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 tesselatus*, 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 sup-port 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.

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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 This fossil was studied by Kristoffersen (2002) and Lindow (2007) in unpublished PhD theses and formally described by Bertelli *et al.* (2010).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 tesselatus* from the middle Eocene of

Fig. 1. Map of Central Europe showing the localities mentioned in the text.

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 *Eocuculus*, 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).

Here I perform the first phylogenetic analysis including *Morsoravis*, *Pumiliornis*, and *Eocuculus*. 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

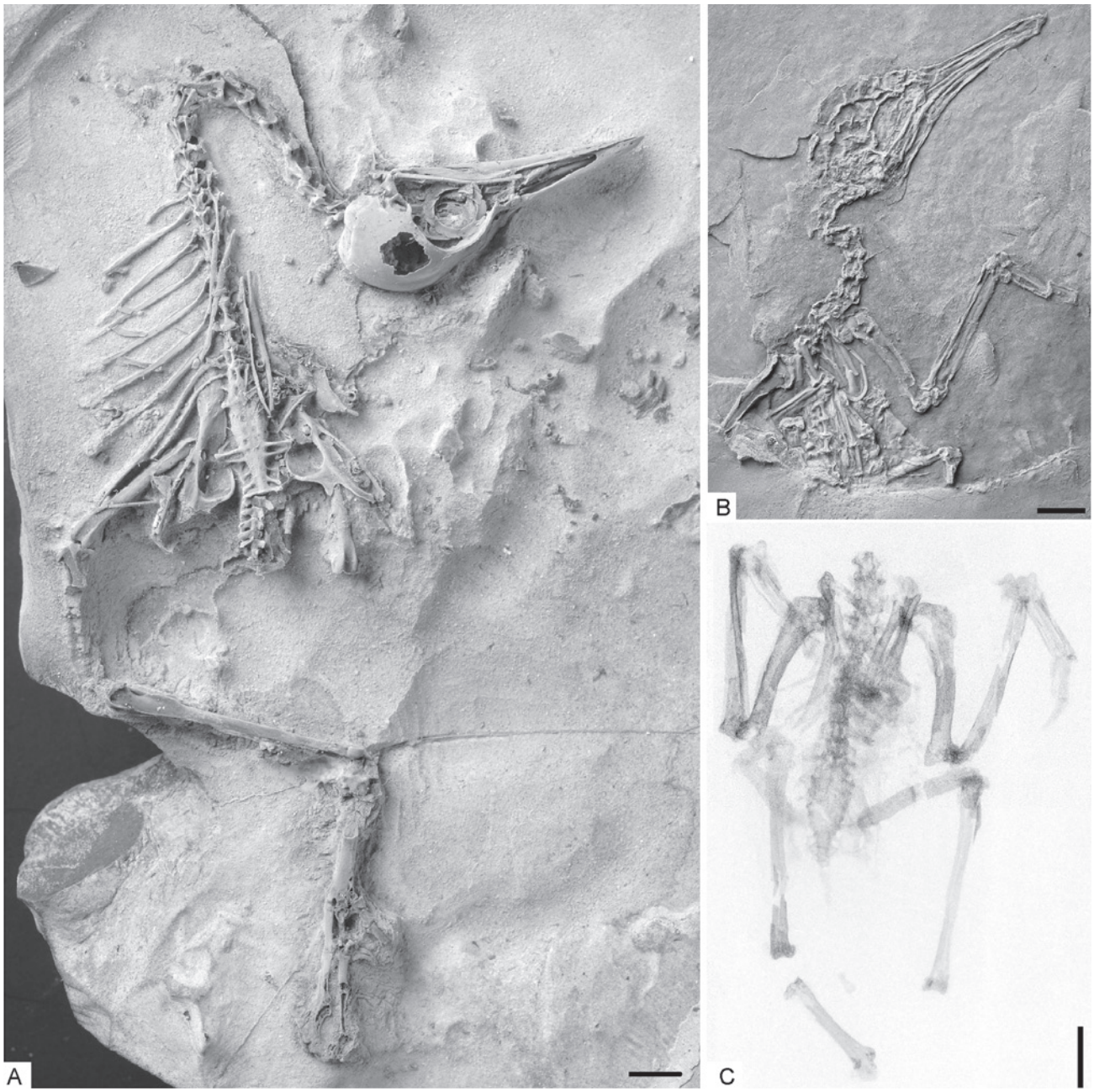

Fig. 2. **A**, *Morsoravis sedilis* from the early Eocene of Denmark (holotype, MGUH 28930); note that the fragile specimen has been damaged after Bertelli *et al.*'s (2010) description, so that the skull roof and most of the right tibiotarsus are now broken. **B**, *Pumiliornis tessellatus* from the 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*.

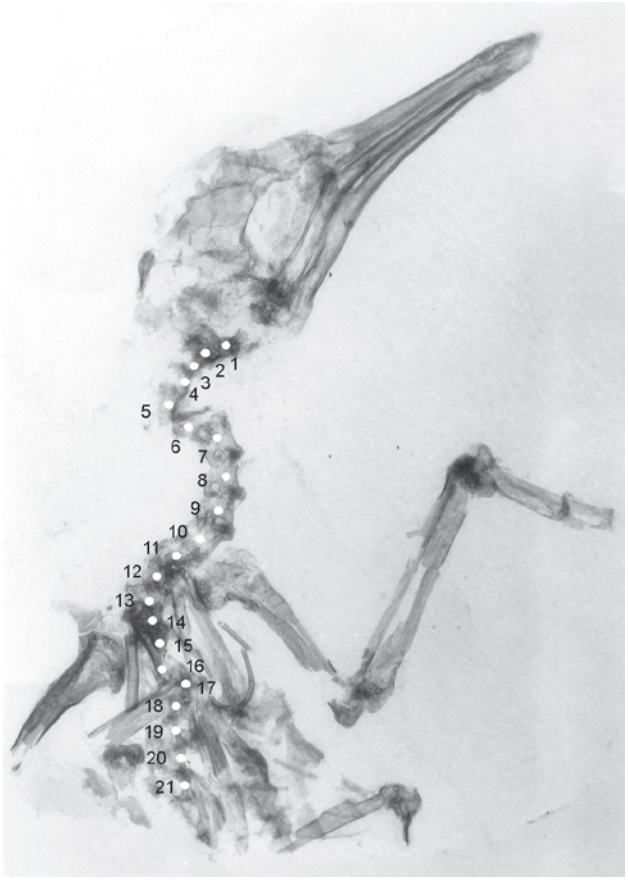

Fig. 3. *Pumiliornis tessellatus* Mayr, 1999 from the middle Eocene of Germany (holotype, SMF-ME 2092A), x-ray photograph. The white dots indicate the position of the presacral vertebrae. Vertebrae 14–16 can not be directly observed and their positions were estimated from the average distance between the vertebral bodies.

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 heterocoelous 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 heterocoelous, 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 pleurocoelous, 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-

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 plantarly 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 Sandcoleidae (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 postcrani-

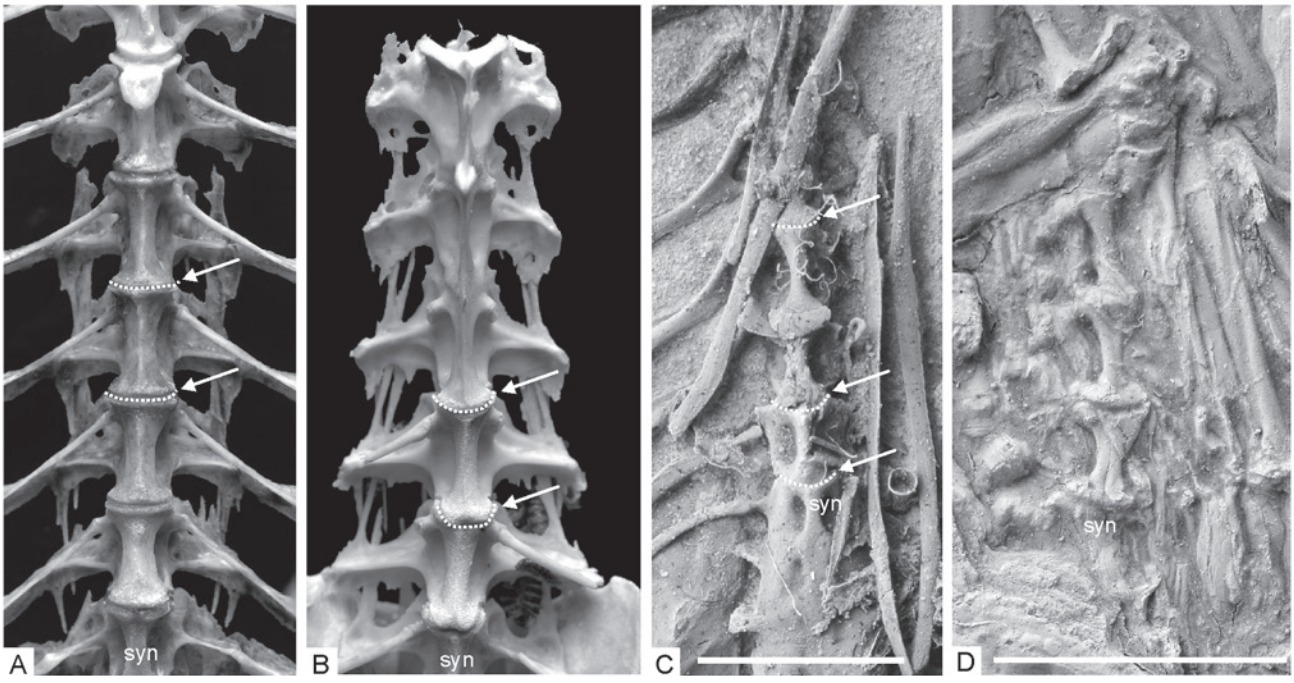

Fig. 4. Caudalmost thoracic vertebrae (ventral views) for comparison. **A**, opisthocoelous vertebrae of *Larosterna inca* (Charadriiformes, Sternidae). **B**, heterocoelous vertebrae of *Scolopax rusticola* (Charadriiformes, Scolopacidae). **C**, *Morsoravis sedilis* (holotype, MGUH 28930). **D**, *Pumiliornis tessellatus* (holotype, SMF-ME 2092A). Dotted lines (arrows) indicate the curvature of the rims of the corpora vertebrarum. Note the presence of pleurocoelous vertebrae in all four species. Abbreviation: syn – synsacrum. The fossil specimens were coated with ammonium chloride. Scale bars equal 5 mm; the pictures of the two extant taxa are not to scale.

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

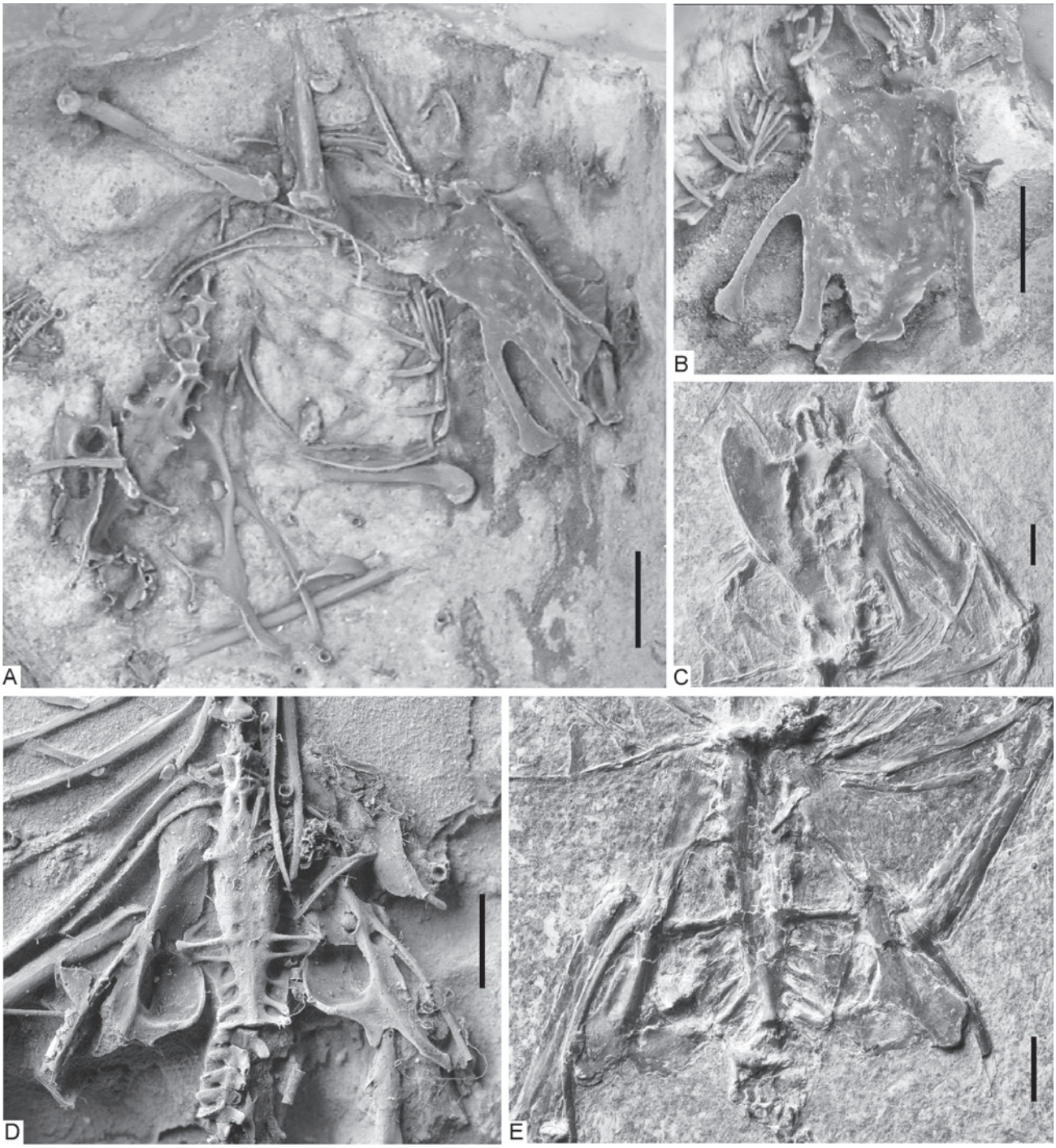

Fig. 5. **A**, partial postcranial skeleton from the Fur Formation (MGUH VP 1289), which may belong to *Morsoravis sedilis* (see text; the specimen is now lost, photo by S. L. Jakobsen). **B**, detail of the sternum of MGUH VP 1289 for comparison to that in C. **C,** *Eocuculus* cf. *cherpinae* from 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).

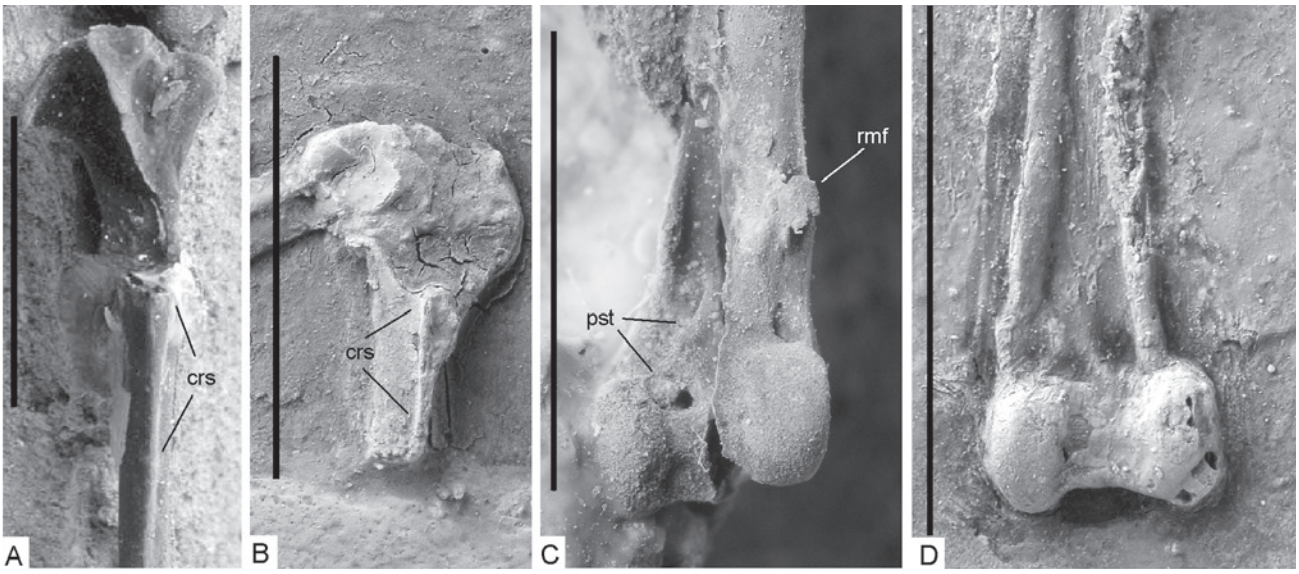

Fig. 6. Tibiotarsus of *Morsoravis sedilis* and *Pumiliornis tessellatus* for comparison. **A**, *M. sedilis* (holotype, MGUH 28930), proximal end of right tibiotarsus in medial view. **B**, *P. tessellatus* (holotype, SMF-ME 2092A), proximal end of left tibiotarsus in medial view. **C**, *M. sedilis* (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.

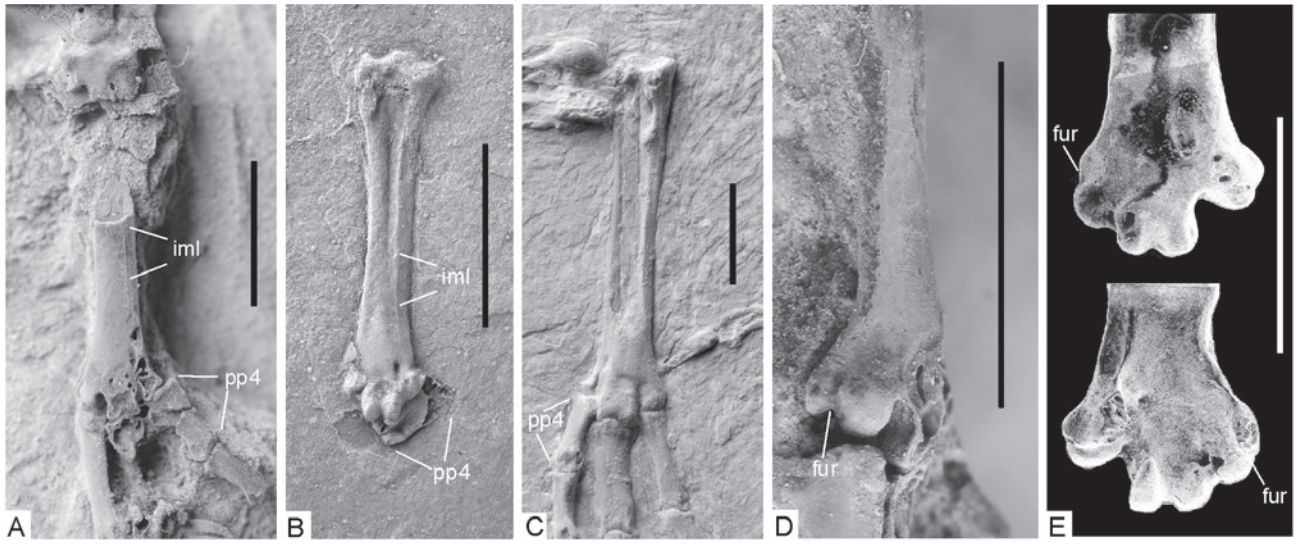

Fig. 7. Tarsometatarsus for comparison. **A**, *Morsoravis sedilis* (holotype, MGUH 28930), left tarsometatarsus in dorsal view. **B**, *Pumiliornis tessellatus* (SMF-ME 2475B), left tarsometatarsus in dorsal view. **C**, *Eocuculus* cf. *cherpinae* (SMF Av 425), right tarsometatarsus in dorsal view. **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.

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*.

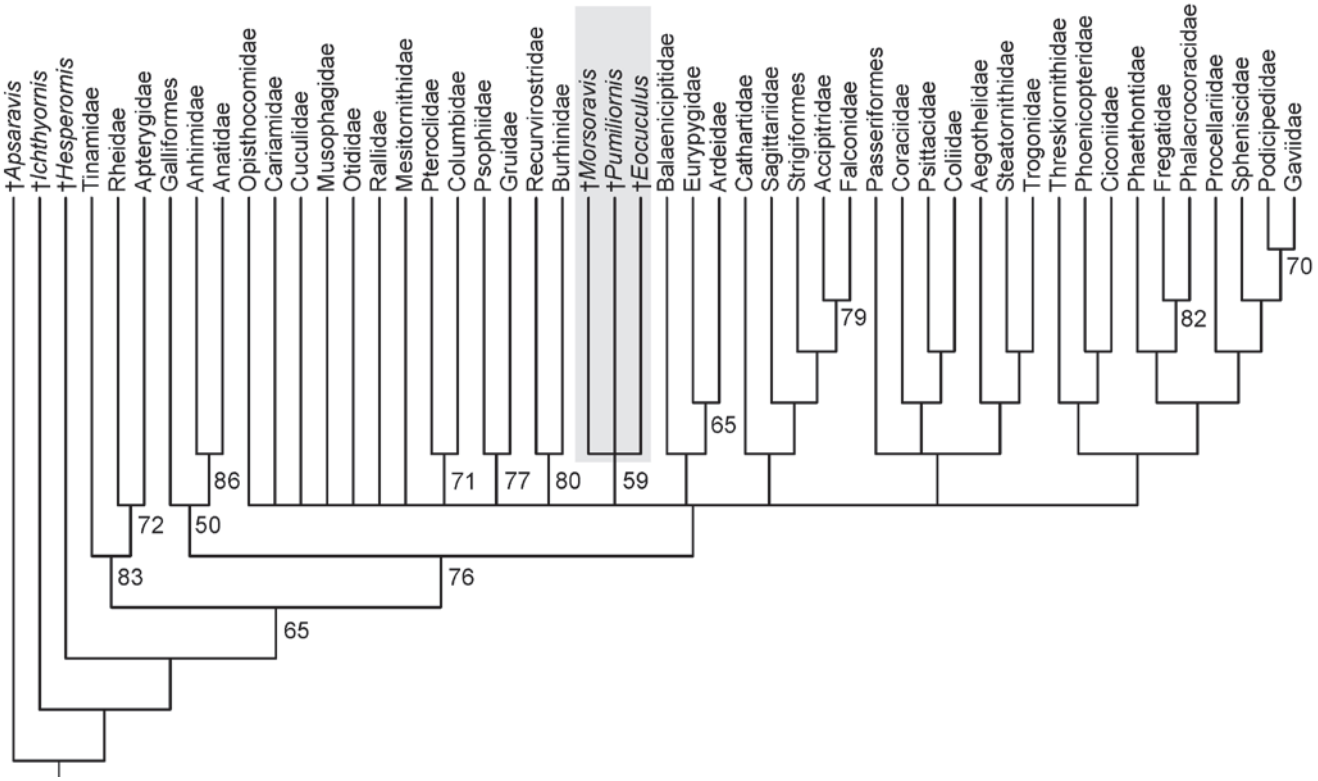

Fig. 8. Strict consensus tree of eight most parsimonious trees (Length = 769, CI = 0.21, RI = 0.47) resulting from analysis of the character matrix in Appendix 2. Unsupported nodes are collapsed, bootstrap support values are indicated next to the nodes. The clade including *Morsoravis*, *Pumiliornis*, and *Eocuculus* is highlighted in gray.

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 (*Balearica*) and Picidae (*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 Suloidea 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 tarsometatarsus 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 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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Appendices

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 rhynchokinetic: 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 maxillopalatini of ossa 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* (Bertelli *et al.* 2010 coded it as unknown).

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 quadrate, 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, Anhimidae, Phoenicopteridae, and Pteroclidae. Character state 2 was scored for Galliformes, 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 Psittaciformes as polymorphic for this character, as pleurocoelous vertebrae occur in some stem group representatives (Halcyornithidae, see Mayr 2002).

65 Coracoid, 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 ilioischiadicum 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 Phallus: 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 vasculare 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
??????????????????????????0????????00??????1?0??????????b?00000??0000000????000000001?000?000010000??001000010??0?????????
??????????????????????????????**????0**
Hesperornis
00?00000?000000000000**1**00000?0100100000?0?0000000??0000201100000000000010200?00???0???????120000100000000001000?????
??????????????????????????????????**??000**
Ichthyornis
00?00000?0??????????????000?a00??00000??00000001O?00?0b?01?000000000101O??0000000001000000
0a0100000000000000100??????????????????????????????????????**??0??**
Rheidae
1001000001001000000000000000001100010O?1111000000000001010000??0**1**001000020O?00???0??00???0?10**1**000000000000001010000??
?0010???0??????1?14??????001000**00000**
Apterygidae
1001000101000000000000000000011**1**000000011110000110010010100O??0000100001O0?00???0??00???0c1000000**0**00000011010000000
0000000000000010a120100??001?000**00000**
Tinamidae
1001000001000000000000000000010000100011110000100a000111000000011000000110110000000000000400000100100000000010000
0010000000000000000100a0100000000**a0000**
Galliformes
1000000000010000001111010100100100100100110**2**1000a10100111a0010001000010001011010100000000031011O1a010010100000000a0
0000000000000000000100100001000010O0**a0000**
Anhimidae
1010000000110?011011110101001001111001001101l0a10
0a1001010101000001000201200101010110000004111010101001000010000000???00????00??00??????????00000?000**00000**
Anatidae
1020000000110?001011110101101001111001001101l0aa000100101010100010000ab011001010101a**0**00000d1010a0001001000000011000O
0110001000ba?00a00a200000000010000**00000**
Opisthocomidae
1000100000000000001101100000101101010000110000110111001110100100111O??111100101110101**1**10000311110000000101001000000000
0000000100000011001000010000l?00**11000**
Podicipedidae
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1a01111?000100001111010000l?10011001400l?0100010011**1000**
Phoenicopteridae
1021000000100?1100101110001011**1**0100100011010101110001211010000000001111110011101011000010211101111111110000011000100
0010000000010000140010010O0?001**10000**
Threskiornithidae
1001010000110011001101100010110101010010001102**0**a011001001110100000000011100100101011100000003111001001011100010000O?00
0001000000001000001000000000100O**10000**
Cariamidae
1000000000111O**1**10011111000001011010100001100000101010000101000001000011011001010100011000021111010010000000101000O?
????1????0??????????????10001??00**10000**
Strigiformes
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0a0100100101011100000002111100000001000010000100001101000l?000010101100000011100**10001**
Recurvirostridae
1000010000010011000001001010100101001000110**2**0000110100000110100100000110010000101110000100201100101101100000001a000?
?????0???0??????????????00000110O**10000**
Burhinidae
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????1????0??????????????00000110O**10000**
Accipitridae
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aa1011001010111100000021110001010010000100001000111011000000001010310000001O?000**10000**
Falconidae
1100000100001011000101100000100101O0a000110010001101O0a11010010000001110110010101111000O0
0b1110011010010000100001000111011000000001000310000001010O0**10011**

Sagittariidae
1100000100a0100101???10000001001110100001100111001110000101000100000000112100101110100000002111101101000000010000000000010100000000001031000000010??00**10000**
Cuculidae
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Musophagidae
10000001000000000001011000001011110000001100000 0a10110001011010000001
1a0010010101010111000200110010100101001000000?0?00?0?1101????0?????????10000100**11000**
Cathartidae
11000000000000011 01???10000011101010010001100100 0a10100101010000000100010010010111110000000211100110100000001000000000100a11000000000100510000001110 00**10000**
Gaviidae
10000000000000?**1**1000111101000110101001000110001001100001010101000000000201000001010100000014011010011001 11?000110000011000000011001010140 01?000001000**10000**
Spheniscidae
10010000000000010001111010001101111010001100000011000010001000000000011010000 0???0??000000101100001100000011011?0000a10000000100001101200 10??000?010**10010**
Phaethontidae
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Fregatidae
1101001?10000?**1**1101101100001110111000000110001001101000010110?10100000112100101011100000102011010001001010010001010 01111100?000000100050000001 00??10**10000**
Phalacrocoracidae
1101101?10100?11a1???1100000110111001000110011001000002**0**0110111010001010110000101110000010311100001100101101001101 0011001?00000000?000210000010 01?10**11000**
Balaenicipitidae
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Eurypygidae
10000100000 10?1100010110000010111100100011000001010000211010100010001110110010101110000000201100000100100001000000? ???????????0???????????000011?00**10000**
Ardeidae
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Ciconiidae
10000000001 10?1101???110000a11010101100011000 0a10001001010100010a000a01111001010111a000a003111011101 1a11000100000010000110000000100000100000100 0?000**10000**
Procellariidae
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Otididae
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Pteroclidae
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Columbidae
10000100000000101 01???10000001011110000001100000011000001101010001000 0a00a11110101110100100201100100100101011000000010000000000000000000010001a00110000**11000**
Rallidae
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Psophiidae
10000000000000010001111000001001010110001100000001000021100010000010002121001010100010000031111010011110000100000 0?????1????0??????????????100000?00**10000**
Gruidae
10000**1**00000a10110000111000101011110110001102**0**0010000002110001000001 0a0212100101011100000003111101001111010000100000000000?000000000001000000000000**10000**
Steatornithidae
11001001001100001 1???10000001001110000101100000001000001001110001000000011001011111100000010110000000010000100000001 00011?001?0?0?0000?0100000011?00**10000**

Psittaciformes
110010010010a00101???1100000100111000000110001001l0aa0001**a**101000a000111011001010111100000021110000a00100011100
0a0100000110000?0101111090101000101000**11a11**
Coliiformes
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1a1010000010110000110010**01**0100000010000011001?0101101051101100001?00**111?0**
Trogonidae
1000100100000000010110100000010011100001011001000110000001011100010000100010010111110100000101100000100101111000000011?1?????01??0?0??008?1??100011000**11010**
Aegothelidae
11000000000??00100000100000010011101000011000100110000001011100000000000010010101110000000001100000100101011000000010??01?001?0?0?1000?0100000011?00**10010**
Coraciidae
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Passeriformes
10000000000000000000011000001 0a10100000011001000110100001011100010000110110010101110 00a000101100000100101111000 0a0a1000011001??00010007b1a0100010000**10a00**
Morsoravis
10**?**00100?**00**?00??????????0?0???010100?0?01102???????10010**1**1000????????????0??????????????????01?11001001 0??????100??**0**?????????????????????????????????????**?1111**
Pumiliornis
10???10?????0?????????????????????1?????0?1???????????01011????0010?0????0?00????111?00??00?011?0??000010???100??0??????????????????????????????????????111
Eocuculus
??11?01?0????????0?000??????1??00??001?1100??0100 10??1100??0??11
Mesitornithidae
10000100?0000111001101100000101101000000110200001001101110001 0?0100001101011101010100010002001101001001011010000000?????????????????????????????????????10110