

Another Charadriiform-Like Bird from the Lower Eocene of Denmark¹

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Received August 17, 2012

Abstract—We describe an exceptionally well-preserved partial skeleton of a new bird from the early Eocene Fur Formation of Denmark. Like other fossils from these marine deposits, the partial skeleton is three-dimensionally preserved and articulated. This new Danish specimen consists of a skull, vertebral column, ribs, pelvis, and hindlimbs. Concerning characters of the pelvis, tibiotarsus and tarsometatarsus, the new fossil bears morphological affinities to charadriiform birds (shorebirds and relatives). A phylogenetic analysis of higher neornithine (modern birds) taxa also supports a close relationship between the new specimen and modern Charadriiformes. The morphologies of the skull and vertebrae, however, distinguish the new fossil from all recent charadriiform families.

Keywords: Fossil birds, Fur Formation, *Scandiavis*, Lower Eocene

DOI: 10.1134/S0031030113110026

INTRODUCTION

In recent years the lower Eocene Fur Formation of Denmark has produced a number of exceptionally preserved fossil birds. Previous research has recognized the presence of several taxa, which also occur in other Eocene localities of Europe, such as the palaeognathous Lithornithidae, the “gruiform” Meselornithidae, the apodiform Eocypselidae, Threskiornithidae and Trogoniformes (Kristoffersen, 1999, 2002a, b; Dyke et al., 2004; Leonard et al., 2005; Lindow, 2007; Mayr, 2009, 2010; Mayr and Bertelli, 2011; Bertelli et al., 2011). Another species, *Morsoravis sedilis*, whose holotype is an exquisitely preserved skeleton, was assigned to Charadriiformes (Bertelli et al., 2010). Charadriiform affinities of *Morsoravis* were, however, questioned by Mayr (2011b), who hypothesized that it is more closely related to the taxon *Pumiliornis* from the early Eocene of Messel.

Here we describe another exceptionally well-preserved avian fossil from the Fur Formation, which was previously identified in an unpublished PhD thesis as a charadriiform bird (Lindow, 2007). We revise some of the characters previously highlighted by the latter author and identify additional features, which constrain the affinities of this bird.

This new specimen is another example of exquisitely preserved Early Eocene avifauna and, as such, is a valuable addition to our knowledge of the diversity of the Fur Formation.

MATERIAL AND METHODS

Anatomical nomenclature follows Baumel and Witmer (1993); all measurements are given in millimetres (rounded to the nearest 0.1 mm). Morphological comparisons were made with fossil and recent material from collections of the Forschungsinstitut Senckenberg, Frankfurt, Germany, and the Museum für Naturkunde, Berlin, Germany. Institutional abbreviations: FU, Moler Museet, Mors, Denmark.

Cladistic analysis. To evaluate the phylogenetic position of the new bird, we performed a cladistic analysis including FU171x within a diverse neornithine sample. Given that FU171x has previously been considered as closely related to Charadriiformes (Lindow, 2007), we have expanded in particular the charadriiform terminals (i.e., Burhinidae, Charadriidae, Haematopodidae, Scolopacidae, Thinocoridae, Rostratulidae, Jacanidae, Laridae, Thinocoridae and Stercorariidae) in our taxonomic sample. The character matrix presented here includes 196 characters (mainly based on Mayr’s 2011b data set); forty-five morphological characters were added from other pre-

¹ The article is published in the original.

vious published analyses (Strauch, 1978; Mayr, 2003, 2004, 2005, 2011a; Mayr et al., 2003; Bertelli et al., 2011). Characters descriptions and codings for the new Danish bird (62 characters) are given in Appendix 2.

The data set was subjected to a parsimony analysis with equal weighting of characters using the phylogenetic program TNT (Goloboff et al., 2008). Heuristic, unconstrained searches for optimal trees were conducted using 1000 replications (random addition sequence of taxa followed by TBR branch swapping) with an extra TBR branch-swapping round on the optimal trees, and followed by application of the parsimony ratchet technique. To estimate the support of groups, we used both absolute and relative Bremer supports calculated on the basis of an incremental sample of 10000 suboptimal trees up to 8.0 units of fit less than the optimals. All support analyses were performed in the phylogenetic program TNT (Goloboff et al., 2008).

SYSTEMATIC PALAEONTOLOGY

AVE S LINNAEUS, 1758

NEO G N A T H A E PYCRAFT, 1900

Genus *Scandiavis* Bertelli, Lindow, Dyke et Mayr, gen. nov.

E t y m o l o g y. The generic name is derived from *scandia* (Latin), in reference to Scandinavia, and *avis* (Latin) meaning bird.

T y p e s p e c i e s. *Scandiavis mikkelsenii* sp. nov.

D i a g n o s i s. Medium-sized bird, with (1) skull with long narial openings, (2) pars symphysialis of mandible with flat ventral surface, (3) presence of a dorsally recurved processus retroarticularis (mandible), (4) third cervical vertebra with distinct subovated processes on dorsal surface of caudal margin, (5) ribs with unfused processus uncinati, pelvis with (6) ilia not fused to synsacrum and (7) deep pits at the base of the spina dorsolateralis ilii, (8) tibiotarsus with relatively long fibula (reaching three-thirds the length of the tibiotarsus), (9) femur with prominent process next to condylus lateralis, (10) tibiotarsus with distinctly notched distal rim of condylus medialis, (11) a rather short tarsometatarsus, not exceeding the femur in length, (12) trochlea metatarsi II plantarly deflected and reaching much less far distally than trochlea metatarsi IV, (13) a wide os metatarsale I, and (14) a short hallux.

G e n e r i c c o m p o s i t i o n. Type species.

C o m p a r i s o n s. Characters 1, 2, 4, 7, 9, 13 are autapomorphic for the new taxon. Characters 3, 6, 7, 10, 12 are shared with extant charadriiform taxa.

Scandiavis mikkelsenii Bertelli, Lindow, Dyke et Mayr, sp. nov.

E t y m o l o g y. The species epithet honours Mr. Bent Søren Mikkelsen, who found the holotype.

H o l o t y p e. Specimen FU171x, incomplete skeleton preserving the skull and mandible, vertebral column, the pelvis and hindlimbs; Coast cliff at Ejerslev, Denmark, Isle of Mors; earliest Eocene Fur Forma-

tion (earliest Ypresian; Beyer et al., 2001). The specimen derives from the stratigraphic level around ash layer +15 of the formation.

D e s c r i p t i o n (Figs. 1–4). **Skull.** In overall proportions, the skull resembles that of the “gruiform” Otididae (Fig. 2). The narial openings are very long but do not extend caudally to the naso-frontal hinge (as they do in schizorhinal nostrils). In addition, the caudal margin of the nostrils is not as rounded as in typical holorhinal nostrils. In their morphology, the nostrils of the new fossil more closely approach the condition found in pseudo-holorhinal birds, such as Turnicidae. The beak is moderately long and measures about half of the total length of the skull. The rostrum maxillae is short, making up less than one third of the total length of the upper bill, and has a broadly rounded tip. Five foramina neurovascularia are visible in a line parallel to the tomial shelf; the caudalmost foramen is situated cranially in a thin groove.

No septum nasale is visible through the external nares. Remains of the processus maxillopalatinus are preserved in the antorbital area. The head of the os lacrimale is wide and not fused to the frontal bone (os frontale); the descending process is long and slender but does not contact the os jugale (Fig. 2). The morphology and position of the os lacrimale corresponds to the condition seen in some Charadriiformes (e.g., Scolopacidae) in that the head of the bone is curved with the ventral end medially inflected, enclosing a large and rounded fenestra orbitonasalis. By contrast, in “gruiform” birds the head of the lacrimal forms a plate that meets the descending process at a right angle. Rostrally, the processus orbitalis of the os lacrimale is excavated by a deep fossa that bears two foramina at the base of this depression. An incomplete and partially articulated sclerotic ring (ossae sclerae) is preserved within the orbit (Figs. 1, 2). Contacting the rostral portion of the scleral ring, the os ectethmoidale is visible. Its morphology also resembles the ectethmoid of Charadriiformes in that it is dorsoventrally narrow. In contrast with many shorebirds it does not fuse to the processus orbitalis of the lacrimal. Unlike *Scandiavis*, in most “Gruiformes” the ectethmoid forms an extended plate unfused to the lacrimal.

In lateral view, the caudal surface of the braincase is somewhat angular with a low foramen magnum. The fossil exhibits a distinct crack through the temporal area and across the cranium (Fig. 2). The position of this break is, however, not comparable to that of a sutura frontoparietalis. Accounting for the morphology and slight displacement at this break, this feature appears to be an artifact of preservation.

The interorbital surface surrounding the orbit forms a well defined supraorbital margin. Unlike many Charadrii and Lari (as well as other groups such as Gaviiformes, Sphenisciformes and Procellariiformes), the frontals of *Scandiavis* lack distinct fossae for salt glands. The septum interorbitale consists of a narrow circular rim that is more developed rostrally

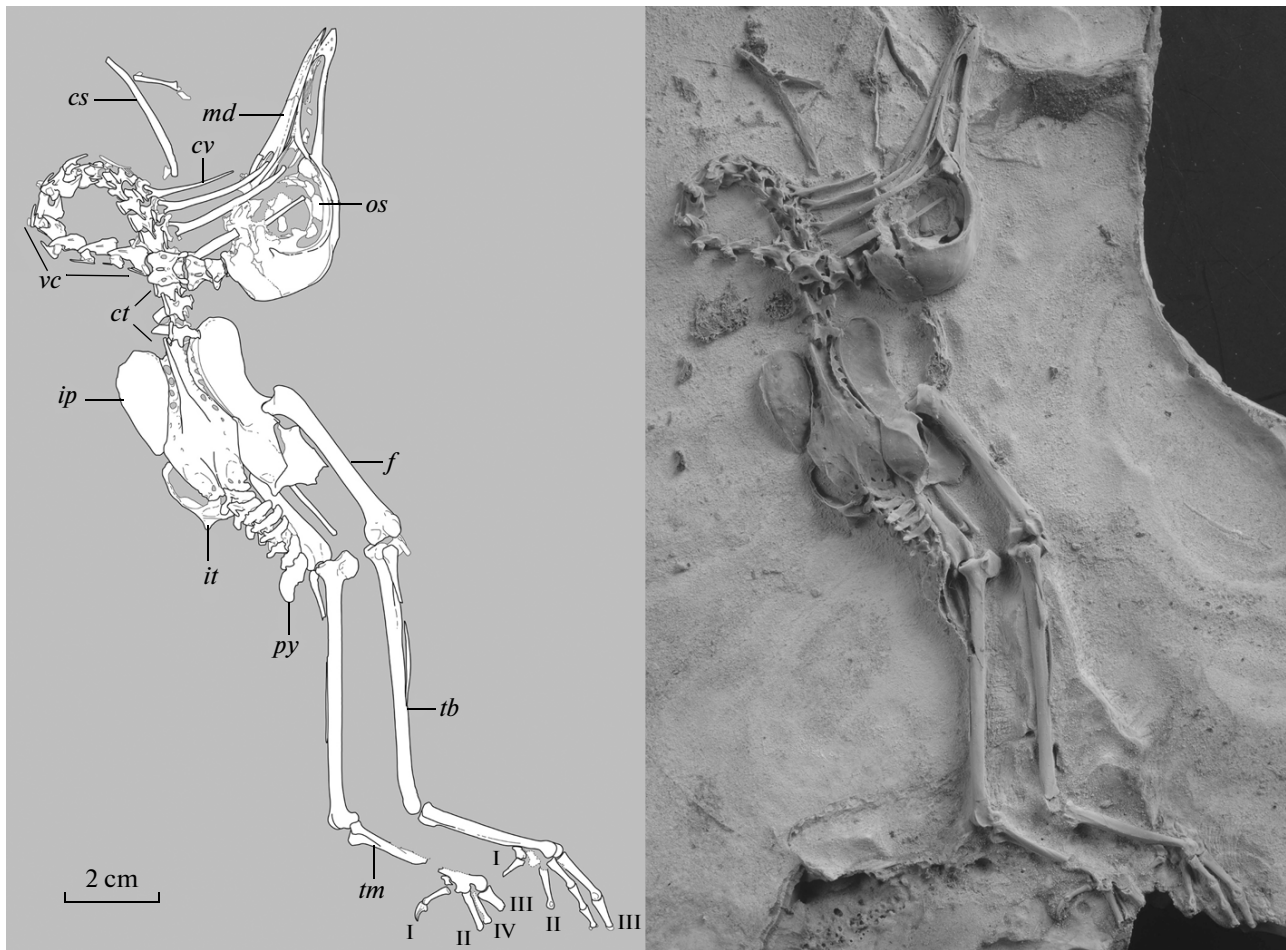


Fig. 1. *Scandiavis mikkelsenii* gen. et sp. nov., holotype FU171x, photograph (right) and interpretative drawing (left) of the slab; Fur Formation, Denmark; early Eocene. Designations: *ct*, thoracic vertebrae; *cs*, costa sternalis; *cv*, costa vertebralis; *f*, femur; *ip*, ala preacetabularis ilii; *it*, spina dorsolateralis ilii; *md*, rostrum mandibulae; *os*, ossa sclerae; *py*, pygostyle; *tb*, tibia; *tm*, tarsometatarsus; *vc*, cervical vertebrae; I hallux; II–IV, digitus II–IV.

(Fig. 2). A large fonticulus orbitocranialis opens dorsal of the caudal portion of this septum. The processus postorbitalis is short and ventrally directed. Bounded by these processes, the temporal area exhibits a small temporal notch (fossa temporalis). Ventrally, the shape of the orbit is delimited by a straight and thin os jugale.

The quadratum is largely exposed in lateral view (Fig. 2). The processus oticus is mostly covered by sediment, and lies close to its natural articulation with the os jugale and braincase. It is slightly displaced caudally, exposing the cotyla quadratojugalis of the condylus lateralis. The processus oticus is very wide and a portion of the articular facet of the capitulum squamosum is discernible. In the otic cavity, a rounded pneumatic opening is visible caudal of the processus oticus. Such pneumatic openings are also present in some Charadriiformes (e.g. *Jacana*, *Thinocorus*, *Rostratula* and most Scolopacidae examined) and most “gruiform” taxa. However, the presence of a single foramen in *Scandiavis* is more similar to the condition

observed in some Charadriiformes, such as Scolopacidae.

The fenestra vestibuli and the cochleae of *Scandiavis* are elongated and about the same size, separated by a slender crista interfenestralis. The recessus tympanicus rostralis appears very well developed. Two openings are visible on the ventral margin of the tympanic cavity; the larger possibly corresponds to the opening for the ostium canalis tubae auditivae, and more caudally a rounded foramen is visible which may correspond to the entrance of the foramen pneumaticum caudale.

In occipital view, the left margin of the foramen magnum is discernible, and its position and plane are relatively low. Immediately lateral of the foramen magnum, the exit for the vena occipitalis externae is represented by a deep sulcus. Dorsal of the foramen, the prominentia cerebellaris is weakly developed. A distinct dorsoventral opening is visible on the exposed surface lateral of the prominentia; the corresponding area that is pierced by the fonticulus occipitalis in

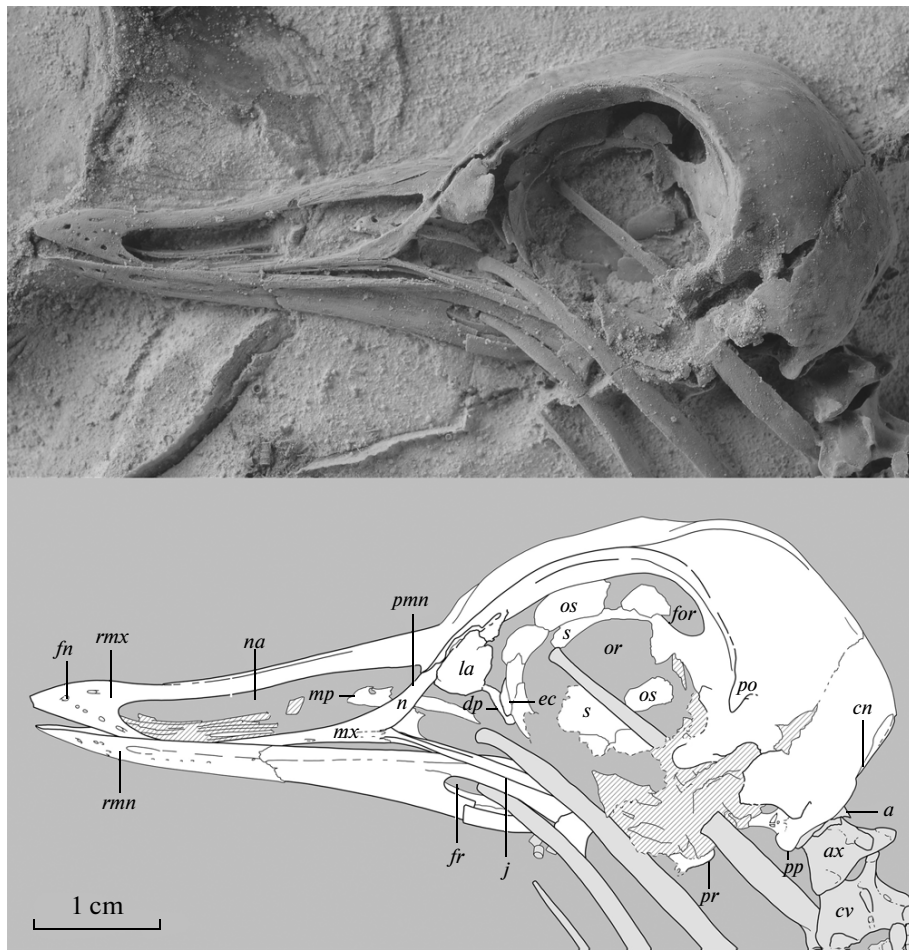


Fig. 2. *Scandiavis mikkelsenii* gen. et sp. nov., holotype FU171x, photograph (above) and interpretive drawing (below) of the skull in left lateral view. Designations: *a*, atlas; *ax*, axis; *cn*, crista nuchalis transversa; *cv*, third cervical vertebrae; *dp*, processus orbitalis of os lacrimale; *ec*, os ectethmoidale; *fn*, foramina neurovascularia; *for*, fonticulus orbitocranialis; *fr*, fenestra rostralis mandibulae; *j*, os jugale; *la*, os lacrimale; *n*, os nasale; *na*, apertura nasi ossea; *mp*, processus maxillopalatinus; *mx*, os maxillare; *os*, ossae sclerae; *or*, fonticulus interorbitalis; *pmn*, processus maxillaris; *po*, processus postorbitalis; *pp*, processus paroccipitalis; *pr*, processus retroarticularis; *rmn*, rostrum mandibulae; *rmx*, rostrum maxillae; *s*, septum interorbitale.

some charadriiform taxa (e.g. *Recurvirostridae*, *Rostratulidae*, *Charadriidae*, and *Scolopacidae*), *core-Gruiformes*, as well as other birds such as *Anseriformes*, and *Phoenicopteriformes*. Whether the openings represent such fonticuli in *Scandiavis* was not possible to determine with certainty; these openings are weakly developed and irregular in outline, which contrasts with the morphology of true fonticuli, which are markedly rounded openings. The crista nuchalis transversa is prominent and forms a sharp caudal border of the occipital area.

Mandibula. The mandibula of *Scandiavis* is shallow and slender. The dorsal surface of the pars symphysialis is unusually flat, with a rounded tip; this morphology contrasts with the pointed condition present in most birds (Fig. 2). The lateral surface of the rostral part displays five foramina neurovascularia. The dorsal margin of the ramus mandibulae slopes, and forms a laterally projecting ledge that defines a distinct lateral

depression (fossa lateralis mandibulae), as in, e.g., some extant Charadriiformes and Rallidae. In the midsection of the mandibula, the lateral surface of the ramus becomes concave, and there is a large and elongated fenestra rostralis mandibulae, which is partially covered by ribs; a portion of the os suprangulare is visible through this fenestra. The caudal section of the mandibula is also partially covered by ribs and by the os jugale, so that it is not possible to discern whether a fenestra caudalis mandibulae was present. The caudal end of the mandible is mediolaterally compressed, bearing a dorsocaudally directed knob-like projection. There is a small, hook-like processus retroarticularis, whose shape resembles the condition found in some Charadriiformes and “Gruiformes” such as Rallidae.

Vertebrae. The praesacral series consists of 20 free vertebrae, i.e., atlas, axis, nine cervicales, two cervicothoracicae, and seven free thoracicae. There is some variation in extant birds concerning the number of free

praesacral vertebrae, with palaeognathous birds and Galloanseres having more than 20 and higher land birds 19 or less (Mayr and Clarke, 2003).

The first cervical vertebra resembles that of some extant “Gruiformes” (e.g. Rallidae) in general morphology (Fig. 2). The dorsolateral portion of the arcus atlantis is exposed and slightly disarticulated, showing the left processus articularis caudalis. The axis is preserved in dorsal aspect and is wider than long, lacking processus costalis or pneumatic openings on the lateral surface of the corpus (Fig. 2). The processus spinosus is rod-like, somewhat elongated and more dorsally than caudally projected in lateral view; this morphology also resembles that of some Charadriiformes (e.g. Scolopacidae) and “Gruiformes” such as Rallidae. By contrast, the processus spinosus is weakly developed in other gruiform taxa (e.g., Gruidae, Psophiidae, Aramidae) or elongated and caudally directed in other charadriiform groups such as Laridae. Caudally, a fovea for elastic ligaments is well developed at the base of this process. The processus articularis caudalis is relatively broad and somewhat double-headed in lateral view, bearing a rather lateral projection with a slightly concave and rounded articular surface. No distinctive bridge-like connection to the processus articularis cranialis was observed in *Scandiavis*.

The third and fourth cervical vertebrae are also exposed in dorsal view (Fig. 2) and their general shape resembles that of some charadriiforms (e.g., Charadriidae, Scolopacidae). Compared with the following vertebra, the morphology of the third vertebra is distinctive. Most notably, its caudal end exhibits a distinctive condition in that it bears two well-marked, subovate processes on the dorsal surface of its caudal margin, which are absent on the fourth cervical vertebra. Similar processes occur in extant Galliformes (e.g., Numididae, Meleagrididae, Tetraoninae), but are absent in charadriiform birds and most “Gruiformes” (except Rallidae), among other birds. In dorsal view, the centrum of the third cervical vertebra is less elongated and caudally wider, while the next, i.e., fourth cervical is distinctly wider at the midsection of the corpus vertebrae. Both cervicals, three and four, have a blade-like processus spinosus, trapezoidal in shape and relatively well developed. This morphology also corresponds to that of most charadriiform groups; by contrast, the first cervical vertebrae are mediolaterally narrow and comparatively more elongated than in shorebirds, with a rounded processus spinosus as in “gruiform” taxa such as Rallidae.

On the lateral surface of the corpus of these vertebrae, a bony bridge connects the ansa costotransversaria to the zygapophysis caudalis enclosing a small foramen in both elements. These openings are particularly developed in cervical four of most charadriiforms. In cranial view, the zygapophysis of cervical four is visible and slightly disarticulated, exposing an elongated suboval articular facet. Ventrally, the foramen transversarium is also exposed and more medially

placed relative to the facet as opposed to a ventral position as in other charadriiforms examined.

Cervical vertebra five is exposed in right dorsolateral view and a well-developed, blade-like processus spinosus can be discerned. This process is somewhat hooked and caudally pointed while cervical six bears a trapezoidal processus. On the cranial side, a distinct lamina arcocostalis and processus costalis appear in these elements, becoming progressively more developed in the following cervicals. The lateral surface of the corpus bears a short and somewhat prominent lateral crest. A similar feature was observed in Charadriiformes (e.g. Charadriidae, Scolopacidae) and Rallidae, although less developed, but in approximately the same position as the crest is located in *Scandiavis*, while other charadriiforms (e.g. Burhinidae) and “gruiforms” (e.g. Otididae, Aramidae) possess an osseous bridge from the midsection of the corpus vertebrae to the processus costalis (Mayr and Clarke, 2003). However, the vertebrae lack a connection between these structures in the fossil and such processes may not represent an incipient development of the bridge. The following vertebrae also have a relatively well-developed lateral crest, which develops into a blade-like process in cervicals eight and nine. On the cranial end of cervical eight, a distinct pair of spine-like processes parallel to the processus costalis appears in the caudal margin of the lamina arcocostalis. From cervical eight onwards, the vertebral column gradually twists and the vertebrae become more ventrally exposed, thus showing two muscular impressions on the ventrolateral surface of the vertebral centrum produced as oval depressions and separated by a prominent ridge. This condition resembles the intermediate groups of cervical vertebrae of most Charadriiformes, in which a marked muscular impression is present on each side and encloses a distinct medial ridge along the ventral surface. The vertebral centrum of cervical nine is more exposed and the processus spinosus becomes distinct; the zygapophysis caudalis is also visible and slightly disarticulated with an elongated suboval articular facet. A wide incisura caudalis is developed on the caudal margin of the vertebra. This condition differs in the intermediate cervicals of charadriiforms in which the caudal margin is less deep and the processus spinosus. The general morphology of the centra is similar to the previously described elements; only the muscular impressions on the ventrolateral sides are more developed in the centrum of cervical nine; this feature is very pronounced in cervical 10. The vertebral corpus of the following elements (10–11) is transversally wider and comparatively shorter in length than previous cervicals (5–9); this is most clearly seen in vertebra 11. A deep lateral excavation is visible on the right lateral side of the corpus of this vertebra. This excavation is deeper and smaller than the previously described ventrolateral muscular depressions; furthermore, they are developed as a pneumatic opening at the cranial end, next to the lamina costotransversaria. The processus costalis of cervical 11 appears slightly

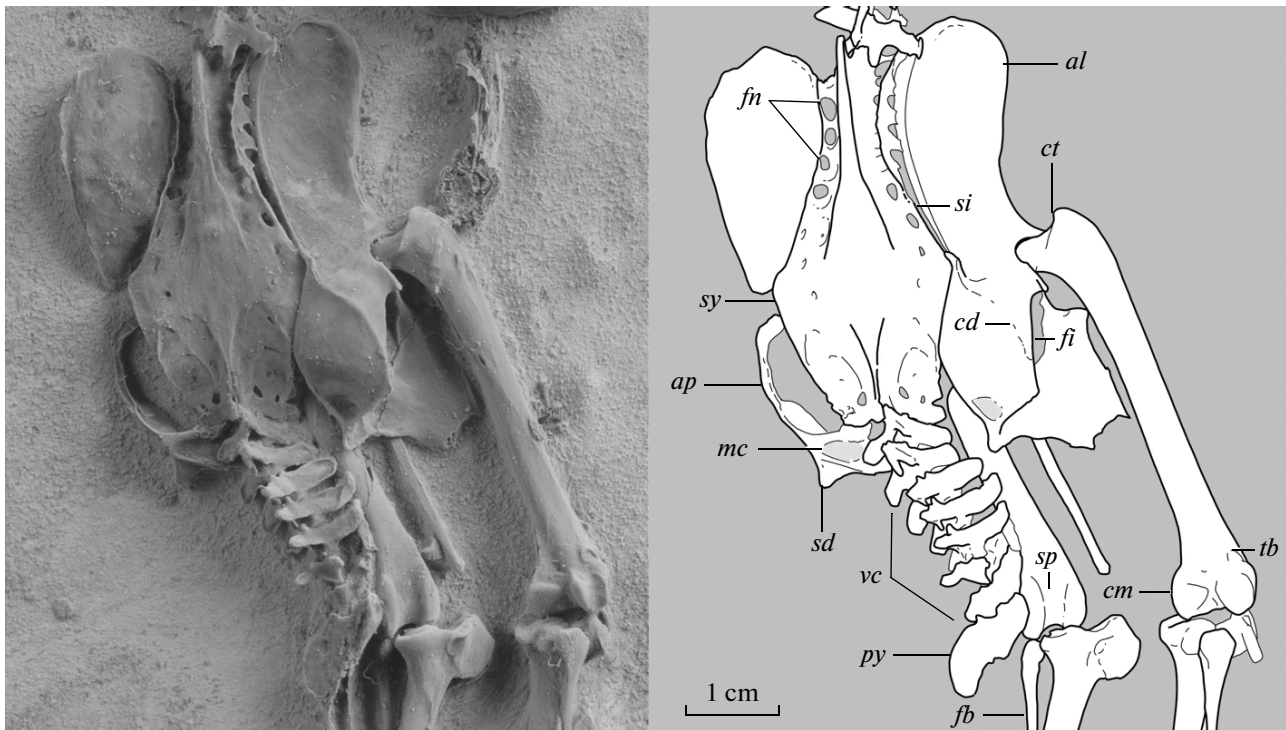


Fig. 3. *Scandiavis mikkelsenii* gen. et sp. nov., holotype FU171x, photograph (left) and interpretive drawing (right) of pelvis and femora in articulation (dorsal view). Designations: *al*, ala preacetabularis ilii; *ap*, ala postacetabularis ilii; *cd*, crista dorsolateralis ilii; *cm*, condylus medialis; *ct*, crista trochanteris; *fb*, fibula; *fi*, foramen ilioischadicum; *fn*, foramina intertransversaria; *mc*?, interpreted as attachment of musculus caudofemoralis; *py*, pygostyle; *sd*, spina dorsolateralis ilii; *si*, sutura iliosynsacralis; *sp*, sulcus patellaris; *sy*, synsacrum; *tb*, tubercle interpreted as attachment area of musculus iliofibularis; *vc*, vertebrae caudalis.

shorter and a relatively similar spine-like process projects from the caudal margin of the lamina.

We distinguish two cervico-thoracic vertebrae (vertebrae 12 and 13) possessing short, floating costae incompletae; these vertebrae are short and transversally wide. The lateral margins of the centra are distinctly arched and become gradually wider in cervical 13. Both processus transversi are preserved; these processes are broad, with large caudal projections.

Seven thoracic vertebrae (14–20) are exposed in *Scandiavis*; these elements are preserved in articulation and unfused. They do not fuse to form a notarium, which is present in few Charadriiformes (e.g., Jacanidae) and some core-Gruiformes (Psophiidae, Aramidae, and Gruidae). The first three thoracic vertebrae (14–16) are exposed in lateral view and appear slightly wider than long; the zygapophysis caudalis reaches far back, interlocking with the corpus of the following vertebra. The incisura caudalis is comparatively wider and more developed than the vertebral body. The centra are dorsoventrally compressed with a strongly concave ventral margin defined by a pair of projections from the cranial and caudal ends. The corpus lack the typical lateral recesses of birds such as Charadriiformes (and also present in *Morsoravis* and other birds). Unlike charadriiforms, the processus transversi possess a thickened lateral rim, and bear a caudally directed process as in Rallidae. The processus

spinosis is rectangular with a marked, thickened dorsal rim, becoming relatively longer in thoracics 15 and 16. The following vertebra (17) and the cranial part of thoracic 18 are covered by cervical four. Thoracics 19–20 that are exposed in dorsal view are wider than long, with a wing-like processus transversus which bears a caudally projected spine-like process.

There are seven free vertebrae caudales, all of which are visible in dorsal aspect (Fig. 3). These vertebrae are wider than long, with well-developed caudally oriented processus transversus; all possess arched processus spinosus. The pygostyle is exposed in right lateral view. It is large and blade-like with a rounded dorsal margin; the caudoventral edge has a thickened rim. There is no well-developed discus pygostyli, and the caudal end of the bone is narrow.

Costae. One cervical rib (costa vertebralis) and five thoracic ribs (costae sternalis) are preserved in the specimen (Fig. 1). Four of the thoracic ribs are in close association with their respective thoracic vertebrae. The cranialmost rib is preserved in articulation (with a visible suture) with a caudodorsally projected processus uncinatus. These processes are also articulated to the third and fourth ribs. The area of a possible processus uncinatus in the caudalmost ribs is obliterated by a crack.

Pelvis. The pelvis of *Scandiavis* is exposed in dorsal view (Fig. 3). It is comparatively wide and short with the preacetabular portion of the ilium being consider-

ably longer than its postacetabular portion. The iliac blades are wide and spatulate and the ala preacetabularis ilii shows a rounded cranial end. The suturae iliosynsacrales are open throughout their entire length, a condition also present in most Charadriiformes, *Procelariiformes*, and *Morsoravis* but it different from most gruiforms—with the exception of Eurypygidae—where both iliac blades are fused to the crista iliosynsacralis, enclosing paired canalis iliosynsacralis.

The dorsal surface of the ala postacetabularis ilii is concave (the left side is mostly broken). The lateral edge is less angular than in most “gruiform” groups—except for Eurypygidae—in which the edge forms a pronounced ledge. A short and rounded crista dorsolateralis ilii projects between the dorsal and lateral sides; this crest prolongs caudally to form a slightly dorsally projected spina dorsolateralis ilii. The morphology of these processes differs from that in Eurypygidae and Rhynochetidae—in these birds the spina is longer and extending farther caudally. One of the most distinctive features of the pelvis of the fossil is the presence of deep pits at the base of the spina (Fig. 3), which probably correspond to the point of attachment of musculus caudofemoralis, a muscle that forms part of the pulley for directional changes of the tail (Baumel and Witmer, 1993: 107). The position of these depressions are comparable to those seen in some Charadriiformes (e.g., Laridae, Scolopacidae) and Rhynochetidae. In the extant taxa, however, they are clearly less developed than in the fossil, in which the pits are notably deeper.

The foramen acetabuli opens at the distal half of the ilium; a small portion of the tuberculum preacetabulare is visible on its ventrocranial margin. A marked processus antitrochantericus projects caudolaterally above the foramen acetabuli. Caudal to the acetabulum, there is a rounded foramen ilioischadicum and the crista dorsolateralis ilii forms a shelf overhanging the foramen and the ala ischii. A closed and circular foramen obturatorium is visible on the right side of the pelvis; this foramen is similar in size to the fused portion of the ischium and pubis.

Only the base of the right ischium is exposed and the distalmost end is missing. The caudal border of this lamina has a smooth appearance, and its morphology indicates that, unlike most charadriiform and gruiform groups, the ischium of *Scandiavis* lacks the distinct incisura marginis caudalis that characterizes the pelvis of Rhynochetidae and Eurypygidae.

A general synsacral ossification is present in the fossil, with several small foramina intertransversaria mainly in the preacetabular area. By contrast, in most recent and fossil Charadriiformes (Mayr, 2000a), the degree of ossification between the processus transversus of adjacent vertebrae is reduced and the synsacrum is heavily perforated by large fenestrae. This condition is also present in the gruiform Eurypygidae and Heliornithidae.

The dorsal surface of the proximal end is excavated by a deep sulcus iliosynsacralis extending caudally as

far as to the middle part of the synsacrum; these depressions are perforated by two parallel rows of foramina intertransversaria. A median crista spinosa synsacri is situated between the grooves; this crest becomes wider caudally and remains separated from the crista iliaca dorsalis. The body of the synsacrum is widest at its midpoint, and forms a rather flat dorsal surface pierced by two small foramina. The remaining caudal portion has deep lateral depressions in shape of two marked ovated scars that may represent the attachment areas of muscles of the tail (musculus levator caudae). At the distal end of the synsacrum, both caudalmost vertebrae remain incompletely fused.

Femur. Both femora are preserved; the right one lies in articulation with the foramen acetabuli and is exposed in caudal aspect, the left femur is mostly visible in cranial aspect (Fig. 3). The morphology and overall proportions of the bone resembles those of the femur of extant Eurypygidae. The crista trochanteris is cranially prominent and well defined. The shaft is not strongly curved and comparatively straight; on the cranial surface, the linea intermuscularis caudalis is very distinct. On the distal end of the right femur, a very pronounced and rounded process lies just proximal to the condylus lateralis that corresponds to the ligamentous ansa for musculus iliofibularis (Fig. 3). A less extreme condition occurs in Charadriiformes (e.g. Laridae, Charadriidae), but unlike the prominent tubercle of the fossil, this structure is only weakly marked. Some other birds such as the “gruiform” Eurypygidae and the Columbidae also possess this slightly elevated process on the lateral margin of the distal femur. A prominent crista medialis supracondylaris extends proximally from a sharp laterally orientated ridge that projects on the proximal articular surface of the condylus medialis. These two crests form the medial and distal borders of a deep fossa poplitea. On the condylus lateralis, the crista tibiofibularis protrudes more cranially than the crista lateralis but is only moderately developed. The shape of this crest is markedly rounded when viewed in lateral aspect, with a sharp proximal edge. The condylus medialis is more cranially projected and wider than the lateral, and defines a wide and deep sulcus patellaris.

Tibiotarsus. Both tibiotarsi are preserved in *Scandiavis*. The right tibiotarsus is exposed in lateral view, the left one in medial view (Fig. 1). The bone is comparatively robust and has similar proportions to the tibiotarsus of extant Rallidae (e.g., *Rallus*). Proximally, the fossa retropatellaris is very deep and relatively large. The facies articularis medialis and incisura tibialis are also distinct but shallow. The crista cnemialis lateralis is slightly hooked, with a thickened lateral edge. A long crista fibularis projects on the lateral surface of the shaft of the tibiotarsus.

The crista cnemialis cranialis is rounded when viewed in lateral aspect (Fig. 3). This crest is projected moderately cranioproximally and distally, not extending to the level of the crista fibularis. This morphology differs from the condition present in charadriiforms in

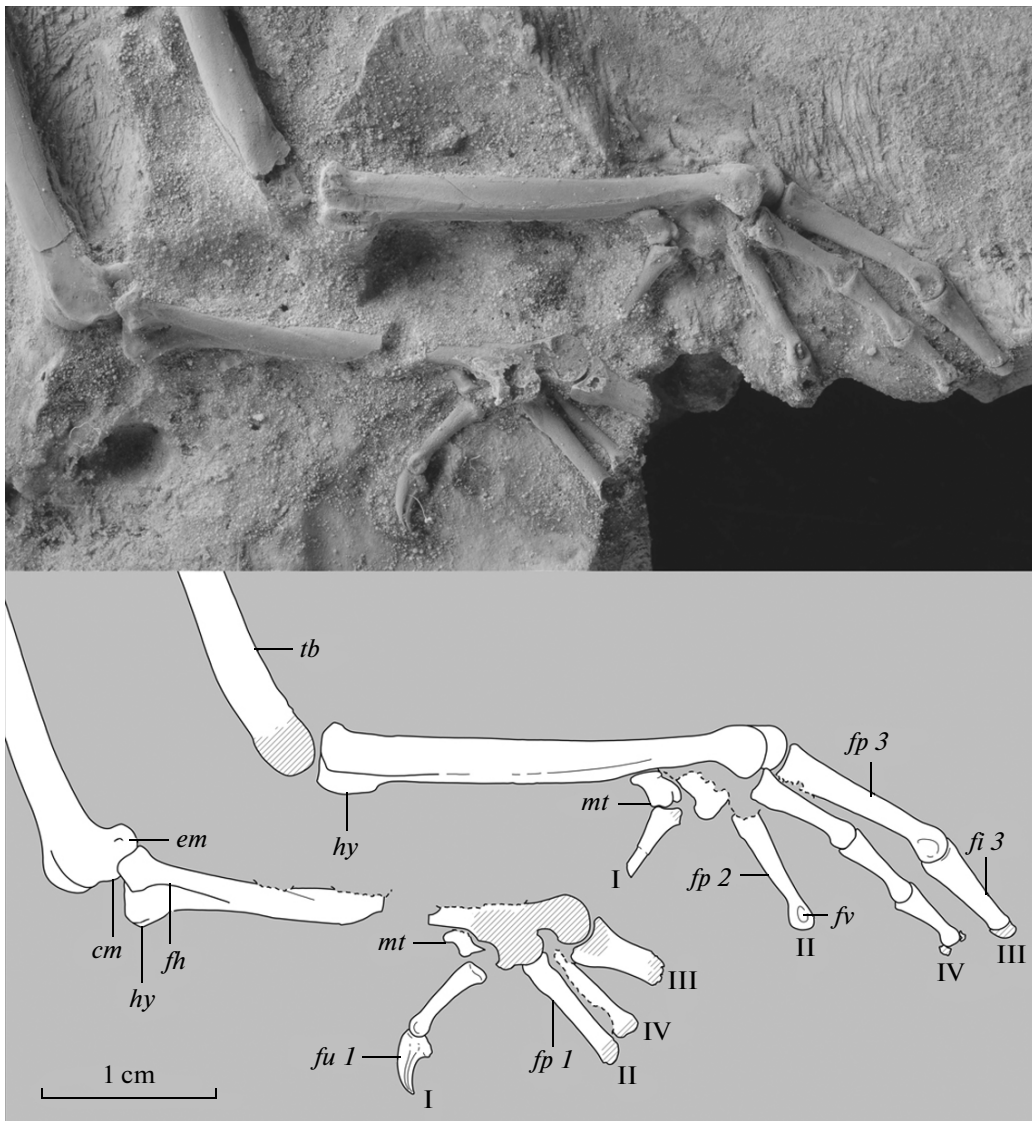


Fig. 4. *Scandiavis mikkelsenii* gen. et sp. nov., holotype FU171x, photograph (above) and interpretive drawing (below) of the tibio-tarsus and tarsometatarsus in lateral view. Designations: *cm*, condylus medialis; *em*, epicondylus medialis; *fh*, fossa parahypotarsalis medialis; *fi*, phalanx intermedia; *fp*, phalanx proximalis; *fu*, phalanx unguis; *fv*, fovea lig. collateralis; *hy*, hypotarsus; *mt*, os metatarsale I; *tb*, tibiotarsus.

which the crest protrudes markedly. A marked muscular depression is present on the medial face of this crest which possibly represents the attachment of the musculus gastrocnemius (facies gastrocnemialis). On the proximal border, a distinct ligamental pit is situated next to the fossa retropatellaris.

On the distal end, the condylus lateralis is mostly covered in sediment, making it difficult to discern anatomical details. The condylus medialis is craniocaudally deep and its distal rim is sharp and distinctly notched in medial view (Fig. 4). This condition is shared by Charadriiformes and it is also present in some Gruiformes (e.g., Psophiidae, Gruidae, Aramidae), among other birds. The medial face of the condylus bears a marked depression enclosing a prominent epicondylus medialis. Adjacent to the proximal margin of the

condylus medialis, the sulcus supratendinalis is barely visible being mostly covered by sediment.

Both fibulae are preserved in association with the tibiotarsi. The proximal head is well developed and club-like. The right fibula is partially broken but the articular facet of the crista fibularis of the tibiotarsus can be discerned.

Tarsometatarsus. Both tarsometatarsi are preserved in close association with the distal end of the tibiotarsus; the left tarsometatarsus is visible in medial aspect, the right in lateral view (Fig. 4). The bone is rather short and does not exceed the femur in length. It is of similar proportions to the tarsometatarsus of some extant Scolopacidae. The hypotarsus is partly hidden in the slab, but has similar proportions to that of *Ral-*

lus. The crista medialis hypotarsi is clearly visible and well developed. This condition is comparable to that of most “Gruiformes”, but it differs from that of Heliorhithidae and Rallidae where the crista is distinctly reduced. Just lateral to this crista, a smaller crista intermedia is partially exposed, but mostly covered by sediment. Whereas a deep fossa parahypotarsalis medialis is present, there is no fossa parahypotarsalis lateralis. In most “gruiforms” and charadriiforms, by contrast, the fossa parahypotarsalis medialis is less marked. No foramina vascularia proximalia are discernible. On the lateral surface of the bone, a distinct groove runs transversally through the mid section of the shaft. The medial surface of the right tarsometatarsus bears two tubercle-like structures on the proximal end, at approximately the position of the tubercle for insertion of musculus fibularis brevis. Adjacent to these tubercles, there is a faint muscular impression in the shape of an oval scar which possibly represents the attachment site of musculus fibularis longus. More medially, two cristae hypotarsales are visible on the proximal end. The dorsal surface of the shaft appears slightly concave and both cristae plantaris lateralis and medialis are very distinct. The os metatarsale I is wide and preserved in articulation with the distal end of both tarsometatarsi (Fig. 4). The trochlea metatarsi II is shorter and displaced more plantarly than the trochlea metatarsi IV, reaching much less far distally than the trochlea metatarsi III. This condition is also similar to most Charadriiformes (and other birds), but differs from most core-“gruiforms” (except e.g., Gruidae and the rallid *Himantornis*), where the distal end of trochlea metatarsi II is at approximately the same level as that of the trochlea metatarsi IV. A groove is present on the dorsal surface above trochleae metatarsorum III and IV, probably in the region of the foramen vasculare distale.

Digits. The toes are comparatively short as opposed to the more elongated condition present in, e.g., most Charadriiformes (Fig. 4). On the left foot, only the first phalanges of the three anterior toes are preserved; on digits II and IV, the phalanx proximalis is more robust and longer than the adjacent one, while on the third toe the three preserved phalanges are short and of similar proportions; the phalanx ungualis bear marked sulcus neurovascularis and their curvature is moderate. The hallux is short and its phalanx proximalis is distinctly more slender than those of the other digits.

Measurements in mm (left/right). Skull (maximum length), 49.5. Femur, —/33.2. Tibiotarsus (from articular surface, or including crista cnemialis, i.e. maximum length), 47.7/—. Tarsometatarsus, 25.5/25.4

Comparisons. The genus *Scandiavis* is monotypic.

Material. Holotype.

DISCUSSION

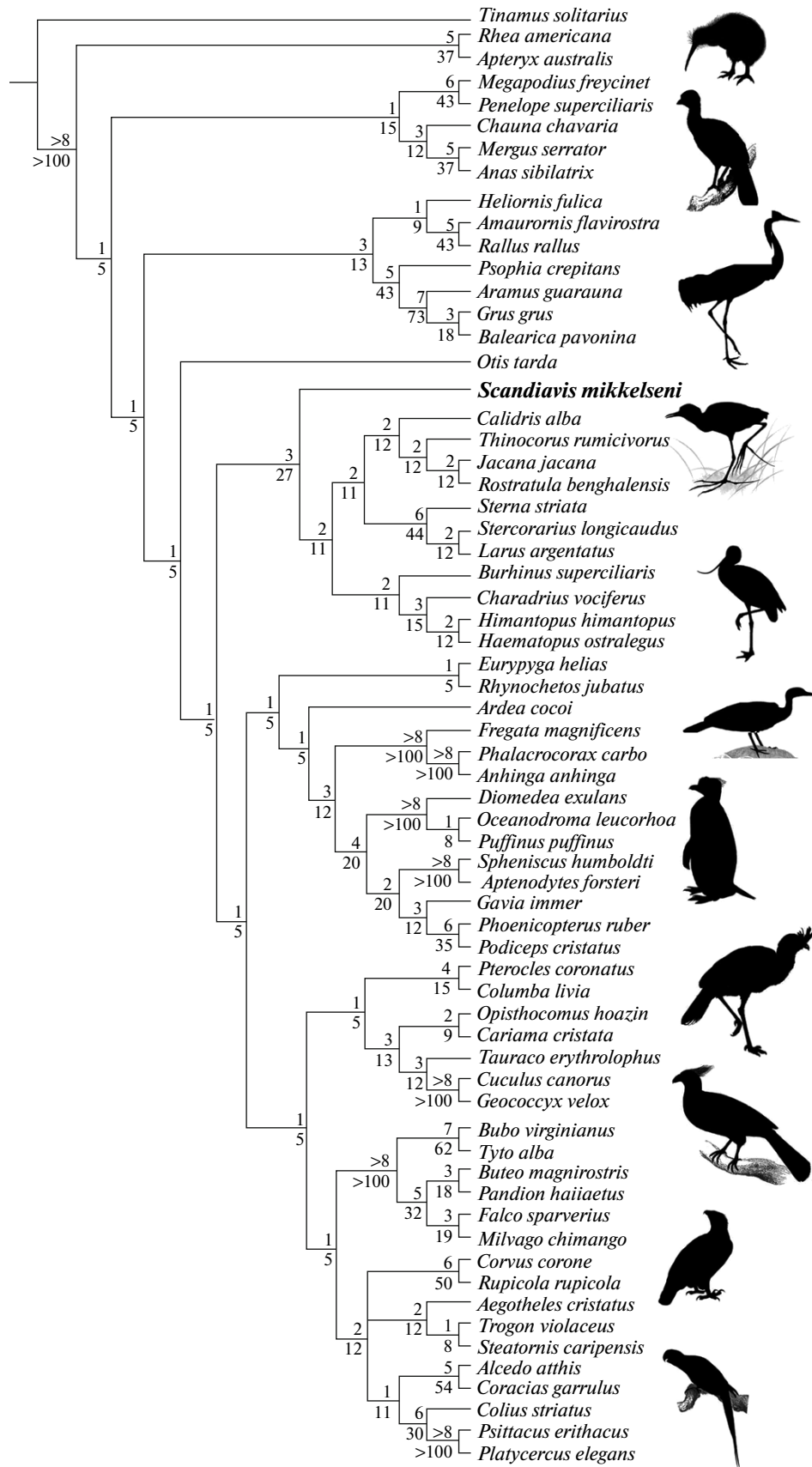
Compared with other birds from the early Paleogene of Europe, *Scandiavis mikkelsenii* gen. et sp. nov. shows some overall similarity to *Morsoravis sedilis* (Bertelli et al, 2010) from the Fur Formation, and *Salmila robusta* (Mayr, 2002) from the middle Eocene of Messel (Germany). As noted in the introduction, the affinities of the former are debated, whereas *S. robusta* was considered most closely related to *Cariamae* (Mayr, 2000b, 2002, 2009). However, the similarities between *Scandiavis mikkelsenii* and either of these two species appear to be superficial, and close comparisons reveal distinct differences.

The skull of *Scandiavis* differs from *Morsoravis*, in which the nostrils are typically schizorhinal and the mandibular tip is pointed, as opposed to the pseudoholorhinal condition and rounded mandibular symphysis of the new Danish bird. *Scandiavis* is also distinguished from *Morsoravis* in lacking diagnostic features such as the typical lateral recesses of the corpora vertebrarum, the ossified retinaculum musculi fibularis on the distal tibiotarsus, the trochleae accessoria metatarsalia II and the metatarsal I with elongated processus articularis tarsometatarsalis, among other characters (Bertelli et al., 2010).

Apart from having a similar general shape of the skull (except for a higher and more robust mandibular ramus), *Scandiavis* differs from *Salmila* in the presence of longer and more slender digits, and the trochlea metatarsi II of the tarsometatarsus is shorter and displaced more plantarly than the trochlea metatarsi IV, whereas the two trochleae are on the same level in *Salmila robusta* (Mayr, 2000b, 2002).

Like many other early Paleogene avian taxa, *Scandiavis* displays a character mosaic, but the new Danish taxon shows most resemblances to “gruiform” and charadriiform birds. In particular, the new fossil agrees with some “gruiform” birds in the presence of dorso-caudal processes on the third cervical vertebrae (only in Rallidae), pneumatic openings on the prootic (considered to be an apomorphy of Gruiformes by Cracraft 1988; see also character 30 of Appendix 2), deep pits on the dorsal surface of the caudal pelvis (only in Rhynchoetidae, see character 180 of Appendix 2). Some of these features are, however, also present in some Charadriiformes, with which *S. mikkelsenii* further agrees in the morphology of the lacrimal-ectethmoid complex, the fact that the iliac blades are not fused to the synsacrum, among other features.

Fig. 5. Strict consensus tree of 2 trees of 923 steps (CI = 0.24; RI = 0.62), Absolute Bremer support (ABS) values are on top of branches, relative Bremer support values (RBS) are below branches. RBS values followed a pattern similar to ABS, i.e., the lowest support and highest conflict correspond to nodes that represent either basal or near-basal dichotomies.



Charadriiform affinities of *Scandiavis* are recovered with relatively low support by our cladistic analyses, which resulted in two most parsimonious trees with almost identical topologies (Fig. 5). Characters that were optimized as apomorphies of this clade are the presence of a descending process of the lacrimal, which does not contact the jugal (character 11: state 1), the distinctly notched condylus medialis of the tibiotarsus (character 95: state 1), the plantarly deflected trochlea metatarsi II, which reaches much less distally than the trochlea metatarsi IV (character 101: state 0) and the fact that the ilia are not fused with the synsacrum (character 178: state 1). We note, however, that among “gruiforms”, these features are also present in Gruidae (characters 11 and 102), Eurypygidae (character 11), Rallidae (character 108), and Psophiidae (character 102).

A phylogenetic placement of *S. mikkelsenii* with regard to the extant avian groups is also made difficult by the fact that the interrelationships of many modern higher-level taxa are still controversial. For example this is the case for the phylogenetic placement of “gruiform” and charadriiform birds, to which *Scandiavis* shows most resemblances. Current phylogenetic analyses based on molecular data congruently do not support monophyly of “gruiform” birds, and the affinities of Otididae, Eurypygidae, and Rhynchotidae remain uncertain (Ericsson et al., 2006; Hackett et al., 2008; Mayr, 2011c). We note, however, that even though an assessment of the phylogenetic interrelationships of the extant birds was beyond the scope of our study, many of the groups (70%) resolved by the analysis are in concordance with recent molecular topologies (Ericsson et al., 2006; Hackett et al., 2008). In particular, this is the case for the interrelationships within Charadriiformes and “core Gruiformes”, i.e., the clade ((Rallidae + Heliornithidae) + (Psophiidae + (Gruidae + Aramidae))).

Clearly, *Scandiavis* is outside crown group Charadriiformes, as it retains plesiomorphic postcranial character states that are absent in the crown group taxa (absence of deep lateral excavations on caudalmost praesacral vertebrae (53 : 0), long hallux (103 : 0) and low number of foramina intertransversaria (177 : 0)), whose alternative states were optimized as synapomorphies of modern charadriiforms. Our analysis further optimized the presence of schizorhinal nostrils (5 : 0) as an apomorphy of crown-Charadriiformes, but the condition of the nostrils is actually unknown for the stem species of Charadriiformes (Mayr, 2011a).

Substantial material of definitive early Eocene (or older) charadriiform birds has not yet been described. Putative late Cretaceous remains are very fragmentary (Olson, 1999; Olson and Parris, 1987; Hope, 1999, 2002), and among the best preserved Paleogene specimens are fossils from the Middle Eocene of Germany and the Lower Oligocene of Germany and France (Mayr, 2000a, 2005, 2009; Mayr and Knopf, 2007).

Charadriiform affinities of *Scandiavis* are tentatively proposed based on the current evidence. Despite the excellent preservation of the holotype, however, the wing and pectoral girdle bones are not preserved and some critical features of the preserved bones are not exposed (e.g., the plantar surface of the hypotarsus). It is to be hoped that future additional data will allow for a more robust hypothesis concerning the phylogenetic placement of *Scandiavis*.

APPENDICES

Appendix 1

Character matrix for phylogenetic analysis. Characters 2, 50, 65, 73, 84, 192 were considered additives. Dashes denotes inapplicable data; questions denotes missing data.

<i>Tinamus solitarius</i>	0010000010	0000000000
0000000001	0001000110	0001000001
0000001101	1000000000	0004100001
0010000001	0000000000	0000000100
0000000-00	0000000001	0000001000
0000000000	010000	011000000-
<i>Rhea americana</i>	0010000010	0100000000
0000000001	100100?110	0000000001
010000200-	00--0--00-	--0-101000
1020000???	0010???0??	???1?14??
0000000-00	001-0000--	--0-000---
0-00000000	00000?	0--?---0--
<i>Apteryx australis</i>	0010001010	0000000000
0000000011	1000000110	0001001001
010000100-	00--0--00-	--0[23]100000
1010000000	0000000000	00010[01]1201
0000000-00	001-0000--	--0-000---
0-00000000	00000?	0--?---0--
<i>Megapodius freycinet</i>	0000000000	1000000111
1010100100	1000010001	1000101001
0001000101	1011000000	0003101101
0000000000	0000000000	0000100100
0100000000	0000000001	0000002100
0000000000	0100?0	0100000000
<i>Penelope supercilialis</i>	0000000000	10-0000111
1010100100	1000010001	1000101001
0001000101	1011000100	0003111101
0000000000	0000000000	0000100100
0000001000	0000000001	0000002100
0000000000	000010	0100000000
<i>Chauna chavaria</i>	0100000002	10-0110111
1010100100	1110010001	1001001001
1000201200	1011011000	0004111000
1000000???	00????00??	00????????
0000001000	0000000000	1001000000
0000000000	000000	0000000000

<i>Anas sibilatrix</i>	0200000002	10-0010111	<i>Buteo magnirostris</i>	1000001000	0101100111
1010110100	1110010001	1010001001	11-0000100	1010000000	1000001000
0001201100	1011010000	0003101000	0001101100	1011111000	0002111000
0011000001	1000100021	?001001200	1000010001	1101100000	0001010310
0000001000	0000000010	1000000000	0100000000	0000000000	1001000000
0000000000	000000		0101000110	10000?	
<i>Mergus serrator</i>	0200000002	10-0010111	<i>Pandion haliaetus</i>	1000001000	0001100111
1010110100	1110010001	1011001001	11-0000100	1010000000	1000000000
0000101100	1011010000	0004101000	0011101100	1011111000	0002111000
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0000001000	0000000010	1000000000	0100000000	00[01]0000000	0001000000
0000000000	000000		010101011?	1000??	
<i>Opithocomus hoazin</i>	0001000000	0000000110	<i>Falco sparverius</i>	1000001000	0101100010
11-0000101	1011000000	0011111001	1010000000	1000101001	1101010000
10--111100	1021010110	0003111100	1011111000	0001111001	1010010000
1000000000	0000001000	0001100100	1101100000	0001000310	0000010100
0110000000	00000000-0	100200-000	0000000000	0001001000	0000000000
0100000000	0000??		10000?		
<i>Cuculus canorus</i>	0000001002	0011101---	<i>Milvago chimango</i>	1000001000	0101100010
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1011010101	0001011000	0010010110	0011101100	1011111000	0001111001
00?1011010	0001100100	001000100[01]	1000010???	??????????	??????????
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0000??			0101000100	1000??	
<i>Geococcyx velox</i>	0000001002	0011101---	<i>Diomedea exulans</i>	1010000000	0101100000
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1011010111	0001001100	1010010110	0011112120	1020010000	0102111000
00?1011010	0001100100	001000100[01]	1021-00000	1100000010	0001000400
0100000000	0001000000	0000000000	0100000000	0010010010	1001100001
0000??			0000000000	000100	
<i>Tauraco erythrophus</i>	0000001000	0000000010	<i>Oceanodroma leucorhoa</i>	1010000000	0001100000
11-0000101	1110000000	00000101100	11-1001100	1110100000	0100101001
0011000100	1011010111	0002001100	0011102100	0020010000	0102011000
1100000?0?	00?0?1101?	??0?0???	0011-00000	1100000010	0001000400
0110000000	0000000000	0002000000	0100000000	0000000000	1001100011
0000000000	0000??		0000000000	000100	
<i>Bubo virginianus</i>	1001001000	0001101---	<i>Puffinus puffinus</i>	1010000000	0001100000
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0000100100	1011110000	0002111100	0011100120	0020010000	0102011000
1100010000	11010001?0	0001010110	0011-00000	1100000010	0001000400
0100010000	0000000000	0001000000	0100000011	0010000010	0001100001
0101010100	10000?		0000000000	000100	
<i>Tyto alba</i>	1001001000	0001101---	<i>Gavia immer</i>	0000000000	00-1100011
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1011110000	0002111100	0000010000	0011010000	0014011010	01100111-0
??????????	??????????	?000011100	1000000011	0010101400	1?00000100
0000000000	0001000000	0000010000	1010000010	1001000000	010000-000
10000?			000000		

<i>Spheniscus humboldti</i>	0010000000	0000100011	<i>Himantopus himantopus</i>	0000100001	1201100010
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102100000	1000000010	0001101200	10?0000?01	0020000???	??00000110
0100100011	0010000010	1001000000	0-10000000	0100000010	1011000011
001010000-	000000			0000000000	020000
<i>Aptenodytes forsteri</i>	0010000000	0000100011	<i>Charadrius vociferus</i>	0000100000	1201100010
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001010000-	000000			0000000000	020000
<i>Phalacrocorax carbo</i>	101101-102	0001111---	<i>Haematopus ostralegus</i>	0000100001	1201100010
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00101011-0	0011110000	0103111000	0110010110	0001100000	0011110000
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0110000001	0011111000	1000000000	1-10001000	0100000010	0000000010
0010000010	000001			0000000000	020000
<i>Anhinga anhinga</i>	001101-102	0001111---	11-0000110	<i>Rostratula benghalensis</i>	0000100000
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<i>Fregata magnificens</i>	101001-100	00-1110110	<i>Jacana jacana</i>	0000100000	1001100000
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<i>Ardea cocoi</i>	0010000000	0001100011	11-0000100	<i>Thinocorus rumicivorus</i>	0000100000
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<i>Phoenicopterus ruber</i>	0200000002	00-1100101	<i>Calidris alba</i>	0000100000	1001100000
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1100001000	0010000110	1001000000	0000001000	0000000010	1011000001
0000000000	00100?			020000	0100002100
<i>Podiceps cristatus</i>	0000000000	1001100011	<i>Stercorarius longicaudus</i>	0000100000	1201100011
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0000000000	00100?			0000000000	020001

<i>Lotus argentatus</i>	0000100000	1201100011	11-1001100	<i>Heliornis fulica</i>	0000000?00	1101100031	11-0000101
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020001				??00??			
<i>Burhinus superciliaris</i>	0000000000	02-1100010	11-0000100	<i>Amaurornis flavirostra</i>		0000000000	0101100011
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020000				0000011000	00001?		
<i>Sterna striata</i>	0000100000	1201100010	11-1000100	<i>Rallus rallus</i>	0000000000	0101100011	11-0000101
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020001				00001?			
<i>Aramus guarauna</i>		0000100700	0101100011	<i>Eurypyga helias</i>	0000100000	10-1100010	11-0000101
11-0010101	1111100002	0001001002	1100000000	1110100000	0000100002	1101000010	0011101000
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0000000000	00001?			0000??			
<i>Grus grus</i>	0000100000	1101100001	11-0010101	<i>Rhynchotos jubatus</i>		0000100000	1001100011
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00001?				0000000000	0000??		
<i>Balearica pavonina</i>		0000100000	0101100001	<i>Otis tarda</i>	0000000000	0001100111	11-0000101
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0100000100	0010000000	1001010000	0100000000	0000000000	1001000000	0100000000	0000000000
0000000000	00001?			000000			
<i>Psophia crepitans</i>	0000000000	0000100011	11-0000101	<i>Cariama cristata</i>	0000000002	1101100111	11-0000101
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0000000000	1101010000	0100000000	0000000000				
0000?0							

1011000110	0002111101	0010000000	1010000???
??12??20??	??2??2???	??10001?20	0100000000
0000000000	0002000000	0000000000	0000000000
70000?			
<i>Psittacus</i> <i>erithacus</i>	1001001002	0000101---	11-0000100
1110000000	0100101100	0111000000	0011101101
1011111000	0002111000	0000010001	1200000100
00011000?0	1011110901	0100010100	0111110000
0010001000	0001000000	0100000000	0000000000
00000?			
<i>Platycercus elegans</i>	1001001002	0000101---	
11-0000100	1110000000	0100100000	0111000000
0011101101	1011111000	0002111000	0010010001
12000001??	??2??2???	??2??2???	?200010100
0110110000	0000001000	0001000000	0100000000
0000000000	00000?		
<i>Pterocles coronatus</i>		0000000000	1010001—
1000000100	1010000001	1000101001	1101000010
0000100111	1011110100	0002011001	0010010100
0010000???	??20?20???	?0?0?1????	?200001100
0110000000	0000000000	0002001000	0100000000
0000000000	00000?		
<i>Columba livia</i>	0000100000	1010101---	1000000101
1110000000	0000100000	1101000010	0000000111
1011110100	1002011001	0010010101	1000000010
0000000000	0000000100	01?0011000	0110?00010
0000000000	0002001000	0100000000	0000000000
00000?			
<i>Alcedo atthis</i>	0000001002	0001110110	11-0000100
1010000000	0000011100	0101100010	0001100100
1011110000	0001011000	0010010101	1000000110
00010001?0	0011000510	0?00003100	0110100001
0000000001	0002000100	0100000000	1000000000
00000?			
<i>Coracias</i> <i>garrulus</i>	0000001002	0001110110	11-0000100
1010000000	0001011100	0101100010	0001100100
1011110000	0001011000	0010010101	1000000?10
00010001?0	0011000510	0?00001100	0110100001
0000000001	0001000000	0100000000	0000000000
00000?			
<i>Colius striatus</i>	0000001002	1010101---	11-0000101
1111000000	0100101100	0101300000	0001000100
1011010100	0001011000	0110010010	1100000100
00011001?0	1011010511	0110000170	0111-00000
0000000000	0000000000	0100000000	0000010000
1000??			

<i>Steatornis caripensis</i>	1001001002	1000011---
1000000100	1110001000	0000100000
0000001100	10211110	?0100000001
1000000000	0001000000	1000000000
<i>Aegotheles cristatus</i>	1000000000	-00100000
1000000100	1111000000	0100100000
0000000100	1011110000	0000011000
1000000010	?201?001?0	?0?1000?01
0100100000	0000001000	0?00000000
1000000000	0000??	
<i>Trogon violaceus</i>	0001001000	0000010110
1000000100	1110001000	1000100000
0001000100	1021110100	0001011000
100000011?	1????201??	0?0?2008?1
0110100000	0000000000	0000000000
1000000000	00000?	
<i>Corvus coram</i>	0000000000	0010000000
1011000000	1000101000	0101100010
1011110001	0001011000	0010010111
00011001??	0001000711	0010001000
0000000001	0000000000	0100000000
00000?		
<i>Rupicola</i> <i>rupicola</i>	0000000000	0010000000
1011001000	1000101000	0101100010
1011110000	0001011000	0010010111
??????????	??????????	?210001000
0000000000	0000000000	0100000000
00000?		
<i>Scandiavis mikkelsen</i>	0?00000?0?	100???????
??20?2??21	101?20?002	??20101001
???????	???????	?20?011?01
000?20????	??????????	???????
????200?20	0?0??200??	???????
00?20?20?	??0???	

Appendix 2

The matrix includes 146 characters from Mayr (2011b), and we have also added fifty previously published characters from the literature; coding modifications and new character states are indicated.² Other published characters or feature descriptions that have been modified are indicated by an asterisk. 62 osteological characters could be scored in *Scandiavis mikkelsen*; was scored as uncertain (?) characters relating to the missing forelimbs, shoulder girdle and sternum (characters 56–67, 69–82, 159–176), and areas not exposed or damaged structures of preserved bones (characters 2, 8, 14–23, 25, 27–29, 34, 35, 37, 41–43, 54, 84, 88, 91, 93, 94, 98–100, 104, 105, 107,

² Previously published descriptions of characters were omitted by the editor.

148, 149, 152, 154–157, 183, 184, 186–188, 190–192, 194–196).

Ch. 1, 2: See Mayr and Clarke (2003; Ch. 2, 3).

Ch. 3: See Mayr (2011b; Ch. 3).

Ch. 4: See Mayr and Clarke (2003; Ch. 5).

Ch. 5*: See Mayr and Clarke (2003; Ch. 6). The narial openings of *Scandiavis* do not extend caudally as far as the naso-frontal hinge, and, in addition, their caudal borders are not slit-like (as it is in schizorhinal nostrils), therefore they were scored as 0 (contrary Lindow, 2007, who coded schizorhinal nostrils as present).

Ch. 6: See Mayr and Clarke (2003; Ch. 7).

Ch. 7: See Mayr and Clarke (2003; Ch. 8). No remains of a septum internasale are visible through the external nares of *Scandiavis* (state 0).

Ch. 8, 9: See Mayr and Clarke (2003; Ch. 9, 10).

Ch. 10*: Palate, degree of fusion of processus maxillopalatini of ossa maxillaria; unfused (0), fusion with os palatinum with loss of identifiable maxillopalatines (Strauch, 1978; ch. 12) (1), extensively fused along their midline, palate directly desmognathous (2). Character description was modified from Mayr (2011b). We scored this character as absent for *Scandiavis* (state 0), since one unfused processus maxillopalatinus is preserved in the holotype.

Ch. 11: See Mayr and Clarke (2003; Ch. 12).

Ch. 12*: Os lacrimale, projection of processus supraorbitalis: absent (0), caudally projecting (1), short and laterally projected (2). The head of the lacrimale is preserved on the skull of *Scandiavis*, and lacks a caudal projection (state 0). This condition is considered non-comparable for *Psophia*, in which the corresponding area shows an apomorphic morphology owing to the formation of small supraorbital ossicles. Character description was modified from Mayr (2011b), where only a caudally projecting process was scored.

Ch. 13, 14: See Mayr and Clarke (2003; Ch. 14, 15).

Ch. 15: See Mayr (2011b; Ch. 15).

Ch. 16: See Mayr and Clarke (2003; Ch. 17). Mayr (2011b) noted variation among taxa of Phalacrocoracidae; examined specimens of *Phalacrocorax carbo* exhibit this condition.

Ch. 17–20: See Mayr and Clarke (2003; Ch. 18–21).

Ch. 21: See Mayr (2011b; Ch. 22).

Ch. 22: See Mayr and Clarke (2003; Ch. 23).

Ch. 23: See Mayr and Clarke (2003; Ch. 24). This character was coded as non-comparable for taxa in which the facet is absent.

Ch. 24, 25: See Mayr and Clarke (2003; Ch. 25, 26).

Ch. 26: Cranium, fonticuli occipitales in adult birds: absent (0), present (1); small openings (2). In *Scandiavis* a weakly developed opening is visible lateral to the cerebellar prominence, but this is considered unlikely to be homologous with the openings that are characteristic of some charadriiform taxa (e.g.

Recurvirostridae, Rostratulidae, Charadriidae, and Scolopacidae) and other groups of birds (anseriforms, phoenicopteriforms, and some gruiform taxa among others); therefore, the condition was scored as a different state (2).

Ch. 27–29: See Mayr and Clarke (2003; Ch. 28–30).

Ch. 30: See Mayr (2011b; Ch. 31).

Ch. 31: See Mayr (2011b; Ch. 32). As in all Neognathae, frontals and parietals are completely fused in *Scandiavis* (state 1); a distinct crack that is an artifact of the preservation is visible through the temporal area of the holotype.

Ch. 32: See Mayr and Clarke (2003; Ch. 33).

Ch. 33: See Mayr and Clarke (2003; Ch. 34). Although the quadrate articulates with the braincase, it is possible to score this character in *Scandiavis*, as the otic and squamosal capitulae are partially exposed and distinct in caudal aspect (state 1).

Ch. 34: See Mayr (2011b; Ch. 36).

Ch. 35–38: See Mayr and Clarke (2003; Ch. 37–40).

Ch. 39: See Mayr and Clarke (2003; Ch. 43).

Ch. 40: Mandible, projection of processus retroarticularis: absent (0); long and strongly mediolaterally compressed (1); narrow and dorsally upcurved (2).

Ch. 41–44: See Mayr and Clarke (2003; Ch. 45–48).

Ch. 45: See Mayr and Clarke (2003; Ch. 50).

Ch. 46: See Mayr and Clarke (2003; Ch. 51). In *Scandiavis*, the third cervical vertebra lacks a connection between processus transversus and processus articularis caudalis (state 0).

Ch. 47–51: See Mayr and Clarke (2003; Ch. 52–56).

Ch. 52: See Mayr (2011b; Ch. 57). Lindow (2007) described that *Scandiavis* had opisthocoelous thoracic vertebrae, a condition characteristic of some charadriiforms; however, there is no evidence on the exposed thoracic vertebrae that indicates this condition; therefore it was scored 1.

Ch. 53: See Mayr (2011b; Ch. 58).

Ch. 54: See Mayr and Clarke (2003; Ch. 59).

Ch. 55: Pygostyle, discus pygostyli greatly enlarged: absent (0), present (1). We have added a coding for *Phaethon* based on additional examined material.

Ch. 56: See Mayr and Clarke (2003; Ch. 62). This character was scored as non-comparable for *Apteryx* and *Rhea*. We have also scored *Fregata* as non-comparable (coracoid and furcula fused).

Ch. 57: See Mayr and Clarke (2003; Ch. 63). This character was scored as non-comparable for *Apteryx* and *Rhea*.

Ch. 58: See Mayr and Clarke (2003; Ch. 64).

Ch. 59: See Mayr (2011b; Ch. 65). Mayr (2005) cited ontogenetic evidence indicating this foramen is non-homologous to the coracoidal fenestra of penguins.

Ch. 60–63: See Mayr and Clarke (2003; Ch. 66–69).

Ch. 64: See Mayr and Clarke (2003; Ch. 70). This character was coded as non-comparable for Opisthocomidae.

Ch. 65–68: See Mayr and Clarke (2003; Ch. 71–74).

Ch. 69*: Humerus crista deltopectoralis strongly protruding and triangular with distinctive angulus: no (0), shaft short and stocky (1); shaft elongated and straight (2). We have added an additional state to this character (Mayr and Clarke, 2003; Ch. 75) to account for the distinct morphology present in some birds such as e.g. Procellariiformes and Charadriiformes. This character was coded as non-comparable for taxa with a reduced crista deltopectoralis (e.g., Spheniscidae, Phalacrocoracidae, Anhingidae, Podicipedidae).

Ch. 70: See Mayr and Clarke (2003; Ch. 76). This character was scored as non-comparable for *Apteryx* and *Rhea*.

Ch. 71, 72: See Mayr and Clarke (2003; Ch. 77, 78).

Ch. 73*: Humerus, fossa musculi brachialis, development: not present or very indistinct (0), present (1), very deep and sharply delimited (2). This character corresponds to characters 79 and 80 of Mayr (2011b) who discriminated the variation of this feature into separated characters (See Mayr and Clarke, 2003; Ch. 79, 80). Due to its highly apomorphic morphology, the humerus of Rheidae, Apterygidae and Spheniscidae was coded as non-comparable for this character. Ordered.

Ch. 74–77: See Mayr and Clarke (2003; Ch. 81–84).

Ch. 78: See Mayr (2011b; Ch. 85).

Ch. 79: See Mayr and Clarke (2003; Ch. 86).

Ch. 80–82: See Mayr and Clarke (2003; Ch. 87–89). These characters were coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 83: See Mayr and Clarke (2003; Ch. 90).

Ch. 84: See Mayr and Clarke (2003; Ch. 91). This character was coded as non-comparable for *Rhea*.

Ch. 85, 86: See Mayr and Clarke (2003; Ch. 92, 93).

Ch. 87: See Mayr (2011b; Ch. 94).

Ch. 88: See Mayr and Clarke (2003; Ch. 95).

Ch. 89: See Mayr and Clarke (2003; Ch. 96). Our scorings for Anatidae and Anhimidae differ from Mayr (2011b).

Ch. 90, 91: See Mayr and Clarke (2003; Ch. 97, 98).

Ch. 92: See Mayr and Clarke (2003; Ch. 99). Contrary to Lindow (2007), who coded it as present, we scored this character as absent for *Scandiavis* (the cristae cnemiales are moderately developed).

Ch. 93: See Mayr (2011b; Ch. 100).

Ch. 94–97: See Mayr and Clarke (2003; Ch. 101–104).

Ch. 98: See Mayr (2011b; Ch. 105). Our scorings for Procellariidae differ from Mayr (2011b).

Ch. 99*: See Mayr (2011b; Ch. 106). Our scorings for Procellariidae differ from Mayr (2011b). This character was coded as non-comparable for *Gavia*, since homology of tendinal furrows/canals was uncertain.

Ch. 100, 101: See Mayr and Clarke (2003; Ch. 107, 108).

Ch. 102*: Trochlea metatarsi IV: not as follows (0); with plantary projecting wing-like flange typical of semizygodactyl birds (1) with large trochlea accessoria (typical of fully zygodactyl feet): (2). *Scandiavis* lacks the trochlea accessoria of trochlea metatarsi IV (state 0) which is present in birds with zygodactyl feet (e.g., Cuculidae, Psittacidae). This character is modified from Mayr (2011b; See Mayr and Clarke, 2003; Ch. 109), we have added an additional state to this character to account for the expansion of the trochlea metatarsi IV in semizygodactyl birds.

Ch. 103–105: See Mayr and Clarke (2003; Ch. 110–112).

Ch. 106: See Mayr (2011b; Ch. 113).

Ch. 107–112: See Mayr and Clarke (2003; Ch. 114–119).

Ch. 113*: See Mayr and Clarke (2003; Ch. 120). Our scorings for Cuculidae and Charadriidae differ from Mayr (2011b).

Ch. 114–137: See Mayr and Clarke (2003; Ch. 121–144).

Ch. 138: See Mayr and Clarke (2003; Ch. 145). Scorings for charadriiform taxa from Woodbury (1998).

Ch. 139–141: See Mayr and Clarke (2003; Ch. 146–148).

Ch. 142–146: See Mayr (2011b; Ch. 149–153).

Ch. 147*: Skull, ectethmoid: greatly reduced or lost: no (0), yes (1). See Bertelli et al. (2011). The ectethmoid is clearly exposed in *Scandiavis* (state 0).

Ch. 148*: Skull, pterygoid, rostral end markedly widened and laterally projected: no (0); yes (1). This condition was listed by Mayr (2008) as a synapomorphy of some “gruiform” taxa (e.g., Rallidae, Gruidae, Aramidae, Psophiidae). We scored this character as non-comparable for Palaeognathae in which palatine and pterygoid are fused.

Ch. 149*: Skull, os laterosphenoidale, large opening dorsocaudally of foramen n. maxillomandibularis: absent or rudimentary (0); present (1). See Mayr (2011a; Ch. 5).

Ch. 150*: Skull, os squamosum, fossa temporalis: short and, in caudal view, separated by wide space (0); deep, meeting or nearly meeting at level of the cerebellar prominence (1). Modified from Mayr (2003; Ch. 16).

Ch. 151*: See Mayr (2011a; Ch. 4).

Ch. 152*: See Mayr (2011a; Ch. 10).

Ch. 153*: See Mayr (2003; Ch. 14) and Mayr (2005; Ch. 19).

Ch. 154*: See Mayr (2005; Ch. 22).

Ch. 155*: See Mayr (2005; Ch. 11).

Ch. 156*: Skull, recessus tympanicus dorsalis, not as follows or small and between articular facets of the quadrate (0), greatly enlarged and situated rostrally to

the articular facets of the quadrates (1). This character is modified from Mayr (2005; Ch. 16).

Ch. 157*: See Mayr et al. (2003; Ch. 15) and Mayr (2005; Ch. 20).

Ch. 158*: Cervical vertebrae, prominent caudolateral projections on ventral side (processus ventrolaterals): absent (0), present (1). See Manegold (2006). These processes are absent in *Scandiavis* (state 0).

Ch. 159*: Furcula, processus acromialis long and slender: no (0); yes (1). This character was coded as non-comparable for Palaeognathae, Opisthocomidae and *Fregata* (furcula and coracoid fused). See Bertelli et al. (2011; Ch. 36).

Ch. 160*: See Mayr et al. (2003; Ch. 31). This character was coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 161*: Coracoid, scapular facet: shallow (0), excavated and cuplike (1). This character was coded as non-comparable for *Rhea*, *Apteryx* and *Fregata*. See Bertelli et al. (2011; Ch. 37).

Ch. 162*: Coracoid, processus procoracoideus extending as a sharp crest along midline of shaft (crista procoracoidei of Livezey, 1998): absent (0); present (1). This character was coded as non-comparable for *Rhea* and *Apteryx*. See Bertelli et al. (2011; Ch. 39).

Ch. 163*: Coracoid, dorsal view, extremitas sternalis forming three pointed projections, facies sternalis distinctly concave: absent (0); present (1). See Mayr (2000a).

Ch. 164*: Coracoid, processus procoracoideus: absent or poorly developed (0), developed with distinct tip markedly deflected towards extremitas omalis (1); well developed, almost contacting or fused to proc. procoracoideus (2). This character is modified from Mayr (2004, ch. 34), we have added an additional state to this character to account for a moderate projection.

Ch. 165*: Coracoid, extremitas sternalis, processus lateralis greatly elongated: absence (0); presence (1).

Ch. 166*: Sternum, corpus sterni extremely elongate and very narrow: no (0); yes (1). Mayr (2007) listed this character as a diagnostic feature of some "Gruiformes" (e.g., Rallidae, Gruidae, Aramidae, Psophiidae).

Ch. 167*: Sternum, spina interna rostri: absent (0); present (1); present and fused to spina externa (2). This character was coded as non-comparable for Opisthocomidae. See Bertelli et al. (2011; Ch. 45).

Ch. 168*: Humerus, incisura capitis: not as follows (0), enclosed by distal projection of caput humeri (1), closed by transverse ridge (2). This character was coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 169*: Humerus, distinctly marked and well-developed 2nd fossa pneumotricipitalis: no (0); yes (1). This character was coded as non-comparable for *Rhea* and *Apteryx*. See Strauch (1978; Ch. 44), Mayr (2011a; Ch. 30), Bertelli et al. (2011; Ch. 55).

Ch. 170*: Humerus, processus supracondylaris dorsalis greatly elongated proximo-distally: absent (0); present (1). This character was coded as non-comparable for *Rhea* and *Apteryx*. See Strauch (1978; Ch. 45), Mayr (2011a; Ch. 33), Bertelli et al. (2011; Ch. 57).

Ch. 171*: See Mayr (2011a; Ch. 31). In some taxa (e.g. Ardeidae, Gaviidae, Threskiornithidae, Spheniscidae) this impressio is also marked but not as developed as in Charadriiformes.

Ch. 172*: See Strauch (1978; Ch. 43) and Mayr (2011a; Ch. 32). Non-comparable for Palaeognathae, Sphenisciformes, *Phalacrocorax* and *Anhinga* since this crista is reduced.

Ch. 173*: See Mayr (2003, ch. 33).

Ch. 174*: Humerus, crista bicipitalis, aspect of ventral border of proximal end of humerus, caudal view: rounded or continuously curving (0); squared off (1). See Bertelli et al. (2011; Ch. 52).

Ch. 175*: See Mayr (2011a; Ch. 34). This character was coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 176*: See Strauch (1978; Ch. 49), Mayr (2011a; Ch. 36), and Bertelli et al. (2011; Ch. 62). This character was coded as non-comparable for *Rhea* and *Apteryx*. Small pneumatic foramina are present in some taxa (e.g., *Cathartes*, *Chauna*, *Fregata*), where they are not as developed as in state 1.

Ch. 177*: Synsacrum, foramina intertransversaria: few small foramina present (0); well developed paired openings (1); several rows of large openings (2). Contrary to Lindow (2007) who described these large fenestrae as present (state 1), we score this character as absent for *Scandiavis* (synsacrum perforated by small foramina intertransversariae). The presence of this condition is typical for Charadriiformes (except Burhinidae), but also occurs in few other birds (Mayr, 2000). This character was coded as non-comparable for *Apteryx*, *Rhea*, *Gavia*, and *Podiceps*.

Ch. 178*: Pelvis, iliac blades and synsacrum fused (0); unfused (1). The sutures between ilia and synsacrum are clearly open in *Scandiavis* (state 1). This character was coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 179: Pelvis, deep pits at the base of the spina dorsolateralis: no (0); yes (1). The position of these depressions are comparable to that seen in specimens of Rhynchotidae and some Charadriiformes (e.g., Laridae, Scolopacidae, Haematopodidae) but clearly less developed than in *Scandiavis* (state 1). This character was coded as non-comparable for *Rhea* and *Apteryx*.

Ch. 180: Pelvis, deep incisura marginis caudalis (deeper than the f. ilioischadicum), with the spinae dorsolateralis ilii reach almost as far caudally as the processus terminalis ischii: no (0); yes (1). This character was coded as non-comparable for Palaeognathae. See Bertelli et al. (2011; Ch. 65).

Ch. 181*: See Mayr et al. (2003; Ch. 50).

Ch. 182: Pelvis, development of crista dorsolateralis ilii: strongly developed, overhanging a marked concavitas infracristalis, convexly bowed if pelvis is viewed from its dorsal side: absent (0); present (1). This character was modified from Mayr et al. (2003; Ch. 52). *Rhea* and *Apteryx* were coded as non-comparable.

Ch. 183*: See Mayr (2005; Ch. 43).

Ch. 184*: See Mayr et al. (2003; Ch. 60).

Ch. 185*: See Mayr (2005; Ch. 46).

Ch. 186*: See Mayr et al. (2003; Ch. 65).

Ch. 187*: Tibiotarsus, ossified retinaculum: absent (0); present (1). See Bertelli et al. (2010).

Ch. 188*: See Mayr et al. (2003; Ch. 62).

Ch. 189*: Tarsometatarsus, trochlea metatarsi II protruding farther distally than trochlea metatarsi III no (0), yes (1).

Ch. 190*: Tarsometatarsus, foramen vasculare distale greatly enlarged, with very marked and wide sulcus extensorius: no (0), yes (1). This foramen is also somewhat large in other taxa (e.g. Accipitridae, Psittacidae) but in these taxa the sulcus extensorius is shallow and less wide. This character is coded as non-comparable in Fregatidae and Spheniscidae where this foramen is reduced. See Mayr (2011a; Ch. 42).

Ch. 191*: See Mayr et al. (2003; Ch. 70).

Ch. 192*: Digi IV, fourth and third phalanx, relative length: fourth phalange longer (0); approximately similar (1); fourth phalange distinctly shorter (2). The presence of a short fourth phalanx in Charadriiformes has been reported by Hesse (1988), and was also considered a synapomorphy of Charadriiformes (except Alcidae) by Mayr (2000b). Ordered.

Ch. 193*: Ungual phalanges nail-like: absence (0); presence (1). See Manegold (2006).

Ch. 194*: External narial openings tubular: absent (0), present (1). Modified from Mayr (2005; Ch. 4).

Ch. 195*: Intratendinous ossification in hindlimbs: absence (0); presence (1). See George and Berger (1966); Bertelli et al. (2011; Ch. 80).

Ch. 196*: Young: precocial or semi-precocial (downy) (0), altricial (naked) (1). After del Hoyo et al. (1996), see also Mayr (2011a; Ch. 49).

ACKNOWLEDGMENTS

We thank Gilles Cuny and Henrik Madsen for their help and for access to fossil material in the Natural History Museum of Denmark in Copenhagen and the Moler Museet (Mors, Denmark) respectively. We also thank Sylke Frahnert and Pascal Eckhoff of the Museum für Naturkunde (Berlin, Germany) for access to osteological specimens. We are very grateful to Sten Jakobsen of the Geologisk Museum of Copenhagen for his preparation of FU171x. We are also indebted to Sven Tränkner of the Forschungsinstitut Senckenberg (Frankfurt, Germany) for photographs

of the material. We also thank V. L. De Pietri for comments and suggestions that improved the manuscript. S.B., B.L. G.M. contributed equally to this project and performed the analysis and description; G.D. acquired funding for the preparation of this specimen provided by the Irish Research Council for Science and Technology (IRCSET 2004/ES0009), which also supported Bent Lindow's PhD. This project was supported by the Alexander von Humboldt Foundation (Grant number 3.1-USA/1127798) and the National Science Foundation (Grant number DEB 0454856).

REFERENCES

- Baumel, J.J. and Winner, L.M., Osteologia, in *Handbook of Avian Anatomy: Nomina Anatomica Avium*, Baumel, J.J., King, A.S., Breazile, J.E., et al., Eds., Publ. Nuttall Ornithol. Club, 1993, no. 23, Second ed., pp. 45–132.
- Bertelli, S., Lindow, B.E.K., Dyke, G.J., et al., A well-preserved “charadriiform-like” fossil bird from the Lower Eocene Fur Formation of Denmark, *Palaeontology*, 2010, vol. 53, pp. 507–531.
- Bertelli, S., Chiappe, L.M., and Mayr, G., A new Messel rail from the Early Eocene Fur Formation of Denmark (Aves, Messelornithidae), *J. Syst. Palaeontol.*, 2011, vol. 9, pp. 551–562.
- Beyer Heilmann-Clausen, C.B. and Abrahamsen, N., Magnetostratigraphy of the Upper Paleocene-Lower Eocene deposits in Denmark, *Newsl. Stratigr.*, 2001, vol. 39, pp. 1–19.
- Cracraft, J., Phylogenetic relationships and trans antarctic biogeography of some gruiform birds, *Geobios*, 1982, vol. 6, pp. 393–402.
- Cracraft, J., The major clades of birds, in *The Phylogeny and Classification of the Tetrapods. Amphibians, Reptiles, Birds*, Benton, M.J., Ed., Oxford: Clarendon Press, 1988, vol. 1, pp. 339–361.
- Dyke, G., Waterhouse, D.M., and Kristoffersen, A.V., Three new landbirds from the early Paleogene of Denmark, *Bull. Geol. Soc. Denmark*, 2004, vol. 51, pp. 77–85.
- Ericson, P.G.P., Anderson, C.L., Britton, T., et al., Diversification of Neoaves: integration of molecular sequence data and fossils, *Biol. Lett.*, 2006, vol. 4, pp. 543–547.
- George, J.C. and Berger, A.J., *Avian Myology*, New York: Academic Press, 1966.
- Goloboff, P.A., Farris, J.S., and Nixon, K.C., TNT, a free program for phylogenetic analysis, *Cladistics*, 2008, vol. 24, pp. 774–786.
- Hackett, S.J., Kimball, R.T., Reddy, S., et al., A phylogenomic study of birds reveals their evolutionary history, *Science*, 2008, vol. 320, pp. 1763–1768.
- Hesse, A., Taxonomie der Ordnung Gruiformes (Aves) nach osteologischen morphologischen Kriterien unter besonderer Berücksichtigung der Messelornithidae, *Cour. Forsch. Senckenb.*, 1988, vol. 107, pp. 235–247.
- Hieronymus, T.L. and Witmer, L.M., Homology and evolution of avian compound rhamphotea, *Auk*, 2010, vol. 127, pp. 590–604.
- Hope, S., A new species of *Graculavus* from the Cretaceous of Wyoming (Aves: Neornithes), *Smiths. Contrib. Paleobiol.*, 1999, no. 89, pp. 261–266.
- Hope, S., The Mesozoic fossil record of Neornithes (modern birds), in *Mesozoic Birds: Above the Heads of Dinosaurs*,

- Chiappe, L.M. and Witmer, L.D., Eds., Berkeley: Univ. California Press, 2002, pp. 339–388.
- Kristoffersen, A.V., Lithornithid birds (Aves, Palaeognathae) from the Lower Palaeogene of Denmark, *Geol. Mijnbouw*, 1999, vol. 78, pp. 375–381.
- Kristoffersen, A.V., The avian diversity in the latest Paleocene-earliest Eocene Fur Formation, Denmark., *Ph.D. Dissertation Thesis*, Copenhagen: University of Copenhagen, 2002a.
- Kristoffersen, A.V., An early Paleogene trogon (Aves: Trogoniformes) from the Fur Formation, Denmark, *J. Vertebr. Paleontol.*, 2002b, vol. 22, pp. 661–666.
- Lemmrich, W. and Der Skleralring der Vogel, *Jen. Zeitschr. Naturwiss.*, 1931, vol. 65, pp. 513–586.
- Leonard, L., van Tuinen, M., and Dyke, G.J., A new specimen of the fossil palaeognath *Lithornis* from the Earliest Palaeogene of Denmark, *Amer. Mus. Novit.*, 2005, no. 3491, pp. 1–11.
- Lindow, B.E.K., The early evolution of modern birds: Fossil evidence from the Lower Eocene Fur Formation of Denmark, *Ph.D. Dissertation Thesis*, Dublin: National University of Ireland, 2007.
- Livezey, B.C. and Zusi, R.L., Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: I—methods and characters, *Bull. Carneg. Mus. Natur. Hist.*, 2006, no. 37, pp. 1–544.
- Manegold, A., Two additional synapomorphies of grebes Podicipedidae and flamingos Phoenicopteridae, *Acta Ornithol.*, 2006, vol. 41, pp. 79–82.
- Mayr, G., Charadriiform birds from the early Oligocene of Céreste (France) and the Middle Eocene of Messel (Hessen, Germany), *Geobios.*, 2000a, vol. 33, pp. 625–636.
- Mayr, G., A remarkable new “gruiform” bird from the Middle Eocene of Messel (Hessen, Germany), *Paläontol. Zeitschr.*, 2000b, vol. 74, pp. 187–194.
- Mayr, G., A new specimen of *Salmila robusta* (Aves: Gruiformes: Salmilidae n. fam.) from the Middle Eocene of Messel), *Paläontol. Zeitschr.*, 2002, vol. 76, pp. 305–316.
- Mayr, G., The phylogenetic relationships of the shoebill, *Balaeniceps rex*, *J. Ornithol.*, 2003, vol. 144, pp. 157–175.
- Mayr, G., Morphological evidence for sister group relationship between flamingos (Aves: Phoenicopteridae) and grebes (Podicipedidae), *Zool. J. Linn. Soc.*, 2004, vol. 140, pp. 157–169.
- Mayr, G., Tertiary plotopterids (Aves, Plotopteridae) and a novel hypothesis on the phylogenetic relationships of penguins (Spheniscidae), *J. Zool. Syst. Evol. Res.*, 2005, vol. 43, pp. 61–71.
- Mayr, G., Avian higher-level phylogeny: well-supported clades and what we can learn from a phylogenetic analysis of 2954 morphological characters, *J. Zool. Syst. Evol. Res.*, 2008, vol. 46, pp. 63–72.
- Mayr, G., *Paleogene Fossil Birds*, Heidelberg: Springer, 2009.
- Mayr, G., Reappraisal of *Eocypselus*—a stem group representative of apodiform birds from the early Eocene of Northern Europe, *Palaeobiodiv. Palaeoenv.*, 2010, vol. 90, pp. 395–403.
- Mayr, G., The phylogeny of charadriiform birds (shorebirds and allies)—reassessing the conflict between morphology and molecules, *Zool. J. Linn. Soc.*, 2011a, vol. 161, pp. 916–934.
- Mayr, G., On the osteology and phylogenetic affinities of *Morsoravis sedilis* (Aves) from the early Eocene Fur Formation of Denmark, *Bull. Geol. Soc. Denmark*, 2011b, vol. 59, pp. 23–35.
- Mayr, G., Metaves, Mirandornithes, Strisores, and other novelties—a critical review of the higher-level phylogeny of neornithine birds, *J. Zool. Syst. Evol. Res.*, 2011c, vol. 49, pp. 58–76.
- Mayr, G. and Bertelli, S., A record of *Rhynchaetites* (Aves, Threskiornithidae) from the early Eocene Fur Formation of Denmark, and the affinities of the alleged parrot *Miopsitta*, *Palaeobiodiv. Palaeoenv.*, 2011, vol. 91, pp. 229–236.
- Mayr, G. and Clarke, J., The deep divergences of neornithine birds; a phylogenetic analysis of morphological characters, *Cladistics*, 2003, vol. 19, pp. 527–553.
- Mayr, G. and Knopf, C., A stem lineage representative of buttonquails from the Lower Oligocene of Germany—fossil evidence for a charadriiform origin of the Turnicidae, *Ibis*, 2007, vol. 149, pp. 774–782.
- Mayr, G., Manegold, A., and Johansson, U., Monophyletic groups within “higher land birds”—comparison of morphological and molecular data, *J. Zool. Syst. Evol. Res.*, 2003, vol. 41, pp. 233–248.
- McKittrick, M.C., Phylogenetic analysis of avian hindlimb musculature, *Miscell. Publ. Univ. Michigan.*, 1991, no. 179, pp. 1–85.
- Olson, S.L., The fossil record of birds, in *Avian Biology*, Farner, D.S., King, J.R., and Parkes, K.C., Eds., New York: Academic Press, 1985, vol. 8, pp. 79–238.
- Olson, S.L., Early Eocene birds from the eastern North America: a faunule from the Nanjemoy Formation of Virginia, *Publ. Virginia Div. Min. Res.*, 1999, no. 152, pp. 123–132.
- Olson, S.L. and Parris, C.D., The Cretaceous birds of New Jersey, *Smiths. Contrib. Paleobiol.*, 1987, no. 63, pp. 1–22.
- Strauch, J.G., The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis, *Trans. Zool. Soc. London*, 1978, vol. 34, pp. 263–345.