On the osteology and phylogenetic affinities of *Morsoravis sedilis* (Aves) from the early Eocene Fur Formation of Denmark

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*Morsoravis sedilis* is a small bird from the early Eocene Fur Formation of Denmark, which in the original description was considered to be most closely related to Charadriiformes. Because *Morsoravis* has subsequently been likened to *Pumiliornis tessellatus*, an equally enigmatic bird from the middle Eocene of Messel in Germany, I perform here the first phylogenetic analysis including the two taxa. This analysis supports a sister group relationship between *Morsoravis* and *Pumiliornis*, and the clade including the two taxa is recovered as the sister taxon of the late Eocene/early Oligocene *Eocuculus*. I report a possible, albeit lost, second specimen of *Morsoravis*, and identify derived characters in support of a sister group relationship between *Morsoravis* and *Pumiliornis*. The analysis did not resolve the higher-level affinities of the clade including *Morsoravis*, *Pumiliornis*, and *Eocuculus*, and did not confirm charadriiform affinities of *Morsoravis*. More data on the osteology of the fossils, as well as an improved understanding of the interrelationships of extant birds, are needed for a well-established phylogenetic assignment of these fossil taxa.

Key words: Aves, *Morsoravis sedilis*, *Pumiliornis tessellatus*, *Eocuculus cheripinae*

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*Morsoravis sedilis* Bertelli *et al.*, 2010 is a small bird from the early Eocene Fur Formation of the island of Mors in Denmark (Fig. 1), which is based on an exceptionally well-preserved partial skeleton lacking both wings and the pectoral girdle (Fig. 2A). This fossil was studied by Kristoffersen (2002) and Lindow (2007) in unpublished PhD theses and formally described by Bertelli *et al.* (2010). These authors considered *M. sedilis* to be most closely related to charadriiform birds, and the species also resulted as sister taxon of Charadriiformes in a phylogenetic analysis performed by Bertelli *et al.* (2010). This placement received, however, only weak support, and *Morsoravis* differs distinctly from charadriiform birds in features of the hind limb, whose osteology indicates perching capabilities and an arboreal way of living (Kristoffersen 2002; Lindow 2007; Bertelli *et al.* 2010). If it was indeed on the stem lineage of Charadriiformes, it would indicate an unexpected ecomorphological diversity of these birds.

Mayr (2009) questioned charadriiform affinities of *Morsoravis* and assumed that it is most closely related to *Pumiliornis tessellatus* from the middle Eocene of...
Here I perform the first phylogenetic analysis including *Morsoravis*, *Pumiliornis*, and *Eoculus*. I further comment on some osteological features of *Morsoravis* and discuss new character evidence for close affinities between this taxon and *Pumiliornis*.

Material and methods

Osteological terminology follows Baumel & Witmer (1993). Phylogenetic analyses were conducted with the Messel in Germany (Fig. 2 B, C). This species is known from two partial skeletons and was compared with “gruiform”, charadriiform, and “ciconiiform” birds in the original description (Mayr 1999). In a later study (Mayr 2008), it was hypothesized that *Pumiliornis* is more closely related to the equally enigmatic taxon *Eoculus*, which is represented by postcranial skeletons from the late Eocene of North America and the early Oligocene of Céreste in France (Chandler 1999; Mayr 2006, 2008).

Fig. 2. A, *Morsoravis sedilis* from the early Eocene of Denmark (holotype, MGUH 28930); note that the fragile specimen has been damaged after Bertelli et al.’s (2010) description, so that the skull roof and most of the right tibiotarsus are now broken. B, *Pumiliornis tessellatus* from the middle Eocene of Germany (holotype, SMF-ME 2092A). C, *Pumiliornis tessellatus*, x-ray photograph of specimen SMF-ME 2475A+B. The specimens in A and B were coated with ammonium chloride. Scale bars equal 5 mm.
heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), using the commands hold 10000, hold/10, mult*1000, and max*. The character matrix (see Appendices) is based on the data set of Mayr & Clarke (2003), which was also used in the analysis of Bertelli et al. (2010). Five additional characters and coding modifications are incorporated (Appendix 1). The emended matrix comprised 47 ingroup taxa and 153 characters. Following Mayr & Clarke (2003), three characters (55, 71, 91) were coded as ordered. In addition to the fossil taxa Morsoravis, Pumiliornis, and Eocuculus, I also added extant Mesitornithidae (Monias benschi) to the analysis as mesites exhibit schizorhinal nostrils and also resemble Morsoravis in other osteological features. The Mesozoic non-neornithine taxa Apsaravis, Hesperornis, and Ichthyornis were used as outgroups.

Consistency index (CI) and retention index (RI) were calculated, as well as bootstrap support values with 1000 replicates, three searches holding one tree per replicate, and TBR branch swapping without max*. For Eocuculus I scored only data obtained from the two reliably identified skeletons (Chandler 1999; Mayr 2006), but not from the tentatively referred wings described by Mayr (2008).

Institutional abbreviations: MGUH - Geological Museum of the University of Copenhagen, Denmark; MNHN - Muséum National d’Histoire Naturelle, Paris, France; SMF - Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Comparison between Morsoravis, Pumiliornis, and Eocuculus

Morsoravis sedilis is about 1.3 times larger than Pumiliornis tessellatus, but as far as comparisons are possible, the two species exhibit a very similar osteology. Detailed comparisons between Pumiliornis and Eocuculus were already made by Mayr (2008), so that I here focus on comparisons between these two taxa and Morsoravis.

The only known skull of Pumiliornis is badly crushed and does not allow the recognition of osteological details, but accounting for the bad preservation it corresponds well with the skull of Morsoravis in overall proportions (Fig. 2). Bertelli et al. (2010) noted that the nostrils of Morsoravis are schizorhinal, and schizorhinal nostrils were also reported for Pumiliornis (Mayr 2008).

Morsoravis has a high number of 21 presacral vertebrae (the cranial portion of the synsacrum was erroneously marked as 22nd vertebra in Bertelli et al. 2010: text-fig. 8). In previous descriptions of Pumiliornis (Mayr 1999, 2008), the vertebral count was not given. The number of presacral vertebrae can, however, be ascertained on the x-ray photograph of the holotype, which substantiates the presence of 21 presacral vertebrae in P. tessellatus (Fig. 3).

Bertelli et al. (2010) stated that the thoracic vertebrae of Morsoravis lack the heteroceleous condition (based on the morphology of vertebra 15 and the contact between the thoracic vertebrae). However, after a re-evaluation of the holotype I note that they actually are heteroceleous, as the ventral sections of the rims of the corpora vertebrarum are curved and do not form straight lines as in opisthocoelous birds (Fig. 4). The thoracic vertebrae of Morsoravis further are pleuroceleous, i.e., with deep lateral depressions, as are those of Pumiliornis and Eocuculus (Fig. 4; Mayr 2008).

The pelvis of the Pumiliornis specimens is poorly preserved, but the Eocuculus pelvis matches well with that of Morsoravis in overall proportions (Fig. 5).

The tibiotarsus of Morsoravis differs from that of Pumiliornis in that it exhibits an ossified pons supratendineus, which is absent in Pumiliornis (Mayr 2008). Unlike Pumiliornis, there is further an ossified retinacu-

Fig. 3. Pumiliornis tessellatus Mayr, 1999 from the middle Eocene of Germany (holotype, SMF-ME 2092A), x-ray photograph. The white dots indicate the position of the presacral vertebrae. Vertebrae 14–16 can not be directly observed and their positions were estimated from the average distance between the vertebral bodies.
lum musculi fibularis (Fig. 6C). Otherwise, however, the bones show a close resemblance. Most notably, the tibiotarsus of Morsoravis also exhibits a marked crest along the medial surface of its proximal end, which was described by Mayr (2008) for Pumiliornis (Fig. 6). This feature has not been mentioned for Morsoravis by previous authors and is here reported for the first time. The known specimens of Eocuculus do not allow recognition of this crest, but the distal end of the tibiotarsus of Eocuculus resembles that of Morsoravis (compare Figs. 6C and 7C).

The tarsometatarsus of Morsoravis corresponds with that of Pumiliornis in overall proportions, but close comparisons are hindered by the fact that the bone is damaged or poorly preserved in all fossils. Both taxa agree in that the foramina vascularia proximalia are widely separated, the shaft is dorsoplantarly flattened, and exhibits an intermuscular line along the lateral portion of its dorsal surface. As detailed by Mayr (2008), the wide proximal phalanx of the fourth toe, together with the plantarily deflected tarsometatarsal trochlea for this toe, suggest the presence of semizygodactyl feet in Pumiliornis (i.e., the fourth toe was spread laterally but not completely reversed as in fully zygodactyl birds). Owing to the preservation of the holotype, presence of this condition can not be established for Morsoravis, but seems likely because of the very wide proximal phalanx of the fourth toe.

The orientation of the slightly laterally spread fourth toe of the Morsoravis holotype, which exhibits its dorsomedial rather than dorsal surface, is also indicative of semizygodactyl feet. The trochlea metatarsi II of Morsoravis has a characteristic morphology in that its medial surface bears a marked groove and is bilobed (Fig. 7D). This condition is very unlike that of Charadriiformes and most other birds but resembles that found in Coliiformes, especially the Eocene Sандcoleidae (Fig. 7E). The trochlea metatarsi II is not well enough preserved in Pumiliornis to safely establish presence or absence of this trait; in Eocuculus it is absent. The trochlea metatarsi III appears proportionally larger in Pumiliornis, but as this trochlea is damaged in the Morsoravis holotype, close comparisons are not possible. As noted by Bertelli et al. (2010), the incisura intertrochlearis medialis of Morsoravis is wider than in Pumiliornis, but this impression may be caused by the fact that the damaged trochlea metatarsi III lacks its dorsal portion.

Morsoravis and Pumiliornis show a close resemblance in the proportions and morphology of the pedal phalanges. Pumiliornis is characterized by a very wide proximal phalanx of the fourth toe (Mayr 2008), which is also present in Morsoravis (Fig. 7).

Elements of the wing and pectoral girdle are not preserved in the Morsoravis sedilis holotype. However, Kristoffersen (2002: pl. 11) assigned a partial postcran-
al skeleton from the Fur Formation to the Zygodactylidae (“Primoscenidae”), which actually matches well with the osteology of *Morsoravis*. Unfortunately, this specimen (Fig. 5A, B), which has the collection number MGUH VP 1289 and which was also figured by Bonde *et al.* (2008: 113), seems to be lost now (S. L. Jakobsen, pers. comm.). With femur and tibiotarsus lengths of ~13.9 and ~23.5 mm respectively (Kristoffersen 2002), it corresponds well with the *M. sedilis* holotype in size, in which these bones measure 14.8/15.2 and 25.6 mm.

![Image of skeleton](image)

**Fig. 5.** A, partial postcranial skeleton from the Fur Formation (MGUH VP 1289), which may belong to *Morsoravis sedilis* (see text; the specimen is now lost, photo by S. L. Jakobsen). B, detail of the sternum of MGUH VP 1289 for comparison to that in C. C, *Eocuculus cf. cherpinae* from the early Oligocene of France (SMF Av 425). D, pelvis (ventral view) of *M. sedilis* (holotype, MGUH 28930). E, *E. cf. cherpinae* from the early Oligocene of France (SMF Av 425). The specimens in A, B, and D were coated with ammonium chloride. Scale bars equal 5 mm.
(Bertelli et al. 2010). As in *Morsoravis* the synsacrum bears two pairs of marked fossae on the ventral surface of its cranial end, and the thoracic vertebrae are pleurocoelous (Fig. 5A). According to Kristoffersen (2002), MGUH VP 1289 exhibits a small processus intermetacarpalis on the carpometacarpus, which was, however, only visible before acid preparation of the fossil, after which the carpometacarpus was hidden by the sternum. The short and broad sternum bears two pairs of deep incisions in its caudal margin and is very different from the sternum of charadriiform birds, but corresponds well with that of *Eocuculus* (Fig. 5).

![Fig. 6. Tibiotarsus of *Morsoravis sedilis* and *Pumiliornis tessellatus* for comparison. A, *M. sedilis* (holotype, MGUH 28930), proximal end of right tibiotarsus in medial view. B, *P. tessellatus* (holotype, SMF-ME 2092A), proximal end of left tibiotarsus in medial view. C, *M. sedilis* (MGUH 28930), distal end of left tibiotarsus in cranial view. D, *P. tessellatus* (SMF-ME 2475B), distal end of right tibiotarsus in cranial view. Abbreviations: crs – crest along medial side of proximal tibiotarsus; pst – pons supratendineus; rmf – ossified retinaculum musculi fibularis. All specimens were coated with ammonium chloride. Scale bars equal 5 mm.](image1)

![Fig. 7. Tarsometatarsus for comparison. A, *Morsoravis sedilis* (holotype, MGUH 28930), left tarsometatarsus in dorsal view. B, *Pumiliornis tessellatus* (SMF-ME 2475B), left tarsometatarsus in dorsal view. C, *Eocuculus* cf. *cherpinae* (SMF Av 425), right tarsometatarsus in dorsal view. D, *Morsoravis sedilis* (holotype, MGUH 28930), distal end of left tarsometatarsus in medial view. E, undetermined species of the coliiform Sandcoleidae from the early Eocene of France (MNHN CB-17347; from Mayr & Mourer-Chauviré 2004), distal end of left tarsometatarsus in dorsal (above) and plantar (below) view. Abbreviations: fur – furrow on medial surface of trochlea metatarsi II, iml – intermuscular line, pp4 – proximal phalanx of fourth toe. The specimens in A–D were coated with ammonium chloride; E is a SEM picture. Scale bars equal 5 mm.](image2)
Results of phylogenetic analysis

Analysis of the character matrix resulted in eight most parsimonious trees (Length = 769, CI = 0.21, RI = 0.47), the strict consensus tree of which is shown in Figure 8. The analysis supports a clade including *Morsoravis*, *Pumiliornis*, and *Eocuculus*, which, however, received only a low bootstrap support of 59%. The following characters were optimized as apomorphies of this clade (numbers refer to the character list): (6) nostrils schizorhinal; (58) caudalmost presacral vertebrae with deep lateral excavations; (74) processus uncinati not fused to ribs; (82) ulna distinctly exceeding humerus in length; (151) tibiotarsus with crest along medial side of proximal end, opposite crista fibularis; (152) tarsometatarsus, foramina vascularia proximalia widely separated; (153) proximal phalanx of fourth toe short and very wide.

Concerning the extant taxa, some clades obtained in the present and Bertelli et al.’s (2010) analysis are not in agreement with well-supported clades based on molecular data, which, for example, recover sister group relationship between Phoenicopteridae and Podicipedidae (Ericson et al. 2006; Hackett et al. 2008; Mayr 2011b). In the present analysis, Podicipedidae were shown to be the sister taxon of Gaviidae, but grouping of these foot propelled diving birds is an artefact of the data set, which includes many characters pertaining to hind limb myology (see discussion in Mayr & Clarke 2003). Likewise, sister group relationship between Steatornithidae and Trogonidae is not supported by all current molecular analyses (Ericson et al. 2006; Hackett et al. 2008).

Discussion

The analysis supports a close relationship between *Morsoravis* and *Pumiliornis*, and also suggests that these early/middle Eocene taxa form a clade together with the late Eocene/early Oligocene *Eocuculus*. *Morsoravis* and *Pumiliornis* are distinguished from all other avian taxa by the unique combination of the following features: (1) beak with schizorhinal nostrils; (2) presence of 21 presacral vertebrae; (3) the thoracic vertebrae are pleurocoelous, i.e., with deep lateral excavations; (4) tibiotarsus with crest along medial side of proximal end; and (5) the proximal phalanx of fourth toe is short and very wide. The clade including *Morsoravis*, *Pumiliornis*, and *Eocuculus* received, however, only low bootstrap support and three of the above features (1, 2, 4) are unknown for *Eocuculus*.
Three characters were optimized as apomorphies of a clade including *Morsoravis* and Charadriiformes in the analysis of Bertelli et al. (2010), that is, the presence of (1) opisthocoelous and (2) pleurocoelous thoracic vertebrae, as well as (3) the absence of a foramen in the caudoventral portion of the pygostyle. None of these features is restricted to Charadriiformes, and the last occurs in many unrelated taxa (e.g., Mayr & Clarke 2003). Based on a re-evaluation of the *Morsoravis* holotype I am confident that the thoracic vertebrae of this taxon actually are heterocoelous (see above; Fig. 4). Moreover, opisthocoelous vertebrae evolved independently within Charadrii and Lari and were probably absent in the stem species of Charadriiformes (Mayr 2011a). Pleurocoelous vertebrae belong to the stem species pattern of charadriiform birds (Mayr 2011a) and have a restricted distribution among extant birds (e.g., Mayr & Clarke 2003). They are, however, present in *Ichthyornis*, a stem lineage representative of Neornithes (Clarke 2004) and the palaeognathous Lithornithidae (Leonard et al. 2005), and were also reported in a number of fossil taxa whose closest extant relatives lack depressions on the vertebral bodies, such as stem group Galliformes (Dyke & Gulas 2002), Piciformes (Mayr & Knopf 2005), and the putatively psittaciform Halcyornithidae (“Pseudasturidae”) (Mayr 2002: fig. 2D).

Kristoffersen (2002) and Lindow (2007) further listed the presence of schizorhinal nostrils as evidence for charadriiform affinities of *Morsoravis*. However, although schizorhinal nostrils probably do belong to the stem species pattern of Charadriiformes (Mayr 2011a), they occur in many other unrelated taxa, such as Threskiornithidae, Mesitornithidae, Columbidae, Gruidae, Trochilidae, and Furnariidae. The same is true for the dorsally curved retroarticular processes of the mandible, which, albeit present in many Charadriiformes, are also found in Galliformes, Threskiornithidae, Mesitornithidae, Rallidae, and some Gruidae (*Balaeica*) and Pididae (*Jynx*).

The present analysis does not resolve the higher-level affinities of the clade including *Morsoravis*, *Pumiliornis*, and *Eocuculus*, but charadriiform affinities of *Morsoravis* are not supported by the morphology of the fossil. *Morsoravis* has an unusually low number of only 12 scleral plates (Bertelli et al. 2010). Most birds, including Palaeognathae and Galloanseres, exhibit a scleral ring with a modal number of 14 or 15 plates, which is likely to be the plesiomorphic condition for Neoaves. In Charadriiformes, the modal number of scleral plates is variable, and whereas 12 or 13 are present in some taxa (Turnicidae, Rostratulidae, Jacanidae, Alcidae), the majority has 15 (Livezey & Zusi 2006). Among extant birds a modal number of 12 plates is otherwise present in Cuculidae, Opisthocomidae, Trochilidae, Coliiformes, and Psittaciformes, whereas Suliformes and Columbiformes have only 11 plates (Lemmrich 1931; Livezey & Zusi 2006).

*Morsoravis* and *Pumiliornis* further share with coliiform and psittaciform birds a crest on the medial surface of the proximal tibiotarsus; as noted above, the peculiar bilobed trochlea metatarsi II of the tarso-metatarsus of *Morsoravis* resembles that of the Eocene Sandcoleidae, which are stem group representatives of Coliiformes (Fig. 4). *Morsoravis* and *Pumiliornis* are, however, distinguished from all “higher land bird” taxa by a high number of 21 presacral vertebrae, which may represent a plesiomorphic feature, because 20 or more presacral vertebrae are present in Mesozoic birds outside Neornithes as well as in palaeognathous birds and Galloanseres (by contrast, “higher land bird” taxa invariably have 19 or fewer presacral vertebrae). I thus note that, although recognition of close affinities between *Morsoravis* and *Pumiliornis* sets them into a phylogenetic context two enigmatic avian taxa with a distinctive morphology, more data on the osteology of the fossils as well as an improved understanding of the interrelationships of extant birds are needed for a well-established phylogenetic assignment of these fossil taxa.

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Appendix

Appendix 1. Character descriptions. Character list follows Mayr & Clarke (2003), with five characters (149-153) newly added and the description of three (15, 44, 94) modified. Concerning Morsoravis, scorings of six characters differ from Bertelli et al. 2010 (who also followed Mayr and Clarke 2003): I completed codings for characters with uncertain scores (10, 11, 36 and 113), and modified the scoring of two characters (3 and 57). Below is a list of characters, whose descriptions or scorings were modified or that were newly added. See Mayr & Clarke (2003) for a complete list of characters and further comments concerning the scoring of the extant taxa.

3 Upper beak, lamellae for filter feeding: absent (0), vestigial (1), well developed (2). Because the keratinous parts of the beak are not preserved in the fossil, I scored this character as unknown for Morsoravis (contrary to Bertelli et al. 2010, who coded it as absent).

6 Nostrils: schizorhinal, i.e., caudal margin slit-like and extending caudally to naso-frontal hinge; cranial kinesis rhynchochonetic: no (0), yes (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Gruidae, and coded it as present (1) for this taxon.

10 Os mesethmoidale reaching rostrally markedly beyond naso-frontal hinge: no (0), yes (1). Bertelli et al. (2010) coded this character as unknown. However, I consider it unlikely that a rostral portion of this structure is broken, which is as fragile as any other portion of the septum orbitale (which is mostly preserved).

11 Palate, processus maxillopalatinus of osa maxillaria fused along their midline: absent (0), present (1). Remains of one unfused processus maxillopalatinus are preserved in the holotype, therefore I scored this character as absent for Morsoravis.

15 Os palatinum, crista ventralis: absent (0), present (1). Character description was modified from Mayr & Clarke (2003), where only a well-developed crista ventralis was scored. Accordingly, this character was scored present in Cariamidae, Gaviidae, Phaethontidae, and Fregatidae, in addition to the taxa coded “1” by Mayr & Clarke (2003).

22 Os palatinum and os pterygoideum fused: yes (0), no (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Hesperornithidae and coded it as absent (1) for this taxon.

31 Os opisthoticum / prooticum, pila otica with cluster of small pneumatic openings: no (0), yes (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Phoenicopteridae, and coded it as present (1) for this taxon.

32 Fronto-parietal suture in adult birds: open (0), closed (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Apterygidae, and coded it as closed (1) for this taxon.

36 Quadratum, processus oticus, pneumatic foramina on dorsal end of caudal surface: absent (0), present (1). The dorsal margin of the caudal surface of the quadrare, which is exposed in the fossil, is not pierced by these foramina; therefore I scored this character as absent for Morsoravis (Bertelli et al. 2010 coded it as unknown).

44 Mandible: not as follows (0), with long and strongly mediolaterally compressed processus retroarticularis (1), with narrow, dorsally upcurved processus retroarticularis (2). Character description was modified from Mayr & Clarke (2003), where only the presence of a retroarticular process was scored. Character state 1 was coded present in Anatidae, Anhingidae, Phoenicopteridae, and Pteroclididae. Character state 2 was scored for Galiformes, Threskiornithidae, Recurvirostridae, Rallidae, Gruidae, and Morsoravis.

57 Thoracic vertebrae: at least part of series amphicoelous or opisthocoelous, i.e., with subround, central articular surfaces that lack the dorsoventral compression and saddle-shaped articular surface seen in heterocoelous vertebrae (0), series completely heterocoelous (1). Scoring of this character differs from Bertelli et al. (2010) concerning Morsoravis, which has heterocoelous thoracic vertebrae. I further corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Phalacrocoracidae, and coded it as absent (0) for this taxon.

58 Caudalmost presacral vertebrae pleurocoelous, i.e., with deep lateral excavations: no (0), yes (1). I coded Psittaci-formes as polymorphic for this character, as pleurocoelous vertebrae occur in some stem group representatives (Halcyornithidae, see Mayr 2002).

65 Coracoide, foramen nervi supracoracoidei: present (0), absent (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Rheidae, and coded it as absent (1) for this taxon.

85 Carpometacarpus, os metacarpale minus strongly bowed, delimiting a large spatium intermetacarpale: no (0), yes (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Anatidae and Opisthocomidae, and coded it as absent (0) for Anatidae and present (1) for Opisthocomidae.

94 Pelvis, foramen ilioischiatricum caudally closed: no (0), yes (1). Character description was modified from Mayr & Clarke (2003), where Rheidae were assigned a separate state.

100 Tibiotarsus, distal end, ossified pons supratendineus: absent (0), present (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Apterygidae and coded it as absent (0).

105 Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal: no (0), yes (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Coliidae.

106 Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1). I corrected the erroneous scoring of this character by Mayr & Clarke (2003) for Coliidae.

113 Osseous claws, pair of canals lateral and medial to tuberculum extensorium: absent (0), present (1). The ungual phalanx bears an open sulcus neurovascularis, therefore I scored this character as absent for Morsoravis (Bertelli et al. 2010 coded it as unknown).

149 Phalloss: present (0), absent (1). Newly added character.

150 Modal number of plates in scleral ring: 14 or more (0), 13 or less (1). Scoring after Lemmrich (1931) and Livezey & Zusi (2006). Newly added character.

151 Tibiotarsus, well-developed crest along medial side of proximal end, opposite crista fibularis: absent (0), present (1). Newly added character.

152 Tarsometatarsus, foramina vascularia proximalia widely separated: no (0), yes (1). Extant Coliidae exhibit only a single foramen vascularis proximale. Newly added character.

153 Fourth toe, proximal phalanx short and very wide: no (0), yes (1). Newly added character.
Appendix 2. Character scorings. Newly added characters and scorings that differ from Mayr & Clarke (2003) or Bertelli et al. (2010) are highlighted. Multistate characters are denoted by “a” (0&1), “b” (1&2), “c” (2&3), and “d” (3&4), unknown character states by “?”. These data are also contained in the supplementary data file Morsoravis.winc which can be imported by the phylogenetic analysis program Winclada. This program is freely available at http://www.cladistics.com/about_winc.htm

Apsaravis

Hesperornis

Ichthyornis

Rheidae

Apterygidae

Tinamidae

Galliformes

Anhimidae

Anatidae

Opisthocomidae

Podicipedidae

Phoenicopteridae

Threskiornithidae

Cariamidae

Strigiformes

Burhinidae

Accipitridae

Falconidae

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