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A new specimen of *Salmila robusta* (Aves: Gruiformes: Salmilidae n. fam.) from the Middle Eocene of Messel

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with 11 figures

Kurzfassung: Ein neues Exemplar des gruiformen Vogels *Salmila robusta* MAYR, 2000 wird aus dem mittleren Eozän von Messel (Deutschland) beschrieben. Es ist unter den am besten erhaltenen Vogelskeletten, die aus Messel bekannt sind und lässt bisher unbekannte anatomische Merkmale dieser Art erkennen. Das neue Exemplar bestätigt die frühere Feststellung (MAYR 2000b), dass *Salmila robusta* abgeleitete Merkmale vor allem mit den Cariamae (zu denen die rezenten Seriemas, Cariamidae, gehören), sowie den Psophiidae (Trompetervögel) teilt. Das Fehlen abgeleiteter Merkmale am Hypotarsus schließt allerdings eine Klassifikation von *Salmila robusta* innerhalb der Cariamae, wie unter Vorbehalt in der Originalbeschreibung angenommen, aus. Statt dessen stützt der gegenwärtige Kenntnisstand am ehesten eine Schwestergruppenbeziehung zwischen *Salmila robusta* und den Cariamae. Zusammen mit den morphologischen Besonderheiten der eozänen Art rechtfertigt dies eine Klassifikation von *Salmila robusta* in eine neue Familie, Salmilidae n. fam.

Schlüsselwörter: Fossile Vögel, Messel, Eozän, Gruiformes, Cariamae, Phylogenie, Salmilidae n. fam.

Abstract: A new specimen of the gruiform bird *Salmila robusta* MAYR, 2000 is described from the Middle Eocene of Messel (Germany). It is among the best preserved bird skeletons known from Messel, and allows the recognition of previously unknown anatomical features of this species. This new specimen confirms previous observations (MAYR 2000b), that *Salmila robusta* shares derived characters mainly with the Cariamae (to which the extant seriemas, Cariamidae, belong) and the Psophiidae (trumpeters). However, the absence of derived features of the hypotarsus precludes classification of *Salmila robusta* within the Cariamae, as tentatively proposed in the original description. Instead, present evidence rather supports sister group relationship between *Salmila robusta* and the Cariamae. Together with the morphological distinctness of the Eocene species, this justifies classification of *Salmila robusta* into a new family, Salmilidae n. fam.

Keywords: Fossil birds, Messel, Eocene, Gruiformes, Cariamae, phylogeny, Salmilidae n. fam.

Introduction

In the last decades, excavations of the Middle Eocene deposits of Messel near Darmstadt (Hessen, Germany) yielded several hundred avian skeletons, which offer an unique insight into the early evolution of birds. So far, more than 30 species have been described which belong to 26 different families (see MAYR 2000a for a survey on the Messel avifauna and SCHAAL & ZIEGLER 1988 for general information on the site). Although the description of most avian taxa from Messel is based on complete skeletons, the osteology of some is only insufficiently known due to the poor bone preservation of the respective specimens. Among these is the gruiform species *Salmila robusta* which was recently described by MAYR (2000b).

Extant Gruiformes (cranes, rails, and allies) are currently classified into eleven families (DEL HOYO et al. 1996), and in the original description, *Salmila robusta* was tentatively assigned to the Cariamae, a taxon which includes the South American Cariamidae (seriemas, two extant species in two genera) and the extinct families Idiornithidae (Eocene and Oligocene of Europe), Bathornithidae (Upper Eocene to Miocene of North America), and Phorusrhacidae (Eocene of Europe, Tertiary of South America, Pleistocene of North America), as well as several other poorly known fossil families (BRODKORB 1967; CRACRAFT 1968; MOURER-CHAUVIRÉ 1981, 1983). A phylogenetic assignment of *Salmila robusta* was especially difficult because of the fact that important osteological features are not visible in the specimens described by MAYR (2000b), and that the species shares most derived similarities not only with the Cariamae but also with the, likewise South-American, Psophiidae (trumpeters, three extant species in a single genus).

Described in this study is a new specimen of *Salmila robusta* which was recently acquired from a private collection by the Hessisches Landesmuseum, Darmstadt, Germany (HLMD), and which was not available at the time the original description was prepared. It is among the best preserved bird skeletons found in Messel so far, and allows the recognition of previously unknown anatomical features. *Salmila robusta* apparently is the sister taxon of several other recent and fossil families (see discussion), and together with the morphological distinctness of the Eocene taxon this justifies its classification into a new family.

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Material and methods

The fossil specimen is deposited in the Hessisches Landesmuseum, Darmstadt, Germany (HLMD). If not indicated otherwise, the anatomical terminology follows BAUMEL & WITMER (1993). The dimensions are in millimeters and refer to the maximum length of the bone along its longitudinal axis. Osteological comparisons have been made with representatives of all recent gruiform families except for the Heliornithidae (finfoots), of which no skeletons were available.

A cladistic analysis with the phylogenetic software PAUP, version 3.1 (SWOFFORD 1993) was performed using a data matrix of 35 anatomical characters (see Appendices I and II for character descriptions and data matrix). The shortest tree was found with the exhaustive search option and the analysis was run with the delayed transformation (DELTRAN) mode; consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis of 1000 replicates.

Systematic Palaeontology

Class Aves LINNAEUS, 1758
Order Gruiformes BONAPARTE, 1854
Salmilidae n. fam.

Type genus: *Salmila* MAYR, 2000.
Other included genera: None.

Diagnosis: Medium-sized birds with (1) furcula very robust; (2) coracoid without well developed foramen nervi supracoracoidei; (3) humerus robust and stout, and with large proximal end; (4) sternum with short margo costalis, one pair of deep incisions in margo caudalis, and tapering trabecula mediana; (5) ulna stout, not exceeding humerus in length, and with very short olecranon; (6) carpometacarpus with portion of trochlea carpalis between processus pisiformis and os metacarpale minus distinctly raised; (7) os metacarpale minus bowed, with proximal end bearing a small tubercle on its ventral side; (8) tarsometatarsus not exceeding ulna in length; (9) hypotarsus with cristae medialis et lateralis hypotarsi separated by distinct sulcus; (10) proximal end of first phalanx of fourth toe with large, medially directing projection.

At least the latter character probably is autapomorphic for the new family.

Salmila MAYR, 2000
Salmila robusta MAYR, 2000
Figs. 1-11

Referred specimen: HLMD.Be.161 (complete articulated skeleton on a slab, formerly in the private collection BEHNKE, Figs. 1, 2).
Dimensions (those of holotype in brackets): humerus, ~55.9 (l), ~53.5 (r) [53.4/56.0]; ulna, 50.0 (l) [~53/~52]; carpometacarpus, 27.1 (l), 26.9 (r) [27.0]; femur, ~49 (r) [~45]; tibiotarsus, ~74.8 (l), ~68 (r) [69.7/64.4]; tarsometatarsus, ~47 (l), ~45.5 (r) [42.9/44.7].

Description and comparison (only those features are mentioned which were not already described by MAYR 2000b):

Skull (Fig. 3): Few additional details of the skull can be seen in the new specimen. Again, it cannot be discerned with certainty whether the beak was holorhinal as in extant Cariamidae and Psophiidae, or schizorhinal as in some of the other gruiform taxa. The narial openings seem to have been more elongated than in extant Psophiidae and Cariamidae, but on the other hand the processus praemaxillaris of the os nasale (Fig. 3) appears to have been wider than in typical schizorhinal birds, e.g. Eurypygidae (sunbittern) and Gruidae (cranes). As in all other gruiform birds, the internarial septum was not ossified. The ossa lacrimalia apparently lack well developed processus supraorbitales which are also absent in extant Psophiidae but present in the Cariamidae and Phorusrhacidae (the bathornithid *Bathornis grallator* also seems to lack these processes, see WETMORE 1944 and OLSON 1985; the skull of other fossil Cariamae has not yet been described). The processus postorbitalis is visible next to the right radius and closely resembles that of the Psophiidae (Fig. 3).

Trachea: Contrary to the other two known specimens of *Salmila robusta*, in HLMD.Be.161 an ossified trachea is preserved.

Vertebrae: *Salmila robusta* had a fairly short neck; as in most other gruiform birds, the most caudal cervical vertebrae bear processus ventrales. It is not clearly visible whether the thoracic vertebrae were fused to form a notarium as in recent Psophiidae, Gruidae, Eurypygidae, and Rhynochetidae (kagus), although it seems to be more likely that they were not (the corresponding vertebrae are overlain by the sternum and are thus not directly visible, however they appear to have been slightly displaced against each other). The free thoracic vertebra directly cranial of the synsacrum lacks a processus ventralis (this vertebra bears a process in *Psophia* and a low ridge in *Cariama*); it further exhibits a well developed pneumatic foramen on each side of the corpus vertebrae (these foramina are also present on the corresponding vertebra of extant Psophiidae and Gruidae, but absent in the Cariamidae). Seven free tail vertebrae can be discerned, and this number was considered to be primitive within Gruiformes by LIVEZEY (1998: 2111). The pygostyle is large as that of the Cariamidae, although its exact shape is not clearly visible (the pygostyle of the Psophiidae is very small).

Coracoid: The coracoid is similar to that of the Psophiidae in the general proportions of its shaft. However, contrary to the latter, there is no prominent crista procoracoidei (terminology after LIVEZEY 1998: 2115) which is an autapomorphic feature of *Psophia*. The new specimen shows, that the coracoid of *S. robusta* does not exhibit a large foramen nervi supracoracoidei in a similar position to that of the Psophiidae, Rallidae (rails) or Gruidae. A foramen nervi supracoracoidei is typically

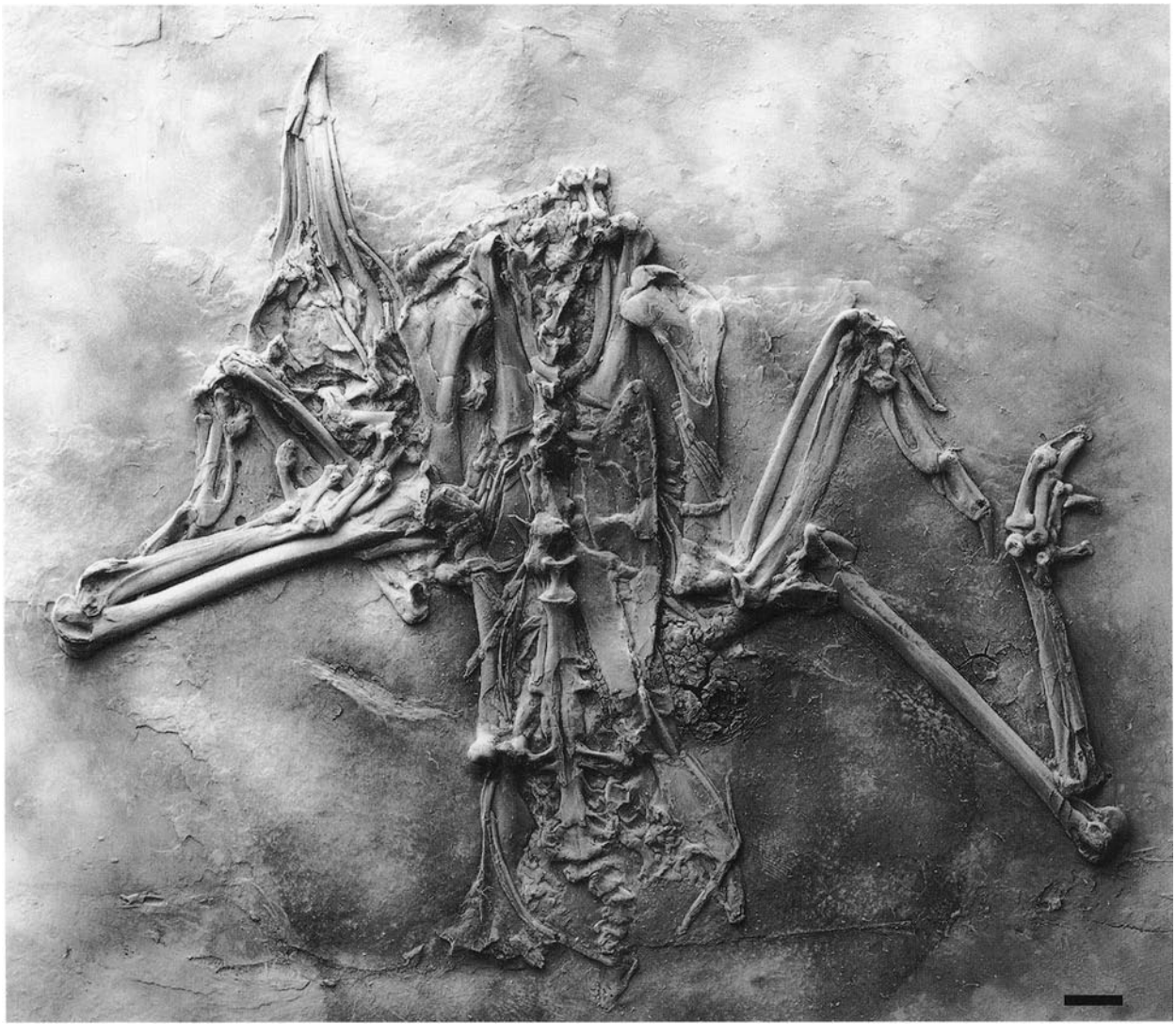

Fig. 1. *Salmila robusta*, referred specimen HLMD.Be.161 (nearly complete skeleton in ventral view); coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.

absent in all extant and fossil Cariamae. At least in ventral view, the processus acrocoracoideus apparently had a similar shape to that of *Idiornis* (see MOURER-CHAUVIRÉ 1983: pl. 4 fig. 8).

Furcula (Fig. 4): The furcula is very robust and the scapus claviculae becomes wider towards the extremitas omalis; the processus acromialis is short and acuminate. In the Cariamidae, as well as in the extinct Idiornithidae (see PETERS 1995: fig. 2) and in the Psophiidae, the furcula is much weaker. Among recent Gruiformes only the Otididae (bustards) have a furcula of similar robustness.

Scapula: The wide corpus of one of the scapulae is visible between the right femur and the vertebral column.

Sternum (Figs. 4, 5): The carina sterni is rather low, the apex carinae is pointed and protrudes strongly cranially as in many recent ducks (Anatidae, e.g. *Anas*, *Aix*), but contrary to extant Gruiformes. A well developed spina externa can be seen next to the sternal end of the left coracoid (a spina externa is absent in the Psophiidae but present in the Cariamidae). The processus craniolaterales are short as in the Cariamidae and Psophiidae. The margo costalis is very short and only 4-5 sternal ribs can be discerned (Fig. 4). The margo costalis of the Psophiidae is very long and eight sternal ribs articulate with the sternum (see BEDDARD 1890: fig. 2), in the Cariamidae the margo costalis also is longer but only five sternal ribs attach to it (Fig. 5). The sternum of the Idiornithidae is unknown, but *Salmila* completely differs from the bathornithid genus *Paracrax* in sternal morphology (see CRACRAFT 1968: fig. 8).

Humerus (Fig. 6): The humerus of *S. robusta* is only poorly preserved in the two skeletons described by MAYR (2000b). In the new specimen for the first time its exact proportions as well as details of the distal end can be discerned. Apart from the rounded crista deltopectoralis, the bone resembles the humerus of the idiornithid genus *Elaphrocnemus* in its overall proportions (see MOURER-CHAUVIRÉ 1983: pl. 1 figs. 3-4). The humeri of extant Cariamidae and Psophiidae are also robust as is that of

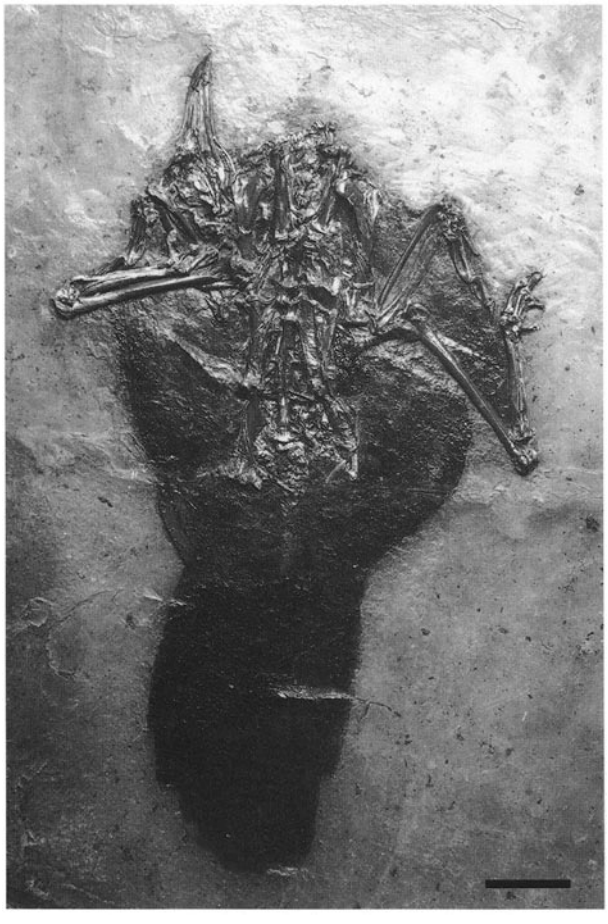

Fig. 2. *Salmila robusta*, referred specimen HLMD.Be.161. Note the well preserved feathering. – Scale bar = 30 mm.

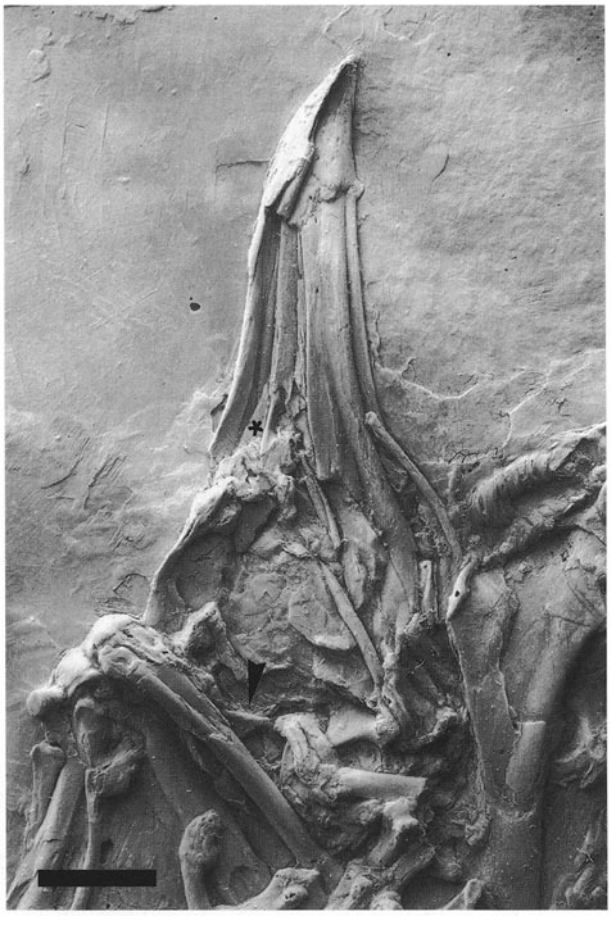

Fig. 3. *Salmila robusta*, referred specimen HLMD.Be.161, skull. The asterisk marks the processus praemaxillaris of the os nasale, the arrow points to the processus postorbitalis. Coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.

Salmila but, probably due to the limited capabilities of sustained flight of these taxa (DEL HOYO et al. 1996), the proximal end of the humerus is much smaller (Fig. 6). A humerus of similar robustness is also found in the Otididae, but the humerus of the other gruiform birds I investigated is much more slender and less robust than that of *S. robusta* (Fig. 6). Contrary to the Cariamidae and Psophiidae, the sulcus transversus of *S. robusta* is distinct and sharply delimited. The crista bicipitalis is small. The distal end of the bone most closely resembles the distal humerus of the Idiornithidae and Psophiidae: The condylus ventralis is globular (in *Cariama* and *Chunga* it is more elongated), the condylus dorsalis is narrow and, as in *Psophia*, its ventral side is excavated; both condyli are separated by a deep incisura intercondylaris which is much shallower in *Cariama* and *Chunga*. The processus flexorius strongly protrudes medially; the shortness of the processus flexorius visible on the poorly preserved humerus of the holotype (see MAYR 2000b) apparently is an artifact of preservation.

Ulna: As already noted by MAYR (2000b), the ulna of *Salmila robusta* closely resembles that of *Psophia*. As in the Psophiidae and Cariamae, both the olecranon and the tuberculum ligamenti collateralis ventralis are poorly developed. The cotyla ventralis is large and appears to have been ovate as in *Psophia* (in the Cariamae it is more circular), though its shape might be a result of the compression of the bone by the overlying sediments.

Carpometacarpus (Fig. 7): The carpometacarpus and the alar phalanges were already described by MAYR (2000b), and the new specimen does not show additional osteological details. The carpometacarpus of *Salmila robusta* closely resembles that of the Idiornithidae and extant Psophiidae (see MOURER-CHAUVIRÉ 1983 and Fig. 7).

Pelvis: MAYR (2000b) considered the pelvis of *S. robusta* to be unusually wide, but in the holotype this impression apparently is largely due to the flattening of the specimen. The new specimen HLMD.Be.161 shows that the overall proportions of the pelvis might instead have been similar to those of the Cariamidae and Psophiidae (although the alae praeacetabulares ilii are not visible). The synsacrum bears two pairs of long processus costales at the level of the antitrochanter, each of which encloses a narrow fenestra. A crista ventralis synsacri is absent (con-

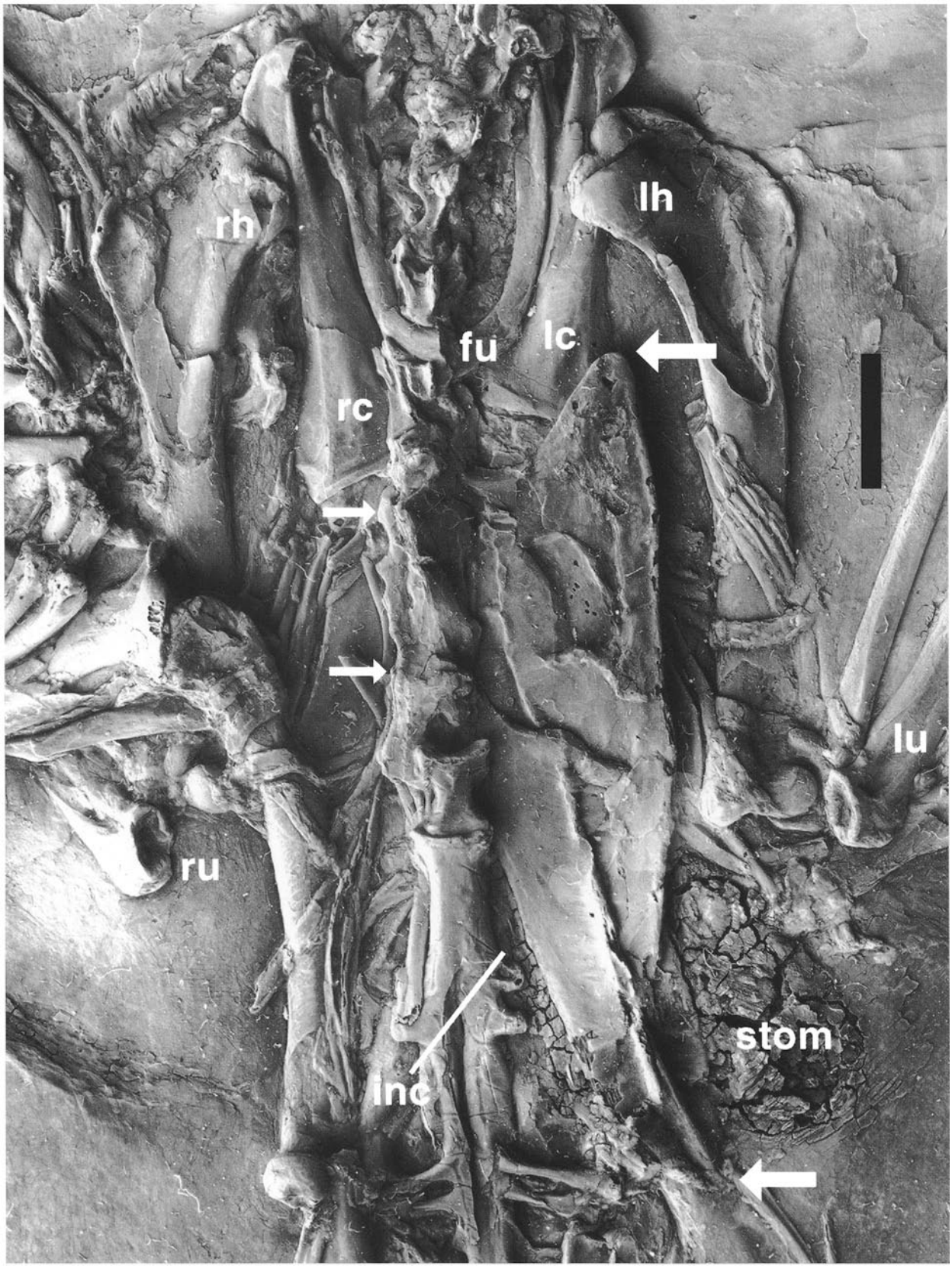

Fig. 4. *Salmila robusta*, referred specimen HLMD.Be.161, detail of the pectoral region. The two small arrows (left side) indicate the margo costalis of the sternum, the two large arrows (right side) the cranial and caudal ends of the sternum. – Abbreviations: fu = furcula, inc = incisura lateralis of sternum, lc = left coracoid, lh = left humerus, lu = left ulna, rc = right coracoid, rh = right humerus, ru = right ulna, stom = stomach content. – Coated with ammonium chloride to enhance contrast. Scale bar = 10 mm.

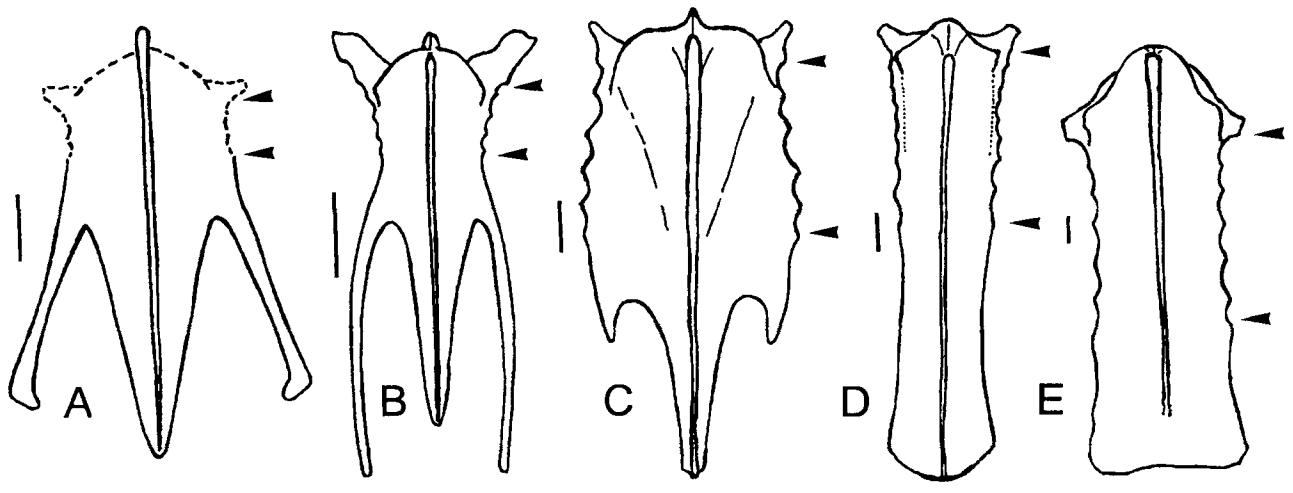

Fig. 5. Sterna in comparison (modified after MAYR 2000b). – **A:** *Salmila robusta* (Salmilidae n. fam.). – **B:** *Gallinula chloropus* (Rallidae). – **C:** *Cariama cristata* (Cariamidae). – **D:** *Psophia viridis* (Psophiidae). – **E:** *Balearica pavonina* (Gruidae). – The arrows indicate the margo costalis. Scale bar = 10 mm.

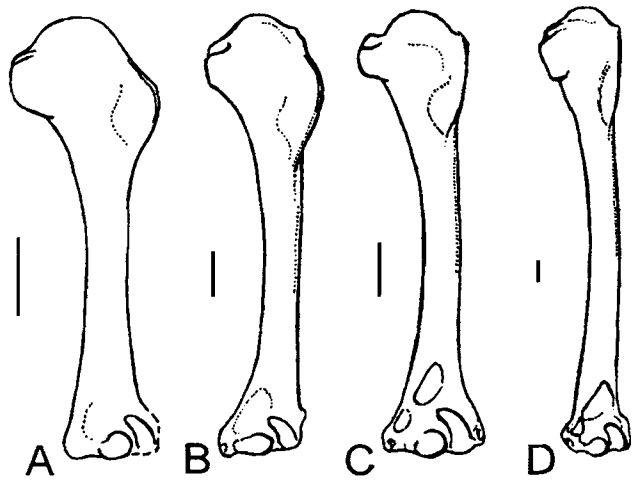

Fig. 6. Left humerus in comparison. – **A:** *Salmila robusta* (Salmilidae n. fam.). – **B:** *Cariama cristata* (Cariamidae). – **C:** *Psophia crepitans* (Psophiidae). – **D:** *Balearica pavonina* (Gruidae). – Scale bar = 10 mm.

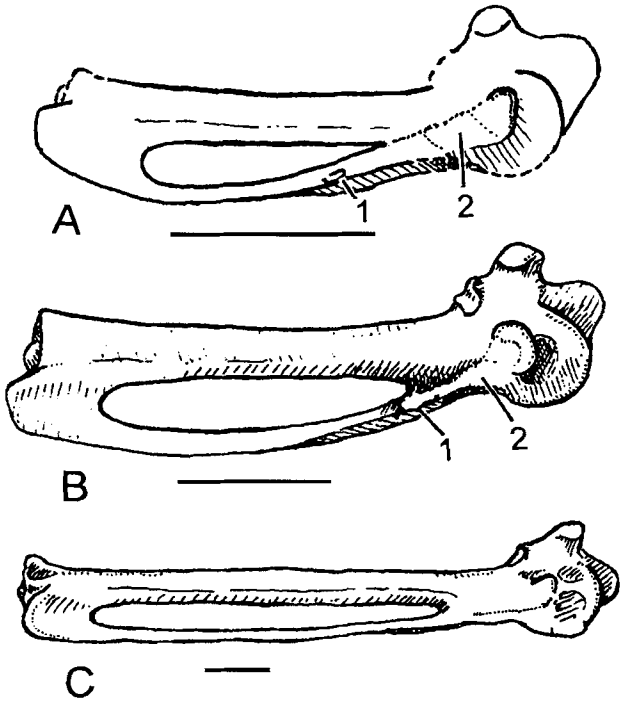

Fig. 7. Right carpometacarpus in comparison. – **A:** *Salmila robusta* (Salmilidae n. fam.). – **B:** *Psophia crepitans* (Psophiidae). – **C:** *Anthropoides virgo* (Gruidae). The numbers indicate (1) the tubercle on the ventral side of the os metacarpale minus, and (2) the raised portion of the trochlea carpalis between the processus pisiformis and the os metacarpale minus. – Scale bar = 10 mm.

trary to extant Psophiidae which exhibit a small medial ridge on the ventral surface of the cranial end of the synsacrum). The incisura caudalis pelvis appears to have been not as deep as in the Psophiidae and Cariamidae, and the margo caudalis of the alae ischii is dorsoventrally higher than in the Cariamidae. Contrary to the statement in MAYR (2000b), there are distinct spinae dorsolaterales ilii. The processus terminalis ischii projects more prominently than in the Psophiidae and Cariamidae; the ossa pubes are very long as in the Cariamidae. The fenestra ischiopubica apparently was narrow as in the Cariamidae and Psophiidae.

Femur: As far as it can be compared, owing to the preservation of the specimen, the femur is very similar to that of *Idiornis* (Idiornithidae) and *Psophia* in its proportions and in the relative curvature of the shaft, whereas the femur of the Cariamidae is stouter and more robust.

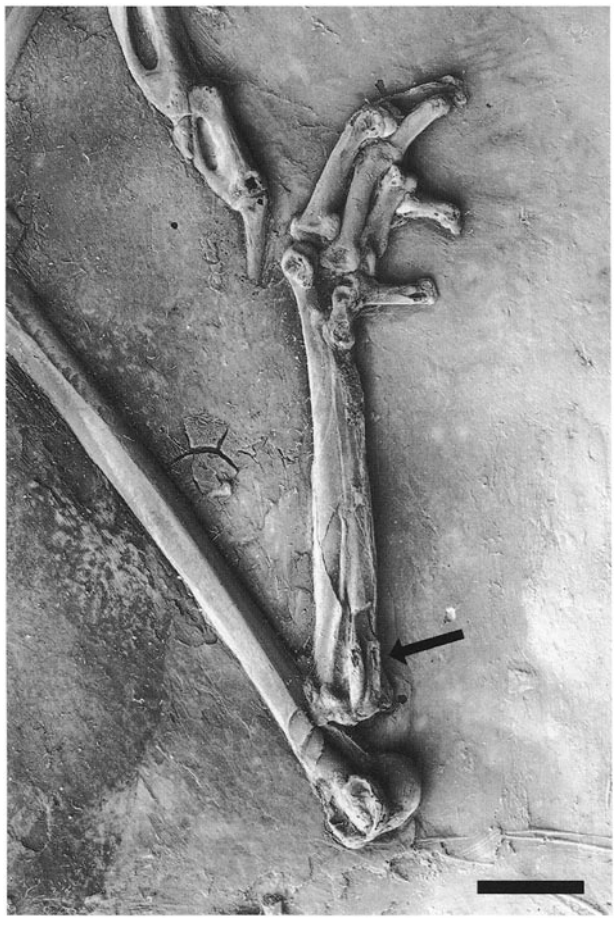

Fig. 8. *Salmila robusta*, referred specimen HLMD.Be.161, left foot. The arrow indicates the hypotarsus; coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.

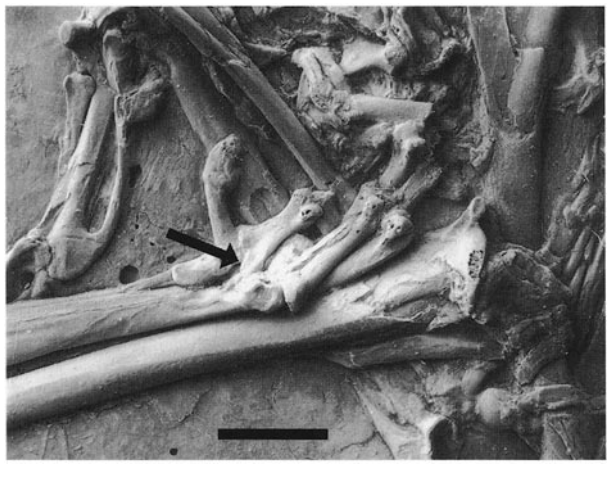

Fig. 9. *Salmila robusta*, referred specimen HLMD.Be.161, detail of right foot. The arrow indicates the marked medially protruding projection on the proximal end of the first phalanx of the fourth toe; coated with ammonium chloride to enhance contrast. – Scale bar = 10 mm.

Tibiotarsus: Due to the pressure of the overlying sediments, the distal ends of the tibiotarsi of the new specimen are medio-laterally compressed and appear to be narrower than they actually were. The distal tibiotarsus of the holotype (SMF-ME.3014) approaches the actual proportions more closely and resembles the corresponding element of the Psophiidae

Tarsometatarsus (Fig. 8): In the new specimen for the first time the hypotarsus is clearly visible, whereas in the holotype only few details can be discerned through the reverse of the transparent slab. It resembles the hypotarsus of the Psophiidae and, to a lesser degree, the genus *Elaphrocnemus* (Idiornithidae), but strongly differs from the block-like hypotarsus of all other Cariamae (including the putative phorusrhacid *Aenigmavis* PETERS, 1987 with which the tarsometatarsus of *Salmila* was compared in the original description). It is elongated and bears two crests which are separated by a distinct sulcus; the crista medialis hypotarsi is more protruding than the crista lateralis hypotarsi, the latter bears a shallow sulcus along its lateral side (visible on the left foot of HLMD.Be.161; Fig. 8). Apparently, the hypotarsus of *Salmila robusta* did not enclose a bony canal (contrary to ANDREWS 1899: 83 and CRACRAFT 1973: fig. 50, the hypotarsus of the two specimens of *Psophia crepitans* examined by me also did not enclose a bony canal, although in one specimen the sulcus is nearly closed). The fossa parahypotarsalis medialis is well developed, and there are low cristae plantares mediales and laterales, as well as a low crista medianoplantaris (which is absent in the Cariamidae and Psophiidae). The fossa metatarsi I is distinct and situated in a similar relative position to that of *Psophia* (in the Cariamidae, but not in the Idiornithidae, see MAYR (2000c), the hallux is greatly reduced). As in all other gruiform birds, both the trochleae metatarsi II and IV bear a wing-like crista on their plantar surface (eminentia plantaris of LIVEZEY 1998: 2122; visible at the left foot of HLMD.Be.161).

Toes (Figs. 8, 9): The proximal end of the first phalanx of the fourth toe bears a very marked medially protruding projection which is also well developed in the Psophiidae but less distinct in the Cariamidae. In the Cariamidae, the phalanges of the second toe are very short so that the distal end of the second phalanx of the second toe extends hardly beyond the proximal end of the second phalanx of the third toe. This feature, which was mentioned by WETMORE (1933: 308) in order to support assignment of the Bathornithidae to the Cariamae, is absent in *S. robusta*. MOURER-CHAUVIRÉ (1983: 136) also noted that in *Idiornis* "la fin de la deuxième phalange du doigt II s'étend à peine au-delà de la base de la deuxième phalange du doigt III". However, in the articulated feet of the Idiornithidae described by PETERS (1995) and MAYR (2000c), the proportions of the pedal phalanges are similar to those of *Salmila robusta*, and the distal end of the second phalanx of the second toe reaches almost as

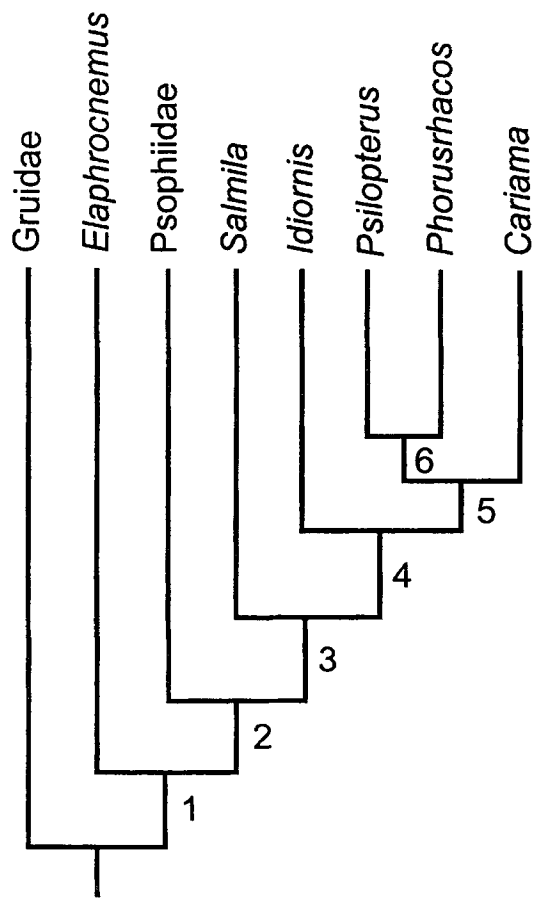

Fig. 10. Single most parsimonious trees resulting from a cladistic analysis of the data matrix in Appendix II with PAUP 3.1 (CI = 0.64, RI = 0.64, RC = 0.41). The nodes are supported by the following diagnostic characters (i.e. those with CI = 1.0): **node 1** - ch. 21; **node 2** - ch. 2, 23, 25; **node 3** - ch. 9, 15; **node 4** - ch. 6, 31; **node 5** - ch. 33, 34, **node 6** - ch. 3, 7, 17, 18, 24, 26. Especially the position of *Elaphrocnemus* departs from current classifications and has to be regarded as tentative (see text).

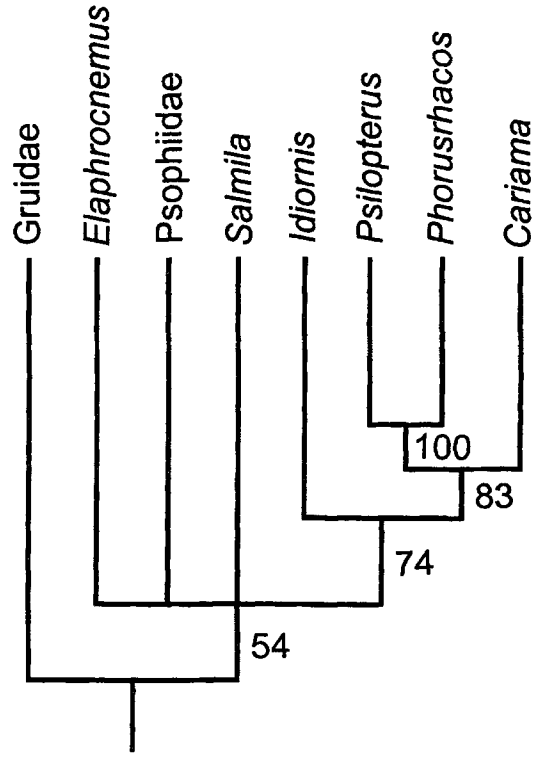

Fig. 11. 50% majority-rule consensus tree of 1000 bootstrapped replicates based on a cladistic analysis of the data set in Appendix II. The numbers indicate the percentage of bootstrapped replicates in which the node was conserved.

far distally as the distal end of the second phalanx of the third toe.

Feathers (Fig. 2): The feathers, which are only visible as indistinct shadows in the holotype, are excellently preserved in the new specimen. The longest primary measures at least 128 mm (measured from the distal end of the phalanx distalis digiti majoris, the tip is not visible). The new specimen confirms that *S. robusta* had a very long, rounded tail as extant Cariamidae and Mesitornithidae (mesites) (the tail of the Psophiidae is very short). The length of the tail feathers increases towards the central rectrices, that of the outermost tail feather is about 91 mm, that of the innermost about 127 mm (measured from the tip of the pygostyle to the tip of the feather). The number of the rectrices cannot be clearly discerned but there seem to have been either 10 or 12 (six pairs of tail feathers were considered to be primitive within the Gruiformes by LIVEZEY 1998: 2127).

Stomach content: As in the holotype, stomach content – a dense layer of carbonized matter – is preserved in specimen HLMD.Be.161 (Fig. 4).

Discussion

The new specimen confirms previous observations (MAYR 2000b) that *Salmila robusta* mainly shares derived similarities with the Psophiidae and recent and fossil Cariamae. The Eocene species also most closely resembles these taxa in the overall morphology of the major limb bones, especially concerning the distal end of the humerus, and the morphology of ulna and carpometacarpus. Its relatively shorter hindlimb elements almost certainly are primitive within gruiform birds (similar limb proportions are, for example, also found in many extant rails) and the characteristic sternal morphology, which distinctly differs from the highly apomorphic one of extant Cariamidae and Psophiidae, might also be

plesiomorphic within the Gruiformes (a similar sternum also occurs in the Rallidae; see Fig. 5 and MAYR 2000b: fig. 4).

In particular, the following derived features are shared by Salmilidae, Psophiidae, and most Cariamae (see also MAYR 2000b):

1. Tip of beak more or less strongly hooked (the hook is especially well developed in the Phorusrhacidae).
2. Ulna with greatly reduced olecranon (except for the phorusrhacid genus *Phorusrhacos* in which the olecranon is well developed).
3. Carpometacarpus with portion of trochlea carpalis between processus pisiformis and os metacarpale minus distinctly raised (Fig. 7; absent in the carpometacarpi which MOURER-CHAUVIRÉ 1983 referred to the genus *Elaphrocnemus* and in those of the phorusrhacid genera *Psilopterus* and *Phorusrhacos*).
4. Os metacarpale minus bowed, with dorsoventrally wide proximal end (the dorsoventrally wide proximal end is absent in the carpometacarpi which MOURER-CHAUVIRÉ 1983 referred to the genus *Elaphrocnemus*). This feature was also considered to be derived by ERICSON (1997: 459).
5. Proximal end of os metacarpale minus bearing a well developed tubercle on its ventral side (Fig. 7; absent in the carpometacarpi, which MOURER-CHAUVIRÉ (1983) referred to the idiornithid genus *Elaphrocnemus*). This feature has also been mentioned for *Phorusrhacos*, the Cariamidae, and Psophiidae by ANDREWS (1899: 72) who noted that he did not "observe this in any but these birds" (which is not quite correct, since the tubercle is also present in few other birds, e.g. rollers, Coraciidae).
6. Fenestra ischiopubica very narrow. This feature was also considered to be derived by ERICSON (1997: 448).

A derived character which is shared by *Salmila robusta* and the Cariamae, but absent in the Psophiidae, is the strongly hooked extremitas omalis of coracoid (only visible in the holotype of *S. robusta* and absent in the coracoids which MOURER-CHAUVIRÉ (1983) referred to the idiornithid genus *Elaphrocnemus*, as well as in the highly apomorphic coracoids of the Phorusrhacidae). In the apparent absence of a well developed foramen nervi supracoracoidei, *Salmila robusta* further agrees with the Cariamae and differs from the Psophiidae, although the polarity of this character (i.e. whether it is derived or primitive within gruiform birds) is uncertain.

However, the new specimen clearly shows that *Salmila robusta* lacks the characteristic block-like hypotarsus which is present in all Recent and fossil Cariamae, except the genus *Elaphrocnemus*, and which was considered to be derived by LIVEZEY (1998: 2121). The Eocene taxon further differs from members of the Cariamae in the more weakly hooked tip of the praemaxilla, and if it is more closely related to the Cariamae it most likely is the sister taxon of the latter. Analysis of the data matrix in Appendix II with PAUP 3.1 also resulted in a sister group relationship between *Salmila robusta* and the Cariamae (of which only those fossil taxa were included from which detailed descriptions of significant parts of the skeleton exist) (Fig. 10). Since the clade (Salmilidae + Cariamae) collapsed in the bootstrap analysis (Fig. 11), this classification, again, has to be regarded as tentative.

Phylogenetic assignment of *Salmila robusta* is aggravated by the fact that, as outlined above, most derived characters are not only shared with the Cariamae but also with the Psophiidae. Similarities between fossil Cariamae and recent Psophiidae were also noted by several earlier authors (ANDREWS 1899; CRACRAFT 1968; OLSON 1974; MOURER-CHAUVIRÉ 1983), and extant seriemas and trumpeters indeed were often considered to be closely related (e.g. BEDDARD 1890; STEGMANN 1978; CRACRAFT 1982). More recent studies, however, supported monophyly of Psophiidae and Rallidae (HOUDE et al. 1997), or of Psophiidae, Gruidae and Aramidae (limpkins) (HESSE 1990; SIBLEY & AHLQUIST 1990).

At the time the original description of *S. robusta* was submitted, a very comprehensive cladistic analysis of the interrelationships between gruiform birds was published by LIVEZEY (1998) which also resulted in monophyly of the taxon (Psophiidae + (Gruidae + Aramidae)). LIVEZEY (1998: tab. 3) listed ten putative synapomorphies of this taxon; of these characters, however, one was incorrectly coded for the Psophiidae (there is no "crista infratrochlearis" on the proximal end of the carpometacarpus), others are of questionable homology (the "rounded indentation" in the cranial margin of the alae praeacetabulares ilii which is of very different shape in Psophiidae and Gruidae/Aramidae, and the "marked heterogeneity of form" of the cervical vertebrae), also present in the Cariamae (the "dorsoventrally broad" crus dorsale fossae on the proximal end of the humerus), or widespread among birds (the presence of a notarium which even within the Gruiformes is also found in Eurypygidae and Rhynochetidae).

A recent phylogenetic analysis of LIVEZEY & ZUSI (2001) which included representatives of all recent higher avian taxa resulted in a completely different phylogenetic tree, but since this analysis was explicitly considered preliminary, it is not discussed further here.

Analysis of the data matrix in Appendix II with PAUP 3.1 resulted in a sister group relationship between the Psophiidae and the taxon (Salmilidae + Cariamae), but the corresponding node also collapsed in the bootstrap analysis.

The relationships between the various taxa of the Cariamae are poorly understood, and in the relative position of the genera *Idiornis* and *Elaphrocnemus* the phylogenetic tree which resulted from the cladistic analysis with PAUP 3.1 strongly differs from current classifications. MOURER-CHAUVIRÉ (1981, 1983) classified the early Tertiary Bathornithidae and Idiornithidae (in which she included the genera *Idiornis* and *Elaphrocnemus*) as subfamilies of the Cariamidae. However, analysis of the data matrix in Appendix II did not support monophyly of Cariamidae and *Idiornis* (the Bathornithidae were not

included since the taxonomy of these birds is very poorly resolved; see OLSON 1985), but instead resulted in monophyly of Cariamidae and Phorusrhacidae with *Idiornis* being the sister taxon of these two families (Fig. 10). *Elaphrocnemus* closely resembles *Idiornis* in the overall morphology of, except for the coracoid, most known skeletal elements and is classified into the Idiornithidae by virtually all recent authors (e.g. BRODKORB 1967; CRACRAFT 1973; MOURER-CHAUVIRÉ 1983). Since several derived features that are shared by *Idiornis*, Phorusrhacidae and the Cariamidae are, however, absent in *Elaphrocnemus* (i.e. ch. 6, 9, 23, 31 of Appendix I), the cladistic analysis resulted in a basal position of *Elaphrocnemus*, even outside the Cariamae (i.e. the taxon including *Idiornis*, Phorusrhacidae, and Cariamidae). Whether this actually reflects the true phylogeny or merely is a result of inadequate character sampling has to be shown by future studies, but so far a close relationship between *Idiornis* and *Elaphrocnemus* has not been supported with derived characters.

To resolve the phylogeny within the Cariamae, a revision of the numerous fossil taxa is in great need, and if classification of *Salmila robusta* as a sister taxon of the Cariamae is correct, this species will be of great importance for outgroup comparisons.

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Literature

ANDREWS, C.W. 1899. On the Extinct Birds of Patagonia. 1. The Skull and Skeleton of *Phororhacos inflatus* Ameghino. – Transactions of the Zoological Society of London **15**: 55-86.

BAUMEL, J.J. & WITMER, L.M. 1993. Osteologia. – In: BAUMEL, J.J.; KING, A.S.; BREAZILE, J.E.; EVANS, H.E. & VANDEN BERGE, J.C., eds., Handbook of avian anatomy: Nomina Anatomica Avium. – Publications of the Nuttall Ornithological Club **23**: 45-132.

BEDDARD, F.E. 1890. On the Structure of *Psophia* and on its Relations to other Birds. – Proceedings of the Zoological Society of London **1890**: 329-341.

BONAPARTE, C.L. 1854. Conspectus systematis ornithologiae. – Annales des sciences naturelles/Zoologie (4) **1**: 105-152.

BRODKORB, P. 1967. Catalogue of fossil birds. Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). – Bulletin of the Florida State Museum (Biological Sciences) **11** (3): 99-220.

CRACRAFT, J. 1968. A Review of the Bathornithidae (Aves, Gruiformes), with Remarks on the Relationships of the Suborder Cariamae. – American Museum Novitates **2326**: 1-46.

CRACRAFT, J. 1973. Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. – Bulletin of the American Museum of Natural History **151**: 1-127.

CRACRAFT, J. 1982. Phylogenetic relationships and transarctic biogeography of some gruiform birds. – In: BUFFETAUT, E.; JANVIER, P.; RAGE, J.-C. & TASSY, P., eds., Phylogénie et Paléobiogéographie. Livre jubilaire en l'honneur de Robert Hoffstetter. – Géobios, Mémoire Spécial **6**: 393-402.

ERICSON, P.G.P. 1997. Systematic relationships of the palaeogene family Presbyornithidae (Aves: Anseriformes). – Zoological Journal of the Linnean Society **121**: 429-483.

HESSE, A. 1990. Die Beschreibung der Messelornithidae (Aves: Gruiformes: Rhynocheti) aus dem Alttertiär Europas und Nordamerikas. – Courier Forschungsinstitut Senckenberg **128**: 1-176.

HOUDE, P.; COOPER, A.; LESLIE, E.; STRAND, A.E. & MONTAÑO, G.A. 1997. Phylogeny and Evolution of 12S rDNA in Gruiformes (Aves). – In: MINDELL, D.P., ed., Avian Molecular Evolution and Systematics: 121-158, San Diego (Academic Press).

DEL HOYO, J.; ELLIOTT, A. & SARGATAL, J. 1996. Handbook of the Birds of the World, vol. 3, Hoatzin to Auks. – 821 p., Barcelona (Lynx Edicions).

LINNAEUS, C. von 1758. Systema naturae per regna tria naturae. – 10th edition, 2 vols., 824 p., Holmiae (L. Salvii).

LIVEZEY, B.C. 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). – Philosophical Transactions of the Royal Society of London (B) **353**: 2077-2151.

LIVEZEY, B.C. & ZUSI, R.L. 2001. Higher-order phylogenetics of modern Aves based on comparative anatomy. – Netherlands Journal of Zoology **51** (2): 179-205.

MAYR, G. 2000a. Die Vögel der Grube Messel – ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. – Natur und Museum **130** (11): 365-378.

MAYR, G. 2000b. A remarkable new "gruiform" bird from the Middle Eocene of Messel (Hessen, Germany). – Paläontologische Zeitschrift **74** (1/2): 187-194.

MAYR, G. 2000c. New or previously unrecorded avian taxa from the Middle Eocene of Messel (Hessen, Germany). – Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe **3**: 207-219.

MOURER-CHAUVIRÉ, C. 1981. Première indication de la présence de Phorusrhacidés, famille d'oiseaux géants d'Amérique du Sud, dans le Tertiaire européen: *Ameghinornis* nov. gen. (Aves, Ralliformes) des Phosphorites du Quercy, France. – Géobios **14** (5): 637-647.

MOURER-CHAUVIRÉ, C. 1983. Les Gruiformes (Aves) des Phosphorites du Quercy (France). 1. Sous-ordre Cariamae (Cariamidae et Phorusrhacidae). Systématique et biostratigraphie. – Palaeovertebrata **13** (4): 83-143.

OLSON, S.L. 1974. [Review of CRACRAFT 1973]. – Auk **91**: 862-865.

OLSON, S.L. 1985. The fossil record of birds. – In: FARNER, D.S.; KING, J.R. & PARKES, K.C., eds., Avian Biology **8**: 79-238, New York (Academic Press).

PETERS, D.S. 1987. Ein "Phorusrhacide" aus dem Mittel-Eozän von Messel (Aves: Gruiformes: Cariamae). – Documents des Laboratoires de Géologie de Lyon **99**: 71-87.

PETERS, D.S. 1995. *Idiornis tuberculata* n. spec., ein weiterer ungewöhnlicher Vogel aus der Grube Messel (Aves: Gruiformes: Cariamidae: Idiornithinae). – In: PETERS, D.S., ed., Acta palaeornithologica. – Courier Forschungsinstitut Senckenberg **181**: 107-119.

SCHAAL, S. & ZIEGLER, W., eds., 1988. Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens. – 315 p., Frankfurt am Main (Kramer).

SIBLEY, C.G. & AHLQUIST, J.E. 1990. Phylogeny and classification of birds: A study in molecular evolution. – 976 p., New Haven, London (Yale University Press).

SINCLAIR, W.J. & FARR, M.S. 1932. Aves of the Santa Cruz Beds. – Reports of the Princeton University Expeditions to Patagonia, 1896-1899, **7** (2): 157-191.

STEGMANN, B. 1978. Relationships of the superorders Alectoromorphae and Charadriimorphae (Aves): a comparative study of the avian hand. – Publications of the Nuttall Ornithological Club **17**: 1-119.

SWOFFORD, D.L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1. – Champaign (Illinois Natural History Survey).

WETMORE, A. 1933. Bird Remains from the Oligocene Deposits of Torrington, Wyoming. – Bulletin of the Museum of Comparative Zoology **75** (7): 297-311.

WETMORE, A. 1944. A new terrestrial vulture from the Upper Eocene deposits of Wyoming. – Annals of the Carnegie Museum **30**: 57-69.

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Appendix I

Character descriptions

1. Skull with well developed, caudally projecting processus supraorbitales: absent (0), present (1).
2. Maxilla with more or less hooked tip: absent (0); present (1).
3. Maxilla dorsoventrally very deep and mediolaterally strongly compressed: absent (0), present (1).
4. Vertebra cranial to synsacrum with pneumatic foramen on each side of corpus vertebrae: absent (0), present (1).
5. Several thoracic vertebrae fused to a notarium: absent (0), present (1).
6. Coracoid, processus procoracoideus fused to processus acrocoracoideus: absent (0), present (1). Not comparable in *Psilopterus* and *Phorusrhacos* in which the processus acrocoracoideus is greatly reduced.
7. Coracoid, processus acrocoracoideus extremely reduced: absent (0), present (1).
8. Coracoid, well developed foramen nervi supracoracoidei: present (0), absent (1).
9. Extremitas omalis of coracoid strongly hooked: absent (0), present (1). Not comparable in *Psilopterus* and *Phorusrhacos* in which the extremitas omalis of the coracoid is greatly reduced.
10. Furcula with weakly developed scapi claviculae: absent (0), present (1).
11. Sternum, margo costalis long, extending over about half the length of the corpus sterni: absent (0), present (1).
12. Sternum, margo costalis with seven or more processus costales: absent (0), present (1).
13. Sternum, caudal margin with: one pair of incisions (0), without incisions (1).
14. Sternum, long and narrow mediolaterally, ventral surface with numerous pneumatic openings: absent (0), present (1).
15. Sternum, spina externa short or absent (0), long and well developed (1).
16. Humerus, proximal end with distinct muscular attachment scar on ventral surface, distal of foramen pneumaticum: absent (0), present (1).
17. Distal end of humerus strongly oblique in relation to longitudinal axis of the shaft: absent (0), present (1).
18. Humerus with reduced proximal end and ulna greatly abbreviated, measuring only about 3/4 of the length of the humerus (both features are related to flightlessness of the respective taxa): absent (0), present (1).
19. Ulna with greatly reduced olecranon: absent (0), present (1).
20. Ulna dorsoventrally compressed: absent (0), present (1).
21. Carpometacarpus, os metacarpale minus distinctly bowed: absent (0), present (1).
22. Carpometacarpus, portion of trochlea carpalis between processus pisiformis and os metacarpale minus distinctly raised, absent (0), present (1).
23. Carpometacarpus, proximal end of os metacarpale minus dorsoventrally wide and bearing a well developed tubercle on its ventral side: absent (0), present (1).
24. Pelvis mediolaterally strongly compressed: absent (0), present (1)
25. Pelvis, fenestra ischiopubica very narrow or completely closed: absent (0); present (1).
26. Pelvis, foramen obturatum completely closed: absent (0); present (1).
27. Femur robust, ratio mediolateral width of midsection of shaft : total length of bone more than 0.09: absent (0), present (1).
28. Tibiotarsus, proximal end with prominent projection lateral to deep fossa retropatellaris, steeply sloping towards facies gastrocnemialis: absent (0), present (1).
29. Tibiotarsus, prominent tubercle distal to the pons supratendineus (considered to be the tuberositas distalis retinaculi musculorum extensorum by LIVEZEY 1998 which is, however, located proximal to this tubercle): absent (0), present (1).
30. Tarsometatarsus greatly elongated and slender: absent (0), present (1).
31. Tarsometatarsus, hypotarsus block-like, plantar prominence without well developed sulci: absent (0), present (1).

32. Proximal phalanx of hallux very short, measuring less than half of the length of proximal phalanx of third toe: absent (0), present (1).
33. Distal end of second phalanx of second toe extending only little beyond proximal end of second phalanx of third toe: absent (0), present (1).
34. Ungual phalanx of second toe "raptorial" (i.e. strongly curved and sharply hooked): absent (0), present (1).
35. Proximal end of first phalanx of fourth toe with marked medially protruding projection: absent (0), present (1).

Appendix II

Data matrix of 35 osteological characters for *Salmila robusta* (Salmilidae n. fam.), Gruidae, Psophiidae, *Idiornis* (Idiornithidae), *Elaphrocnemus* (currently also classified into Idiornithidae), Phorusrhacidae (*Phorusrhacos* and *Psilopterus*), and Cariamidae (*Cariama*); see Appendix I for character definitions. Outgroup comparisons are based on a hypothetical ancestor, unknown character states are indicated by "?".

	0 0 0 0 0 0 0 0 0 1 1 1 10 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5
Ancestor	0 0 0 ? 0 0 0 ? 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Idiornis[a, b]	? ? ? ? ? 1 0 1 1 1 ? ? ? ? ? 0 0 0 1 0 1 1 1 0 ? ? 0 0 0 1 1 0 0 0 0
Elaphrocnemus[a]	? ? ? ? ? 0 0 1 0 ? ? ? ? ? ? 0 0 0 1 1 1 0 0 ? ? ? 0 0 0 1 0 ? ? ? ?
Cariama	1 1 0 0 0 1 0 1 1 1 1 0 0 0 1 1 0 0 1 1 1 1 1 0 1 0 1 1 0 1 1 1 1 1 0
Psilopterus[c]	1 1 1 ? 0 ? 1 1 ? ? 1 0 ? 0 ? 0 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 1 0
Phorusrhacos[d]	1 1 1 ? ? ? 1 1 ? ? ? ? ? ? ? ? 1 1 0 1 1 0 1 1 1 1 1 0 1 1 1 1 1 1 0
Salmila	0 1 0 1 ? 0 0 1 1 0 0 0 0 0 1 ? 0 0 1 ? 1 1 1 0 1 ? ? ? 0 0 0 0 0 0 1
Psophiidae	0 1 0 1 1 0 0 0 0 1 1 1 1 1 0 1 0 0 1 1 1 1 1 0 1 0 0 1 1 1 0 0 0 0 1
Gruidae	1 0 0 1 1 0 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0

[a] after MOURER-CHAUVIRÉ (1983) and own observation (casts of humeri and tarsometatarsi of *Elaphrocnemus*)
[b] after PETERS (1995), and MAYR (2000c)
[c] after SINCLAIR & FARR (1932) and own observation
[d] after ANDREWS (1899) and own observation