**Pumiliornis tessellatus** n. gen. n. sp., a new enigmatic bird from the Middle Eocene of Grube Messel (Hessen, Germany)

Gerald Mayr

Abstract

*Pumiliornis tessellatus* n. gen. n. sp. is described from the Middle Eocene of Grube Messel (Hessen, Germany). This bird combines “gruiform” and “charadriiform” characters with a columbiform foot and therefore resembles *Rhynchaeites messelensis* Wittich, a species also found in Messel. *Pumiliornis tessellatus* can be clearly distinguished from all extant taxa, but it has not been possible to ascertain whether the similarities it shares with *Rhynchaeites messelensis* are synapomorphic, symplesiomorphic or convergent.

**Keywords:** Messel, Eocene, birds, *Rhynchaeites messelensis*

Kurzfassung

*Pumiliornis tessellatus* n. gen. n. sp. wird aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland) beschrieben. Dieser Vogel vereinigt „gruiforme“ und „charadriiforme“ Merkmale mit einem columbiformen Fuß und ähnelt darin der ebenfalls in Messel gefundenen Art *Rhynchaeites messelensis* Wittich. *Pumiliornis tessellatus* läßt sich klar gegenüber allen rezenten Taxa abgrenzen, aber es konnte nicht geklärt werden, ob die Übereinstimmungen mit *Rhynchaeites messelensis* synapomorph, symplesiomorph oder konvergent sind.

**Schlüsselwörter:** Messel, Eozän, Vögel, *Rhynchaeites messelensis*

Introduction

In both the number of individual skeletons and the number of species, birds constitute a considerable part of the land vertebrates so far found in Messel. Most of them belong to the “land bird assemblage” of Olson (1985). A survey was conducted by Peters (1992); more recently the systematic position of some of the small “higher land birds” has been analyzed by Mayr (1998). In many cases, despite an extensive knowledge of their osteology, the phylogenetic position of some birds from Messel still cannot be determined. The species presented in this paper belongs among these taxa with uncertain systematic affinities.
Methods

It has not been possible to carry out an exhaustive phylogenetic analysis in the course of this paper due to the almost completely unresolved systematic position of most higher avian groups. This would have required the inclusion of a large number of taxa. The osteological terminology follows Baumel & Witmer (1993). Dimensions were mainly taken from x-ray photographs, but were confirmed by measuring the individual bones. They represent the overall length of the bone along its longitudinal axis. Concerning the length of the claws, the distance of the tuberculum extensorium to the apex phalangis has been measured.

Systematics

Type species: Pumiliornis tessellatus n. gen. n. sp., only known species of the genus.

Diagnosis: Small anisodactyl bird, which differs from all other avian genera in the combination of the following characters:

- long and slender bill, probably schizorhinal
- furcula without apophysis furculae
- stout humerus with broad proximal end
- carpometacarpus slender with broad symphysis metacarpalis distalis
- short and dorso-ventrally flattened tarsometatarsus with a low hypotarsus
- trochlea metatarsorum II and IV considerably shorter than trochlea metatarsi III
- well-developed hallux

Autapomorphic for the genus Pumiliornis is the caudally displaced apex carinae.

Etymology: pumilio (Lat.): dwarf, ornis (Gr.): bird.

Pumiliornis tessellatus n. gen. n. sp. (fig. 1)


Diagnosis: As for genus. Measurements see tabs. 1-2.

Type locality: Grube Messel, Hessen, Germany.

Type horizon: Geiseltalium, Middle Eocene.

Referred specimen: SMF ME 2245A and B (fig. 1c and d), articulated skeleton lacking the skull and the toes in the collection of the Forschungsinstitut Senckenberg, Frankfurt a.M. (Germany). Excavation 29-390, found on 18.5.1987.

Etymology: tessellatus (Lat.): mosaic – because of the mosaic distribution of characters typical for different higher avian taxa.

Description and comparison: In order to make comparisons more easy, the terms “Gruiformes” and “Charadriiformes” as used in this paper include the families listed by Wetmore (1960), although the monophyly of these two taxa is not supported by any derived character. The terms are therefore enclosed in quotation marks.

Skull (fig. 2): The lacrimal-ectethmoid complex is large and plate-like (fig. 2: 1). As in Eurypygidae ("Gruiformes"), it ends with a thin processus orbitalis which touches the jugal bar (SMF ME 2092A). The interorbital bridge is narrow (fig. 2: 2). The interorbital septum might have been fenestrated as this region is transparent on the x-ray photograph. A processus postorbitalis is not visible. The processus oticus of the quadratum can be seen from the caudal side and is broad medio-laterally. The beak is long, straight and slender. It is not possible to ascertain whether its tip is blunt or pointed. The processus maxillaris of the os nasale is thin (fig. 2: 3, fig. 2). The nares appear to be schizorhinal: a slit extends over approximately two thirds of the length of the bill and divides a ventral bar from a dorsal bar; the single dorsal bar is visible from its ventral side (a similar preservation has been described by Peters 1987 for the bill of Juncitarsus merkeli). The proximal end of the ventral bar (fig. 2: 4) is broad as in Rhynchaelites messelensis Wittich (see Peters 1983: 6), but due to the poor preservation these observations are somewhat uncertain. The rami mandibulae are moderately broad; a fenestra mandibulae has not been found. The pars symphysialis of the mandible (fig. 2: 5) reaches about one fifth of its total length. In

Fig. 1: Pumiliornis tessellatus n. gen. n. sp. a: SMF ME 2092A (holotype). b: SMF ME 2092B (holotype). c: SMF ME 2245A. d: SMF ME 2245B. Covered with ammoniumchloride to enhance contrast. Scale bar = 10 mm.
Tab. 1: Length of limb bones (left/right) in millimetres.

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<tr>
<th></th>
<th>Humerus</th>
<th>Ulna</th>
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Tab. 2: Length of the pedal phalanges in millimetres.

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<td>−1.9</td>
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its proportions the skull resembles that of some “Charadriiformes”, e.g. *Vanellus* (Charadriidae).

**Vertebrae:** The cervical vertebrae are short. In specimen SMF ME 2475, ten presacral vertebrae can be counted. The ventral side of the corpus vertebrae of the most caudal cervical vertebrae is formed by a ridge (SMF ME 2475B) like in some “charadriiform” birds, e.g. *Glareola* (“Charadriiformes”, Glareolidae) or *Recurvirostra* (“Charadriiformes”, Recurvirostridae). The thoracic vertebrae are free, not fused to a notarium (SMF ME 2092A). In specimen SMF ME 2092B, six caudal vertebrae can be identified (STRAUCH 1978 reported 5-9 caudal vertebrae for the “Charadriiformes”). Details of the pygostyle are not visible.

**Coracoid** (fig. 4): The coracoid is long and slender. It might have been only weakly pneumatic since in specimen SMF ME 2475 the shaft, in contrast to most other bones, is not crushed. The extremitas omalis resembles that of some “gruiform” birds (e.g. Rallidae) and exhibits a distinct impressio ligamenti acrocoraco-humeralis (fig. 4: 1). The facies articularis scapularis (fig. 4: 2) is very shallow in contrast to all “charadriiform” and “gruiform” birds (except for the Cariamidae) in which it is cup-like (fig. 4: 3) – a shallow facies articularis scapularis is more typical for many “higher” land birds. A broad processus procoracoideus is present (SMF ME 2475A, right side) which bears a small articulation facet for the scapula (fig. 4: 4), like in some Rallidae, e.g. *Porphyrio porphyrio*. The ventral side of the extremitas omalis shows an elevation of approximately triangular shape (fig. 4: 5). The processus glenoidalis is short proximo-distally.

The morphology of the extremitas omalis of the coracoid distinguishes *P. tessellatus* from all “charadriiform” birds among which the processus acrocoracoideus is longer, the sulcus musculi supracoracoidei deeper.

A foramen nervi supracoracoidei, which is present in many “Gruiformes” and “Charadriiformes” (fig. 4: 6), is not visible. The processus lateralis of the sternal end is short.

**Furcula:** The furcula is U-shaped. Both the scapus clavliculae and the extremitas sternalis claviculae are slender. An apophysis furculae seems to be absent (SMF ME 2475B, right side; SMF ME 2475A, left side) and resembles that of *Rhynochetos jubatus* (“Gruiformes”, Rhynochetidae). Among the “Charadriiformes”, the furcula bears a distinct apophysis furculae, the extremitas omalis tapers off to a point.

**Scapula** (fig. 4): The acromion is long and shows a small enlargement for the articulation with the furcula on its dorsal side (fig. 4: 7 – like in *Glareola*, “Charadriiformes”, Glareolidae). The distal end of the corpus scapulae is slightly inflected.

**Ribs:** In specimen SMF ME 2475A, eight vertebral ribs can be counted, although this might not be the complete number. Sternal ribs are not identifiable.

**Sternum:** Some details of the sternum are visible in specimen SMF ME 2092A. It seems to be rather short and broad in contrast to the more elongated sternum of most “Gruiformes” and “Charadriiformes”, although this might partially be a result of the flattening of the bone. Most remarkably the apex carinæ is displaced.
caudally, like in the Mesitornithidae (“Gruiformes”) and in other birds, e.g. Opisthocomidae and many Galliformes. Neither the presence nor the absence of a spina externa can be confirmed with certainty. It is also not possible to determine the height of the carina sterni. The margo caudalis bears four incisurae (SMF ME 2092A, left side). The trabeculae are broad but their caudal ends are not preserved, therefore it is not possible to determine the depth of the incisurae.

**Humerus:** The humerus is stout, its shaft slightly bowed and its proximal end broad dorso-ventrally. The crista deltoidpectoralis is rounded and low and reaches about one fifth of the total length of the bone. The crista bicipitalis is small. Only a few details can be seen from the caudal side of the proximal end (SMF ME 2475A): the tuberculum dorsale is deepened and not as conspicuous as that of the “Charadriiformes”. The fossa pneumotricipitalis appears to be single, the capitulum humeri is only slightly turned towards the cranial side.

The processus supracondylaris dorsalis is small and fuses with the epicondylus dorsalis. The tuberculum supracondylare ventrale is large. The processus flexorius is well developed and resembles that of the Eurypygidae and Cariamidae (both “Gruiformes” – the processus flexorius of the “Charadriiformes” is much shorter). Its ventral side does not show the distinct pit which is found in many “Charadriiformes” and “Gruiformes”. The condylus ventralis of *P. tessellatus* is more cylindrical than that of the “Charadriiformes”, its articulation surface is flattened. The sulcus scapulotricipitalis is shallow.

**Ulna** (fig. 5): The ulna is distinctly longer than the humerus. Systematically relevant details of the distal end are not visible. The proximal end (SMF ME 2475A, left side) most closely resembles that of some “charadriiform” birds, e.g. the genera *Larus* (Laridae) and *Glareola* (Glareolidae) and, but less so, that of some Threskiornithidae (e.g. *Geronticus eremita*): the olecranon is short and blunt (fig. 5: 1). The cotyla ventralis is shallow and appears to be circular although only its dorsal half can be seen (fig. 5: 2), the cotyla dorsalis is small (fig. 5: 3), the incisura radialis marked (fig. 5: 4). The tuberculum ligamenti collateralis ventralis is low. The proximal end of the ulna is inflected towards the cranial side of the bone (SMF ME 2475B, right side).

**Radius:** The radius is stout and sigmoidally bowed, but no closer details of this bone are visible.

**Carpometacarpus** (fig. 4): The carpometacarpus is slender. Both the os metacarpale majus and the os metacarpale minus are of equal length and run in parallel. The spatium intermetacarpale appears to be narrow, although this could be a result of the flattening of the
Bone. The symphysis metacarpalis distalis is long. The processus extensorius is low and slightly bent ventrad, the processus pisiformis is centrally positioned. A fossa supratrochlearis is absent. The dorsal side of the trochea carpalis bears a short ridge along its cranial half (SMF ME 2475B, left side). A sulcus tendinosus is not visible. The carpometacarpus resembles that of some “Charadriiformes” (e.g. Glareolidae) and “Gruiformes” (e.g. Rallidae), but it is relatively shorter (see tab. 3).

Other elements of the wing (fig. 4): The phalanx proximalis digiti majoris shows an oval fossa ventralis and a short processus internus indicis at its distal end (fig. 4: 8). The phalanx distalis digiti majoris is long, its tip is broad and rounded. The os carpi ulnare shows no peculiarities and resembles that of the Eurypygidae (“Gruiformes”) and many other birds. The crus breve and the crus longum are short and of equal length.

Pelvis: The cranial part of the pelvis (SMF ME 2475A, x-ray photograph) is not as long and slender as in many “Gruiformes” (e.g. Rallidae) and “Charadriiformes”. The alae praeacetabulares ilii do not meet the dorsal midline ridge of the synsacrum.

Femur: No details of this bone are visible.

Tibiotarsus: The cristae cnemiales laterales and craniales are enlarged (SMF ME 2475B). The crista cnemialis lateralis has a triangular shape and resembles that of many “charadriiform” birds. The crista fibularis reaches one quarter of the length of the tibiotarsus, the length of the fibula cannot be determined. The distal end of the tibiotarsus is deflected against the longitudinal axis of the bone. The condylus medialis is only slightly smaller than the condylus lateralis (while it is distinctly smaller within most “Charadriiformes” and “Gruiformes”). Its longitudinal axis is inclined to that of the condylus lateralis. The incisura intercondylaris is wide, the trochlea cartilaginis tibialis shallow.

Tarsometatarsus (fig. 6): The tarsometatarsus is short (approximately half the length of the tibiotarsus), flattened and becomes broader towards its distal and proximal ends. The hypotarsus is small and very low. No cristae plantares and no fossae parahypotarsales are present. The eminentia intercondylaris is moderately developed. The trochlea of the distal end are arranged on a bow. The trochleae metatarsorum II and IV are considerably shorter than the trochlea metatarsi III and are turned plantad. Both trochleae seem to be cylindrical, but due to their poor state of preservation no details are visible. The trochlea metatarsi III is short and broad and shows a distinct groove which expands on the dorsal side of the tarsometatarsus into a depression. The trochlea metatarsi III most closely resembles that of the Columbiformes – within all “Gruiformes” and “Charadriiformes” this trochlea is longer than broad. No incisurae intertrochleares can be identified between the trochleae.

The dorsal side of the shaft above the trochleae is convex. The foramen vasculare distale is of average size, neither large nor small. A fossa metatarsi I is not visible.

In its proportions and in the morphology of the distal end, the tarsometatarsus resembles that of *Archaegoganga larvatus* (Columbiformes, Pterooclidae; see Mourer-Chauviré 1993: pl. 3 e, f). However, it differs from that species in the lower hypotarsus.

Toes (fig. 6): All toes have the usual number of phalanges and are stout. The third toe is the longest (slightly longer than the tarsometatarsus), the second

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**Fig. 5:** *Pumiliornis tessellatus* n. gen. n. sp., proximal end of ulna (SMF ME 2475A, left side). Scale bar = 5 mm. 1 = olecranon; 2 = cotyla ventralis; 3 = cotyla dorsalis; 4 = incisura radialis; 5 = humerus; 6 = radius.

**Fig. 6:** *Pumiliornis tessellatus* n. gen. n. sp., foot (reconstructed after SMF ME 2092 and SMF ME 2475). Scale bar = 5 mm.
As found in many early Tertiary birds, *Pumiliornis tessellatus* n. gen. n. sp. shows a mosaic distribution of features typical for several modern taxa, which is based upon the simultaneous occurrence of derived and primitive characters. This species differs from birds of the “higher land bird assemblage” of Olson 1985 (i.e. the “anomalognate” birds of Garrow 1874) in the morphology of the proximal ulna, the slender carpometacarpus and the low hypotarsus. While the carpometacarpace and the ulna resemble the corresponding elements of many “charadriiform” or “gruiform” birds, respectively, the humerus and the tarsometatarsus certainly would not have been assigned to these groups if found isolated. The feet of *P. tessellatus* closely resemble those of doves (Columbiformes, Columbidae), but apart from the (probably, see description) schizorhinal bill there is no derived character uniting *P. tessellatus* with this order. All Columbiformes (Columbidae + Pteroclidae) differ from *P. tessellatus* in the form of the humerus (crista deltopectoralis larger), the carpometacarpus (os metacarpale minus more bowed) and the proximal end of the ulna (cotyla dorsalis larger).

*Pumiliornis tessellatus* shows considerable overall similarity in its osteology and in its proportions (tab. 3) to *Rhynchaeites messelensis* Wittich, the first fossil bird having been described from Messel (see fig. 7):

1. the bill is long and slender
2. the bill is schizorhinal with a dorso-ventrally unusually broad basal segment of the ventral bar – this character has been listed by Peters (1983) as one synapomorphy of the taxon (*R. messelensis* + Threskiornithidae)
3. an apophysis furculae is absent
4. the ulna is longer than the humerus
5. the carpometacarpus is slender
6. the symphysis metacarpalis distalis is long – Hoch (1980) cited this character in order to support a monophyly of the taxon (*R. messelensis* + Scolopacidae)
7. the tarsometatarsus is shorter than the femur
8. the hypotarsus is low
9. the trochlea metatarsorum II and IV are distinctly shorter than the trochlea metatarsi III
10. the toes are short as are their claws

Hoch (1980) already pointed at the mosaic distribution of “charadriiform” and columbiform characters in *R. messelensis* and referred it to “the Charadrii on the basis of numerous skeletal features. It deviates from all living and known fossil shorebirds by having a strong perching foot” (Hoch 1980: 33). In his revision of the species, Peters (1983) placed *R. messelensis* within the Threskiornithidae. As *P. tessellatus* and *R. messelensis* have been found at the same site and are of the same age, it might be tempting to assume a close relationship. Yet,
Tab. 3: Proportions of the limb bones of *Pumiliornis tessellatus* in comparison. HU = humerus, UL = ulna, CM = carpo-metacarpus, TT = tibiotarsus, TM = tarsometatarsus, n = number of individuals. * = SMF ME 1045 and specimen IX in Peters (1983).

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“Charadriiformes”

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“Gruiformes”

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Columbiiformes

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most of the features mentioned above seem to be plesiomorphic. Only characters (2) and (6) might be derived, but the presence of (2) is not certain for *P. tessellatus* (see description) and both also occur in the Threskiornithidae; besides, character (6) is found in many “charadriiform” birds, too.

Moreover, apart from size, there are many features in which *P. tessellatus* differs from *R. messelenis*:

1. the shorter and stouter humerus with a larger proximal end
2. the longer hallux – the ratio of hallux: tarsometatarsus is 0.27 for *Rhynchaetes* (after specimen IX in Peters 1983), and 0.33 for *P. tessellatus*
3. the proximal phalanges of the second and the third toe are longer than the following phalanx in *R. messelenis* but shorter in *P. tessellatus*
4. the tarsometatarsus which shows no crista plantaris

Of course, differences cannot be quoted in order to refute a close relationship between two taxa. But since some of those listed above are quite fundamental, and as there are only a few derived characters shared by *P. tessellatus* and *R. messelenis*, the resemblances between the two taxa might be due to convergence or symplesiomorphy.

Apart from the schizorhinal bill there is no derived character shared between *P. tessellatus* and “charadriiform” or “gruiform” birds. Closer examination revealed many characters in which both orders differ from the fossil species. A phylogenetic analysis is aggravated, however, as neither the monophyly of the “Gruiformes” nor the monophyly of the “Charadriiformes” has been convincingly established with derived characters so far. All “Charadriiformes” differ from *P. tessellatus* in the morphology of the extremitates omales of the furcula and of the coracoid (see description), the more elongated sternum, the longer and more slender tarsometatarsus (see tab. 3) and the short or entirely lost hallux (except for Jacanidae, Dromadidae). The polarity of these characters is uncertain. But according to their occurrence among the other neognathous birds, the following are derived features of the “Charadriiformes” absent in *P. tessellatus* (the distribution of some characters within the “Charadriiformes” has been adopted from Strauch 1978):

1. the large processus supracondylaris dorsalis of the humerus (except for Burhinidae, Jacanidae, Alcidae)
2. the double fossa pneumotricipitalis of the humerus (except for Jacanidae, some Glareolidae)
3. the troclea metatarsi II which is shorter and turned more plantad than the trochlear metatarsarum III and IV (except for Burhinidae)

It is more difficult to differentiate *P. tessellatus* from the “Gruiformes”. Cracraft (1988: 351) mentioned a “large fenestra/foramen in the skull immediately posterior to the facet for the medial head of the quadrate” in order to support a monophyly of the “Gruiformes”. Unfortunately, this part of the skull is not visible in *P. tessellatus*. Most “gruiform” birds are considerably larger and deviate from the fossil species in:

1. the more slender sternum having a margo caudalis with no or only one pair of incisurs
2. the proportions of the wing – the ulna of “gruiform” birds has approximately the same length as
the humerus or is shorter (except for Gruidae, Aramidae, Otididae)

(3) the larger cotyla dorsalis of the ulna and the less marked incisura radialis (except for Gruidae)

Character (2) is probably plesiomorphic within neo-
gnathous birds, as the ulna is not longer than the hune-
rus in Cretaceous birds, too (see MARTIN 1995). More-
over, both “gruiform” and “charadriiform” birds differ
from P. tessellatus in the form of the humerus, which in
the latter two orders is more elongated with the proxи-
mal end being smaller.

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