrae with well-developed processus ventrolaterales (Fig. 3; Manegold, 2006). Livezey (2011: 394) assumed that the “process in flamingos illustrated by Manegold (2006) is not homologous with the facies articularis of ‘processus postlateralis’ of grebes, which is associated with a unique insertio accessorius [sic] tendinis m. longus colli ventralis (Zusi and Storer, 1969)”. It is, however, unknown, whether the latter authors did indeed study Phoenicopteriformes with regard to this character, and occurrence of a derived myological feature does not necessarily preclude homology of the osteological structures. In *Juncitarsus*, processus ventrolaterales are present (Fig. 3A);
- humerus with distinct muscle scar at insertion site of musculus scapulohumeralis cranialis (Olson and Feduccia, 1980: Fig. 27; Mayr, 2004: Fig. 2). This character is present in *Juncitarsus*, *Palaelodus*, and Podicipediformes, but only weakly developed in Phoenicopteridae. Livezey (2011: 394) stated that “[t]his impressio insertii [sic] also occurs in loons, whereas the associated muscle is absent in *Phoenicopterus ruber* and most Ciconiiformes (Vanden Berge, 1970), voiding homology and the synapomorphy.” Livezey’s reference to Vanden Berge (1970) is, however, misleading as this latter author did report the muscle in flamingos and wrote that within the studied birds the “muscle was found only in the Ardeidae, *Phoenicopterus chilensis*, and *Phoenicoparrus jamesi*; it is absent in *Phoenicopterus ruber* and in all other ciconiiforms examined” (Vanden Berge, 1970: 305);
- tibiotarsus, distal rim of condylus medialis distinctly notched (Mayr, 2004). Livezey (2001: 394) stated that “[t]his assessment is erroneous”, but this is certainly not

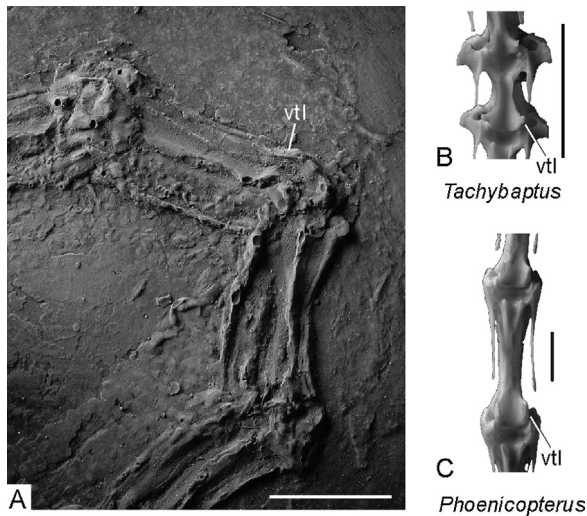


Fig. 3. Cervical vertebrae of **A:** *Juncitarsus merkelii* (Juncitarsidae, cast of holotype, SMF A 295, coated with ammonium chloride) in comparison to the fifth cervical vertebra (ventral view) of **B:** *Tachybaptus ruficollis* (Podicipediformes) and **C:** *Phoenicopterus ruber* (Phoenicopteriformes). Abbreviation: vtl, processus ventrolateralis. Scale bars equal 10 mm.

Fig. 3. Vertèbres cervicales de **A:** *Juncitarsus merkelii* (Juncitarsidae, moulage d'holotype, SMF A 295, recouvert de chlorure d'ammonium, et comparaison avec la cinquième vertèbre cervicale (vue ventrale) de **B:** *Tachybaptus ruficollis* (Podicipédiformes) et **C:** *Phoenicopterus ruber* (Phoenicoptériformes). Abréviations : vtl, processus ventrolateralis. Barres d'échelle = 10 mm.

the case, as shown by Fig. 4D–G. In fact, notching does not only occur on the condylus medialis, but also on the condylus lateralis (Fig. 4). The condylus medialis of *Juncitarsus* also exhibits a notch (Peters, 1987);

- hypotarsus pedicellate, with three well-developed crests (cristae medialis, lateralis and intermedia), which are plantarily fused to form canals in Palaelodidae and Podicipediformes (Fig. 5G–J). Extant Phoenicopteridae only exhibit two hypotarsal crest, which are separated by deep sulci for the flexor tendons. According to the phylogeny proposed in this study (see below), this condition is an apomorphy of Phoenicopteridae. In its proportions, the hypotarsus of *Juncitarsus* closely resembles that of *Palaelodus* (Fig. 5H, I).

The following seven characters are synapomorphies of Mirandornithes to the exclusion of *Juncitarsus*:

- at least four thoracic vertebrae fused and forming a notarium (Mayr, 2004). *Juncitarsus* lacks extensively fused thoracic vertebrae (Olson and Feduccia, 1980; Peters, 1987), and only two vertebrae form a notarium in *J. merkelii* (Fig. 6);
- ulna, tuberculum ligamenti collateralis ventralis greatly elongated (new character; “attachment of the anterior articular ligament” of Olson and Feduccia, 1980: 55). *Juncitarsus* lacks an elongated tuberculum ligamenti collateralis ventralis, the shape of which agrees with the condition found in most neornithine birds (Fig. 5A–C);
- phalanx proximalis digiti majoris craniocaudally narrow (ratio length to craniocaudal width more than 4.5; Mayr,

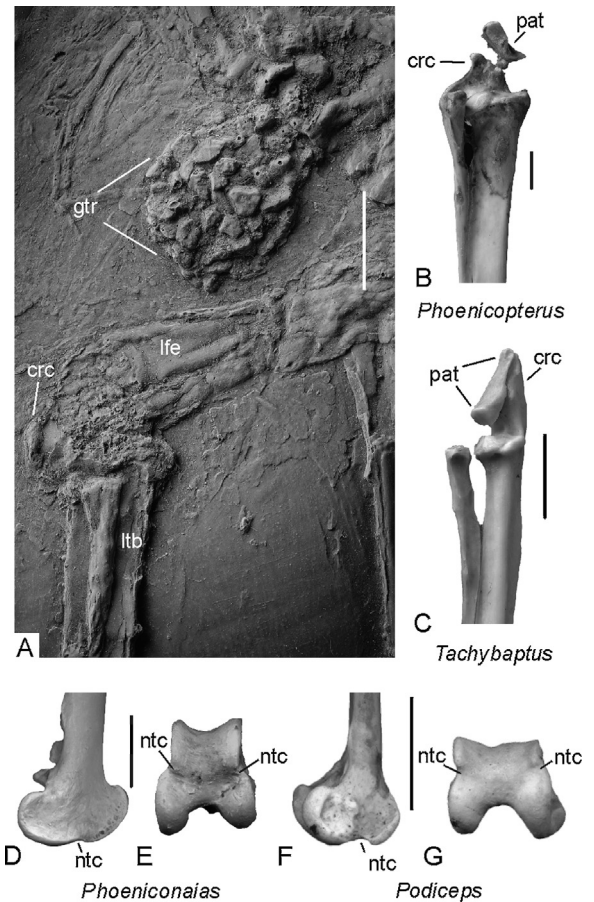


Fig. 4. **A:** Detail of the holotype of *Juncitarsus merkelii* (Juncitarsidae, cast of holotype, SMF A 295, coated with ammonium chloride) with gastroliths and left knee joint in comparison to the proximal end of the left tibiotarsus (caudal view) and patella of **B:** *Phoenicopterus ruber* (Phoenicopteriformes) and **C:** *Tachybaptus ruficollis* (Podicipediformes). **D–G:** distal end of right tibiotarsus of **D, E:** *Phoeniconaias minor* (Phoenicopteriformes) and **F, G:** *Podiceps grisegena* (Podicipediformes) in **D, F:** medial and **E, G:** distal view. Abbreviations: crc, cristae cnemiales; gtr, gastroliths; lfe, left femur; ltb, left tibiotarsus; ntc, notches in distal rims of condyli medialis et lateralis; pat, patella. Scale bars equal 10 mm.

Fig. 4. **A:** Détail de l'holotype de *Juncitarsus merkelii* (Juncitarsidae, moulage d'holotype, SMF A 295, recouvert de chlorure d'aluminium, avec gastrolithes et articulation du genou gauche, en comparaison avec la tibiotarse gauche (vue caudale) et rotule de **B:** *Phoenicopterus ruber* (Phoenicoptériformes) et **C:** *Tachybaptus ruficollis* (Podicipédiformes). **D–G:** Terminaison distale du tibiotarse droit de **D, E:** *Phoeniconaias minor* (Phoenicoptériformes) et **F, G:** *Podiceps grisegena* (Podicipédiformes) en vues médiale (**D, F**) et distale (**E, G**). Abréviations : crc, cristae cnemiales; gtr, gastrolithes; lfe, fémur gauche; ltb, tibiotarse gauche; ntc, encoches dans les bordures distales des condyli medialis et lateralis; pat, rotule. Barres d'échelle = 10 mm.

2004). It has been previously noted (Mayr, 2004) that the phalanx proximalis digiti majoris of *Juncitarsus* is proportionally wider than that of flamingos and grebes, and corresponds in its proportions with the usual condition found in most neornithine birds (Mayr, 2004: Fig. 2);

- patella enlarged (new character) and cristae cnemiales of tibiotarsus projecting markedly beyond proximal articular surfaces. Mayr (2004) noted that Phoenicopteriformes and Podicipediformes share enlarged cristae

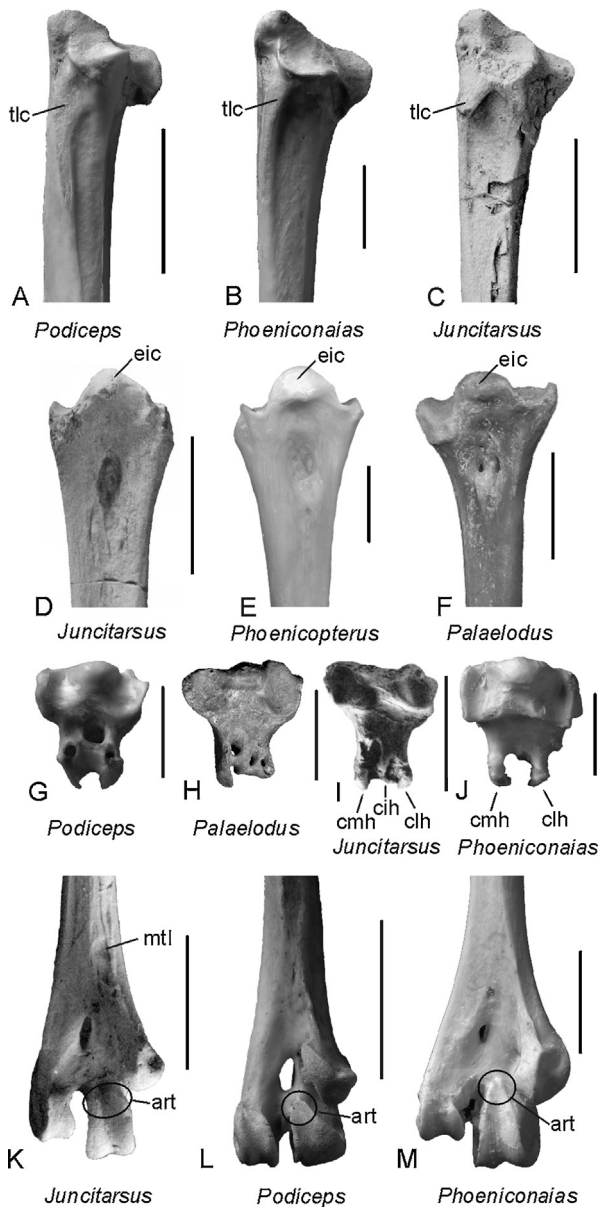


Fig. 5. Proximal end of left ulna of **A:** *Podiceps grisegena* (Podicipediformes), **B:** *Phoeniconaias minor* (Phoenicopteriformes), **C:** *Juncitarsus gracillimus* (Juncitarsidae, from [Olson and Feduccia, 1980](#): Fig. 28C). Proximal end of right tarsometatarsus (cranial view) of **D:** *J. gracillimus* (from [Olson and Feduccia, 1980](#): Fig. 26A), **E:** *Phoenicopterus ruber* (Phoenicopteridae), **F:** *Palaelodus* sp. (*Palaelodidae*, uncatalogued specimen in the collection of Senckenberg Research Institute Frankfurt). Right tarsometatarsus (proximal view) of **G:** *Podiceps cristatus* (Podicipediformes), **H:** *Palaelodus* sp. (specimen as above), **I:** *J. gracillimus* (from [Olson and Feduccia, 1980](#): Fig. 26B; left side, reversed to facilitate comparisons), **J:** *P. minor*. Distal end of left tarsometatarsus (plantar view) of **K:** *J. gracillimus* (from [Olson and Feduccia, 1980](#): Fig. 25E), **L:** *P. grisegena*, **M:** *P. minor*. Abbreviations: art, proximal portion of plantar surface of trochlea metatarsi III (encircled area); cih, crista intermedia hypotarsi; clh, crista lateralis hypotarsi; cmh, crista medialis hypotarsi; eic, eminentia intercotylaris; mtl, fossa metatarsi I; tlc, tuberculum ligamenti collateralis ventralis. Scale bars equal 10 mm; scale bars for *J. gracillimus* are approximate and based on the figures in [Olson and Feduccia \(1980\)](#).

Fig. 5. Terminaison proximale de l'ulna gauche de **A:** *Podiceps grisegena* (Podicipédiformes), **B:** *Phoeniconaias minor* (Phoenicoptérimorphes),

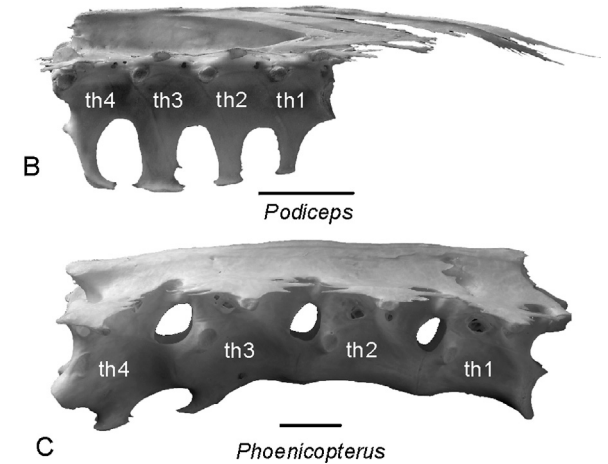
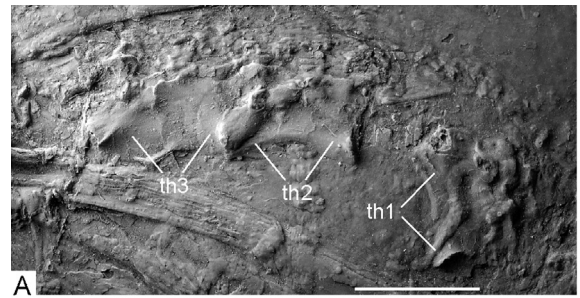


Fig. 6. **A:** Caudal thoracic vertebrae of *Juncitarsus merkei* (Juncitarsidae, cast of holotype, SMF A 295, coated with ammonium chloride) in comparison to the notarium of **B:** *Tachybaptus ruficollis* (Podicipediformes) and **C:** *Phoenicopterus ruber* (Phoenicopteriformes). The thoracic vertebrae are numbered. Scale bars equal 10 mm.

Fig. 6. **A:** Vertèbres thoraciques caudales de *Juncitarsus merkei* (Juncitarsidae, moulage d'holotype, SMF A 295, recouvert de chlorure d'ammonium), en comparaison avec le notarium de **B:** *Tachybaptus ruficollis* (Podicipédiformes) et **C:** *Phoenicopterus ruber* (Phoenicoptérimorphes). Les vertèbres thoraciques sont numérotées. Barres d'échelle = 10 mm.

cnémiales of the tibiotarsus, but it went unnoticed that flamingos also exhibit an enlarged patella ([Fig. 4B, C](#)). The formation of a hypertrophied patella has been listed as a character distinguishing grebes from loons (e.g., [Stolpe, 1935](#)), and an enlarged patella is here considered

C: *Juncitarsus gracillimus* (Juncitarsidae, d'après [Olson et Feduccia, 1980](#), Fig. 28C). Extrémité proximale du tarsométatarsaire droit (vue crâniale) de **D:** *J. gracillimus* (selon [Olson et Feduccia, 1980](#); Fig. 26A), **E:** *Phoenicopterus ruber* (Phoenicopteridae), **F:** *Palaelodus* sp. (*Palaelodidae*, spécimen non répertorié de la collection du Senckenberg Research Institute de Francfort). Tarsométatarsaire droit (vue proximale) de **G:** *Podiceps cristatus* (Podicipédiformes), **H:** *Palaelodus* sp. (spécimen comme plus haut), **I:** *J. gracillimus* (d'après [Olson et Feduccia, 1980](#), Fig. 26B; côté gauche, retourné pour faciliter la comparaison), **J:** *P. minor*. Terminaison distale du tarsométatarsaire gauche (vue plantaire) de **K:** *J. gracillimus* (d'après [Olson et Feduccia, 1980](#); Fig. 25E), **L:** *P. grisegena*, **M:** *P. minor*. Abréviations: art, portion proximale de la surface plantaire de trochlea metatarsi III (zone entourée d'un cercle); cih, crista intermedia hypotarsi; clh, crista lateralis hypotarsi; cmh, crista medialis hypotarsi; eic, eminentia intercotylaris; mtl, fossa metatarsi I; tlc, tuberculum ligamenti collateralis ventralis. Barres d'échelle = 10 mm; les barres d'échelle pour *J. gracillimus* sont approximatives et basées sur les figures in [Olson et Feduccia, 1980](#).

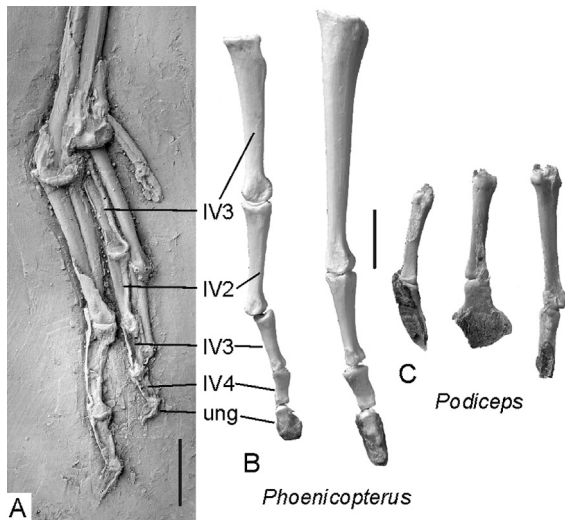


Fig. 7. A: right foot of the holotype of *Juncitarsus merkei* (Juncitarsidae, cast of holotype, SMF A 295, coated with ammonium chloride) in comparison to **B:** the fourth (left) and third (right) toes of *Phoenicopterus ruber* (Phoenicopteriformes), and **C:** the penultimate and ungual phalanges of the three anterior toes of *Podiceps cristatus* (Podicipediformes). The phalanges of the fourth toe are numbered; note the short penultimate (fourth) phalanx of the fourth toes of *Juncitarsus* and *Phoenicopterus*. Abbreviation: ung, ungual phalanx. Scale bars equal 10 mm.

Fig. 7. A: Pied droit de l'holotype de *Juncitarsus merkei* (Juncitarsidae, moulage d'holotype, SMF A 295, recouvert de chlorure d'ammonium), en comparaison avec **B:** le quatrième doigt (gauche) et le troisième doigt droit de *Phoenicopterus ruber* (Phoenicopteriformes) et **C:** l'avant-dernière phalange et l'ongle des trois doigts antérieurs de *Podiceps cristatus* (Podicipédiformes). Les phalanges du quatrième doigt sont numérotés ; à noter la quatrième avant-dernière phalange, courte, des quatrième doigts de *Juncitarsus* et *Phoenicopterus*. Abréviations : ung, phalange ongle. Barres d'échelle = 10 mm.

a synapomorphy of grebes and flamingos, with equally large patellae occurring only in Suloidea (Phalacrocoracidae, Anhingidae, Sulidae), Sphenisciformes, the extinct Plotopteridae, and some Anseriformes. A large patella cannot be observed in the holotype *J. merkei* (Fig. 4A);

- tarsometatarsus, proximal portion of plantar surface of trochlea metatarsi III elongate and of subtriangular shape (new character). As noted by Olson and Feduccia (1980), *Juncitarsus* differs from extant flamingos (and grebes) in that the proximal margin of the plantar surface of the trochlea metatarsi III is straight (Fig. 5K–M). The latter condition is found in Mesozoic non-neornithine birds, Palaeognathae and most neognathous birds and is thus plesiomorphic for neornithine birds;
- absence of fossa metatarsi I (this study) and reduction of hallux (Mayr, 2004). *Juncitarsus* has a well-developed fossa metatarsi I (Fig. 5K–M), which is likely to be correlated with the fact that the hallux is proportionally longer than in extant Phoenicopteriformes and Podicipediformes (Mayr, 2004);
- ungual phalanges dorsoventrally flattened and widened (Manegold, 2006). Livezey (2011: 394) stated that the “state in flamingos is much more similar to that in storks (e.g. *Ciconia* and *Mycteria*) than the unique state found in grebes”. As shown in Fig. 7, this statement is, however, erroneous and the ungual phalanges of flamingos, as well

as the penultimate phalanx of the third toe, are unusually flattened (albeit to a lesser degree than in grebes). In *Juncitarsus*, the ungual phalanges are not flattened (Fig. 7A).

The status of two derived characters shared by Phoenicopteriformes and Podicipediformes cannot be evaluated for *Juncitarsus*, and these either constitute synapomorphies of *Juncitarsus* and Mirandornithes, or apomorphies of Mirandornithes:

- unusually high number of at least 23 praesacral vertebrae (Mayr, 2004). Livezey (2011: 394) criticized this character because “the states were delimited by unequally wide ranges of counts, and ordering inflated the influence of the character”. These possible analytical issues do, however, not challenge the status of this feature as a synapomorphy of grebes and flamingos, because the high vertebral count found in these taxa clearly is derived within Neoaves and occurs in very few other groups (Mayr and Clarke, 2003). The number of praesacral vertebrae of *Juncitarsus* is unknown, as an exact count is not possible in the *J. merkei* holotype;
- processus spinosus of fourth through seventh cervical vertebrae forming a marked ridge (Mayr, 2004). The original definition of this character (Mayr, 2004) also included a strong elongation of the vertebrae, but such is absent in *Tachybaptus* and *Podilymbus* (skeletons of the latter were not available in 2004). Livezey (2011: 393) correctly noted that “this feature is much more prominent and serially extensive (third through 14th vertebrae) in flamingos than in grebes (fourth through seventh vertebrae)”, but this does not necessarily render “sequential homology of states among taxa questionable”, as grebes and flamingos have a similar vertebral count and the definition of the character includes only those vertebrae that exhibit the derived morphology. The vertebrae of *Juncitarsus* are not well enough preserved for an unambiguous assessment of the presence or absence of this feature.

Apart from two plesiomorphic features, which distinguish *Juncitarsus* from charadriiform birds (humerus with single pneumatic foramen and without processus supracondylaris dorsalis), Olson and Feduccia (1980: 48) listed three derived characters in support of phoenicopteriform affinities of *Juncitarsus*:

- the fact that the cervical vertebrae are “modified similarly to modern Phoenicopteridae”;
- a humerus with a distinct muscle scar at the insertion site of musculus scapulohumeralis cranialis, and;
- a tarsometatarsus with a high and broad eminentia intercotylaris (“intercotylar knob”).

None of these characters constitutes, however, strong evidence for a sister group relationship between *Juncitarsus* and Phoenicopteriformes. As detailed above, most of the derived features of the cervical vertebrae of flamingos are also found in grebes, and the marked scapulohumeralis cranialis scar is a synapomorphy of Mirandornithes. The

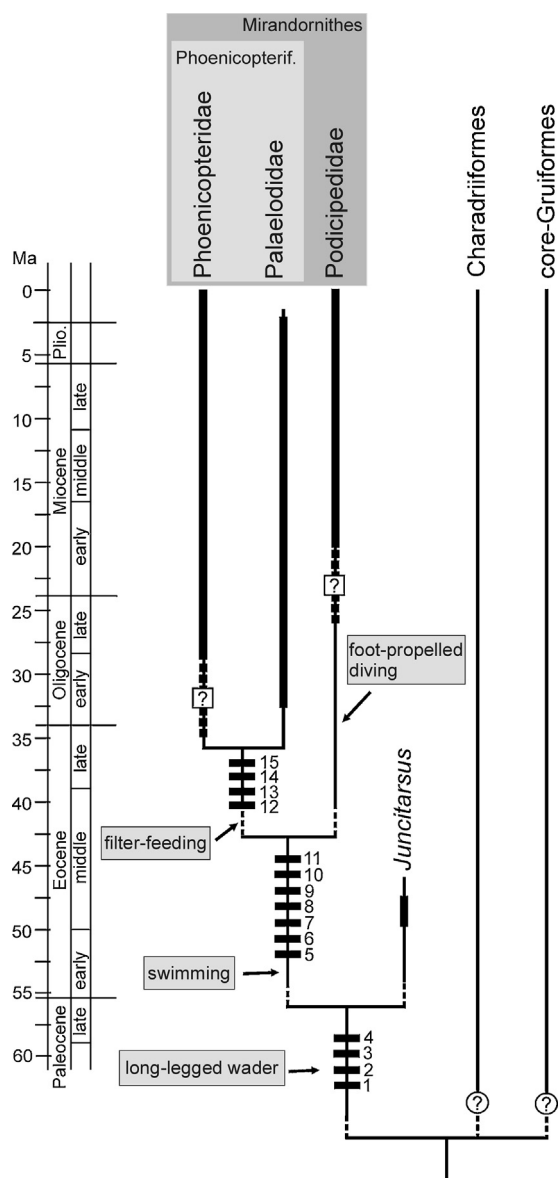


Fig. 8. Phylogenetic interrelationships of *Juncitarsus*, Podicipediformes, Palaelodidae, and Phoenicopteridae as proposed in the present study, with the temporal distribution of fossils assigned to *Juncitarsus* and Mirandornithes indicated by darker bars (based on data from Mayr (2009), Mlíkovský (2002), Olson and Feduccia (1980), Worthy et al. (2010)). Question marks in square fields denote an uncertain fossil record, those in circles tentative phylogenetic affinities (see text). Hypothesized transitions into new ecological zones are indicated in the shaded fields. Proposed apomorphies are numbered: 1, cervical vertebrae with well-developed processus ventrolaterales; 2, humerus with distinct muscle scar at insertion site of musculus scapulohumeralis cranialis; 3, tibiotarsus, distal rim of condylus medialis distinctly notched; 4, hypotarsus pedicellate, with three well-developed crests; 5, at least four thoracic vertebrae fused and forming a notarium; 6, ulna, tuberculum ligamenti collateralis ventralis greatly elongated; 7, phalanx proximalis digiti majoris cranio-caudally narrow; 8, patella greatly enlarged; 9, tarsometatarsus, proximal portion of plantar surface of trochlea metatarsi III elongate and of subtriangular shape; 10, fossa metatarsi I absent and hallux greatly reduced; 11, ungual phalanges dorsoventrally flattened and widened; 12, deep lower mandible; 13, presence of fonticuli occipitales; 14, elongation of cervical vertebrae; 15, presence of tubercle on distal tibiotarsus, laterodistal of pons supratendineus.

eminencia intercotylaris of *Palaelodus* is not as strongly raised as in extant Phoenicopteridae (Fig. 5D–F) and more closely resembles that of Podicipediformes, so that the prominent eminencia of *Juncitarsus* and modern flamingos probably evolved convergently, possibly in functional correlation with the greatly elongated legs of these birds.

In summary, the osteology of *Juncitarsus* is in better agreement with a sister group relationship to Mirandornithes than with an assignment to Phoenicopteriformes (Fig. 8). *Juncitarsinae* Peters, 1987, which were considered to be a taxon within Phoenicopteriformes, is thus elevated to a family-rank taxon, *Juncitarsidae* (Peters, 1987).

3. *Juncitarsus* and the higher-level affinities of flamingos and grebes

Molecular data do not provide unequivocal evidence for the closest extant relative of the flamingo/grebe clade. In studies with a comprehensive taxon sampling that include β -fibrinogen sequences, Phoenicopteriformes and Podicipediformes are placed in a taxon termed “Metaves”, which was hypothesized to constitute one of the two major lineages of Neoaves (all extant birds except Palaeognathae and Galloanseres; Ericson et al., 2006; Fain and Houde, 2004; Hackett et al., 2008). A metavian clade is, however, not obtained in analyses excluding β -fibrinogen sequences and, because of the lack of independent complementary evidence, likely to be an artifact of this gene (Mayr, 2011a; McCormack et al., 2013; Morgan-Richards et al., 2008). Mayr (2011a) hypothesized close affinities between flamingos and grebes and the Madagascan Mesitornithidae (mesites), because combined sequence data from *c-myc*, *RAG-1*, *myoglobin*, and *ornithine decarboxylase* support a clade (Mesitornithidae + [Phoenicopteriformes + Podicipediformes]), whereas β -fibrinogen sequences result in sister group relationship between Mesitornithidae and Phoenicopteriformes

Fig. 8. Interrelations phylogénétiques de *Juncitarsus*, des Podicipédiformes, des Palaelodidae et des Phoenicopteridae, telles que les propose l'étude ici présentée, avec la distribution dans le temps des fossiles attribués à *Juncitarsus* et Mirandornithes indiqués par des barres foncées, sur la base des données de Mayr (2009), Mlíkovský (2002), Olson et Feduccia (1980) et Worthy et al. (2010). Les points d'interrogation dans les carrés correspondent à un enregistrement fossile incertain, ceux situés dans des cercles à des affinités phylogénétiques non assurées (voir texte). Les transitions hypothétiques dans de nouvelles zones écologiques sont indiquées dans les champs ombrés. Les apomorphies proposées sont numérotées comme suit : 1, vertèbres cervicales avec processus ventrolaterales développé ; 2, humérus avec cicatrice de muscle visible sur le site d'insertion du musculus scapulohumeralis cranialis ; 3, tibiotarse, bordure distale du condylus medialis nettement entaillée ; 4, hypotarse pédicellé, avec trois crêtes bien développées ; 5, au moins quatre vertèbres thoraciques fondues et formant un notarium ; 6, ulna, tuberculum ligamenti collateralis ventralis très allongé ; 7, phalanx proximalis digiti majoris cranio-caudalement étroite ; 8, rotule très élargie ; 9, tarsométatars, portion proximale de la surface plantaire de trochlea metatarsi III allongée et de forme subtriangulaire ; 10, fossa metatarsi I absente et hallux très réduit ; 11, phalanges ongle aplaties et élargies dorso-ventralement ; 12, mâchoire inférieure profonde ; 13, présence de fonticuli occipitales ; 14, élongation des vertèbres cervicales ; 15, présence de tubercule sur le tibiotarsus distal, latéro-distal de pons supratendineus.

(Ericson et al., 2006: Figs. ESM-4 and ESM-6; see also Kimball et al., 2013).

In analyses of nuclear sequences exclusive of β -fibrinogen data, Phoenicopteriformes and Podicipediformes group with either Otididae (bustards), Musophagidae (turacos), and Columbiformes (doves and sandgrouse; McCormack et al., 2013: Fig. 2A; see also Kimball et al., 2013: Fig. 5B), Eurypygidae (sunbittern) and Phaethontidae (tropicbirds; McCormack et al., 2013: Fig. 2B), or the clade (Mesitornithidae + Mirandornithes) results in a polytomy with Charadriiformes and core-Gruiformes (Rallidae, Heliornithidae, Psophiidae, Aramidae, and Gruidae) (Ericson et al., 2006: Fig. ESM-6). Analyses of nuclear gap characters identifies Pelecanidae (pelicans) as sister taxon of flamingos and grebes (Yuri et al., 2013: Fig. 3), whereas some mitochondrial data support sister group relationship between the Phoenicopteriformes/Podicipediformes clade and Charadriiformes (Brown et al., 2008: Fig. 2; Morgan-Richards et al., 2008; Pratt et al., 2009: Fig. 1; see also Cracraft et al., 2004: Fig. 27.6). An analysis of nuclear PEPC sequences, albeit with a restricted taxon sampling, also resulted in sister group relationship between Phoenicopteriformes and Charadriiformes (Sorenson et al., 2003: Fig. 3).

Obviously, thus, molecular data do not unambiguously identify the closest extant relative of Mirandornithes. However, although there is a fairly wide array of taxa that group with flamingos and grebes in sequence-based studies, Musophagidae, Columbiformes, Pelecanidae, and Phaethontidae are identified as close relatives only in singular data sets, and a sister group relationship is not supported by complementary evidence. That a close relationship between Charadriiformes and Mirandornithes is found in multiple analyses is particularly noteworthy, because charadriiform affinities of flamingos were already assumed before publication of the molecular results, with the shorebird-like morphology of *Juncitarsus* playing a central role in the establishment of this hypothesis (Olson and Feduccia, 1980; Peters, 1987).

Peters (1987) noted that *Juncitarsus* and flamingos share with Charadriiformes (except Alcidae, see below) a derived morphology of the fourth toe, in which the fourth phalanx is shorter than the third (Fig. 7). This feature is present in only few other neornithine birds (Palaeognathae, Otididae, Sphenisciformes, Procellariiformes, Ardeidae, Balaenicipitidae, and Scopidae; Hesse, 1990: 13). In all other taxa, including Podicipediformes, the fourth phalanx is longer than the third, which is the plesiomorphic condition that also occurs in *Archaeopteryx* (Hesse, 1990). Based on the here proposed phylogenetic interrelationships of *Juncitarsus*, Phoenicopteriformes, and Podicipediformes (Fig. 8), it is equally parsimonious to assume that shortening of this phalanx occurred independently in *Juncitarsus* and Phoenicopteriformes, or that a short fourth phalanx is plesiomorphic for Mirandornithes and was secondarily elongated in Podicipediformes. That such can indeed occur is exemplified by Alcidae, which are phylogenetically nested within other Charadriiformes (e.g., Fain and Houde, 2007; Mayr, 2011b), and which are the only charadriiform birds with a long fourth phalanx.

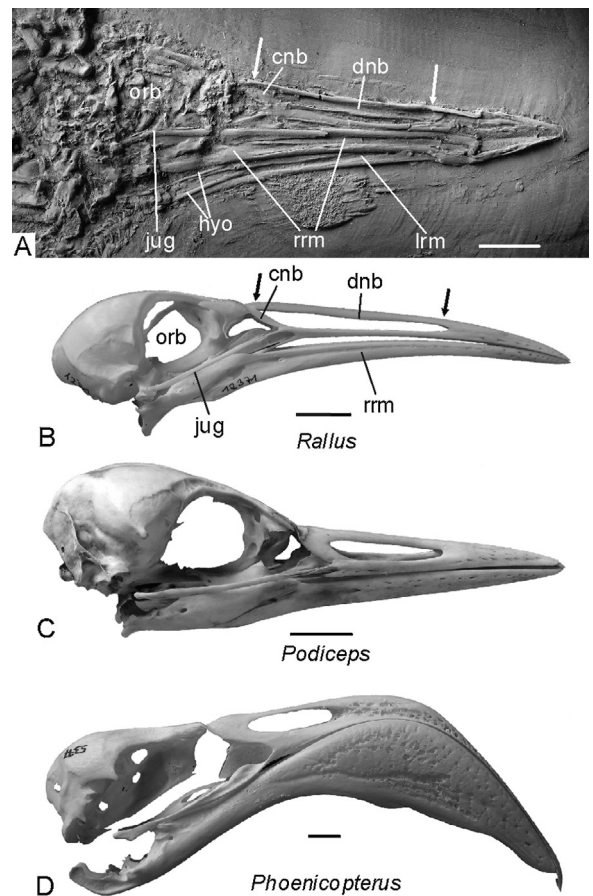


Fig. 9. Comparative views of skulls. **A:** *Juncitarsus merkei* (Juncitarsidae, cast of holotype, SMF A 295, coated with ammonium chloride). **B:** *Rallus sanguinolentus* (Rallidae). **C:** *Podiceps grisegena* (Podicipediformes). **D:** *Phoenicopterus ruber* (Phoenicopteriformes). The arrows in **A** and **B** indicate the caudal and rostral ends of the nasal opening. Abbreviations: cnb, caudal nasal bar, formed by processus maxillaris of os nasale and processus nasalis of os maxillare; dnb, dorsal nasal bar, formed by processus praemaxillaris of os nasale and processus frontalis of os praemaxillare; hyo, ceratobranchialia of hyoid; jug, jugal bar; lrm, left ramus mandibulae; orb, right orbita; rrm, right ramus mandibulae. Scale bars equal 10 mm. **Fig. 9.** Crânes en comparaison. **A:** *Juncitarsus merkei* (Juncitarsidae, moulage d'holotype, SMF A 295, recouvert de chlorure d'ammonium). **B:** *Rallus sanguinolentus* (Rallidae). **C:** *Podiceps grisegena* (Podicipédiformes). **D:** *Phoenicopterus ruber* (Phoenicopteriformes). Les flèches dans **A** et **B** indiquent les extrémités caudale et rostrale de l'ouverture nasale. Abréviations: cnb, barre nasale caudale, formée par processus maxillaris de l'os nasale; dnb, barre nasale dorsale, formée par processus praemaxillaris de l'os nasale et processus frontalis de l'os praemaxillare; hyo, ceratobranchialia de l'hyoïde; jug, barre jugale; lrm, ramus mandibulae gauche; orb, orbite droite; rrm, ramus mandibulae droit. Barres d'échelle = 10 mm.

Peters (1987) further assumed that *Juncitarsus* had schizorhinal nostrils, which are indicative of rynchokinosis, and which are a derived characteristic of some charadriiform and "gruiform" birds (e.g., Zusi, 1984). However, although the nostrils of *Juncitarsus* are very long as in, e.g., some species of Rallidae (Fig. 9), their caudal ends are not slit-like and do not reach the nasofrontal hinge as in truly schizorhinal birds. In any case, schizorhinal nostrils would not constitute unambiguous evidence for charadriiform affinities, because Charadriiformes include schizorhinal and holorhinal taxa, and from the

phylogenetic interrelationships of the extant taxa it cannot be deduced, which condition was present in the stem species of the clade (Mayr, 2011b).

For grebes, “gruiform” affinities were also previously discussed (see Olson, 1985), and Zusi and Storer (1969) found that Podicipediformes share a derived morphology of the cervical musculus longus colli ventralis with the sister taxa (e.g., Ericson et al., 2006; Hackett et al., 2008) Eurypygidae and Rhynochetidae (kagu). Manegold (2006) correlated this feature with a derived morphology of the vertebrae also present in flamingos, i.e., the presence of marked processus ventrolaterales; these likewise occur in *Juncitarsus* (Fig. 3A) and thus belong to the groundplan of the clade (*Juncitarsus* + Mirandornithes). Like mesites, the sunbittern and the kagu further share a notarium and derived properties of the β -fibrinogen gene with grebes and flamingos. An extensively fused notarium is, however, absent in *Juncitarsus* (Fig. 6), and thus probably evolved convergently in the clade (Eurypygidae + Rhynochetidae) and in Mirandornithes.

In overall morphology, e.g., with regard to the shape of the major wing bones and the short and plantarly deflected trochlea metatarsi II, *Juncitarsus* clearly corresponds better with Charadriiformes and core-Gruiformes than with Mesitornithidae, Eurypygidae, and Rhynochetidae. *Juncitarsus* and Mirandornithes further share with Charadriiformes and core-Gruiformes several derived characters that are absent in Mesitornithidae, Eurypygidae, and Rhynochetidae, such as a distinctly notched distal rim of the condylus medialis of the tibiotarsus (Fig. 4). One of the key apomorphies of grebes, the presence of lobed feet, is otherwise also only known from the “gruiform” sungrebes (Heliornithidae) and coots (Rallidae), and the charadriiform phalaropes (Phalaropidae), and may constitute a case of parallelism in closely related taxa.

Although the closest extant relatives of Mirandornithes can ultimately be identified only through congruent results of future analyses of molecular or morphological data, Charadriiformes remain among the candidate taxa, and it is to be hoped that future studies will yield data for a robust phylogenetic placement of Mirandornithes, Charadriiformes, and the putatively closely related “gruiform” birds.

4. Discussion and conclusion

Because of their highly divergent life habits and morphology, flamingos and grebes are certainly among the most interesting examples for the evolution of disparate morphologies among birds. It has been detailed previously that the very divergent morphologies of extant Phoenicopteriformes and Podicipediformes are bridged by the Palaelodidae, which combine flamingo-like skull features with a foot morphology reminiscent of that of grebes (Mayr, 2004). Palaelodids are known from very abundant material and especially the species *Palaelodus ambiguus* is represented by thousands of bones representing virtually every skeletal element (e.g., Cheneval and Escuillié, 1992; Milne-Edwards, 1871; Worthly et al., 2010). Although the osteology of *Palaelodus* is comparatively well known, many features, especially of the skull, have not yet been

evaluated in light of the novel hypothesis of a sister group relationship between flamingos and grebes. Such a revision of palaelodid morphology is beyond the scope of this study, but it should be noted that contra Mayr (2009), who hinted at the possibility that palaelodids are the sister taxon of Podicipediformes, phoenicopteriform affinities of *Palaelodus* are well supported by several shared derived features, including a deep lower mandible, the presence of occipital fontanelles on the cranium (Cheneval and Escuillié, 1992), the elongation of the cervical vertebrae, and the presence of a tubercle on the distal tibiotarsus, laterodistal of the pons supratendineus. Future studies will also have to evaluate the exact affinities of other taxa assigned to Palaelodidae, such as the New World *Megapalaelodus*, at least some species of which show plesiomorphic features suggesting a position outside Mirandornithes (i.e., a low number of vertebrae fused into the notarium and a truncate proximal plantar articulation facet of the trochlea metatarsi III; e.g., Agnolin, 2009).

Palaelodus exhibits swimming adaptations, such as a mediolaterally compressed tarsometatarsus and proximally elongated cristae cnemiales of the tibiotarsus (Mayr, 2004), which are absent in *Juncitarsus*. A number of other derived characteristics of Phoenicopteriformes and Podicipediformes, which are also absent in *Juncitarsus* and thus likely evolved after the split of the latter from the lineage leading to modern flamingos and grebes, may also be correlated with the transition from a wading to a swimming habit, such as the extensively fused notarium, the large patella, closure of the hypotarsal canals, and flattening of the ungual phalanges. The life habits of *Juncitarsus* are poorly known, but the extremely elongated legs suggest that it was a wading bird, which probed for food in a lacustrine environment (Peters, 1987). That *Juncitarsus* was not yet adapted for filter feeding is not only indicated by the shape of its long and pointed beak, but also by the presence of numerous gastroliths in the *J. merkei* holotype (Fig. 4A), which suggest a diet consisting of harder items (Peters, 1987). Whereas the stem species of Mirandornithes was likely to be a bird with swimming adaptations, such were probably absent in the stem species of the clade (*Juncitarsus* + Mirandornithes) and evolved after the divergence of *Juncitarsus* and Mirandornithes (Fig. 8).

Removal of *Juncitarsus* from the stem lineage of Phoenicopteriformes is of significance for the calibration of molecular data, and currently there exists no unambiguous Eocene record of Phoenicopteriformes, whose earliest fossils date from the Early Oligocene (Mayr, 2009). The earliest described fossils of Podicipediformes are from the Early Miocene (Mayr, 2009). The fossil record would thus be broadly congruent with a divergence date of crown group Mirandornithes in the mid-Paleogene, some 45 million years ago, as suggested by a recent calibrated molecular phylogeny (Brown and van Tuinen, 2011).

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