



THE BIRDS FROM THE PALEOCENE FISSURE FILLING OF WALBECK (GERMANY)

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ABSTRACT—Almost 70 years after their discovery, more than 450 isolated avian bones from the Paleocene fissure filling of Walbeck are described. *Fissuravis weigelti* gen. et sp. nov. is represented by a coracoid with a very large cotyla scapularis and short processus acrocoracoideus and tentatively assigned to the palaeognathous Lithornithidae. Another coracoid of a large flightless bird, misidentified as a mammalian scapula before, is assigned to the Gastornithidae and is the earliest fossil record of this taxon. Most other bird bones from Walbeck belong to *Walbeckornis creber* gen. et sp. nov., which is represented by all major limb elements; this species resembles charadriiform birds and the ‘gruiform’ Messelornithidae, but its plesiomorphic morphology in combination with the poorly resolved higher level phylogeny of extant birds does not allow a definitive phylogenetic assignment. Several coracoids, humeri, and tarsometatarsi are assigned to *Gradiornis walbeckensis* gen. et sp. nov., which resembles some species of the Cariamae in overall morphology. A tarsometatarsus and a tentatively referred praemaxilla of the strigiform *Berruornis* are described as a new species, *B. halbedeli*. A few other unnamed taxa are represented by fragmentary remains. All of the sufficiently well-preserved avian taxa belong to terrestrial forms, and by its species poorness the Walbeck avifauna sharply contrasts with the very diverse avifaunas known from the earliest Eocene of Europe.

INTRODUCTION

Very little is known about Paleocene birds (Mayr, 2005a). Most of the few described European fossils come from the Reims area in France, where remains of the large flightless Gastornithidae (Anserimorphae) and Remiornithidae (Palaeognathae), the strigiform *Berruornis*, putative Messelornithidae, and a taxon of uncertain affinities (*Eupterornis*) were identified (Lemoine, 1878, 1881; Martin, 1992; Mourer-Chauviré, 1994, 1995; Buffetaut, 1997). From the early Paleocene of Sweden, *Scaniornis* was described, a presumably aquatic bird whose phylogenetic affinities are uncertain (Dames, 1890; Ericson and Tyrberg, 2004). Pelagornithidae, large marine pseudo-toothed birds, occur in the Paleocene of England and North Africa (Harrison, 1985; Bourdon, 2005). Also from the Paleocene of North Africa, Bourdon et al. (2005) described fossils of the Prophaethontidae. Few and mostly fragmentary remains of Paleocene birds are further known from the former Soviet Union (*Eopuffinus*, *Zhylgaia*, *Tshulia*; Nessonov, 1992) and China (*Qinornis*; Xue, 1995); the phylogenetic affinities of these taxa are uncertain.

From the uppermost Cretaceous or lowermost Paleocene of New Jersey in North America (Olson, 1994; Parris and Hope, 2002) various avian specimens with some ‘charadriiform’ features were assigned to the ‘form family’ Graculavidae (*Graculavus*, *Telmatornis*, *Laornis*, *Palaeotringa*; Olson and Parris, 1987; Benson, 1999). Also from the New Jersey deposits, a humerus was tentatively identified as belonging to Procellariiformes (*Tythostonyx*; Olson and Parris, 1987), and another humerus classified into Anseriformes (*Anatalavis*; Olson, 1999). Other Paleocene North American bird remains were referred to the palaeognathous Lithornithidae (Houde, 1988), the anseriform Presbyornithidae (Olson, 1994; Benson, 1999), the Prophaethontidae (Olson, 1994), and Strigiformes (*Ogygoptynx*; Rich and Bohaska, 1976).

The only South American Paleocene avian specimens are from Brazil and Argentina and belong to large palaeognathous birds,

possibly stem group Rheidae (*Diogenornis*; Alvarenga, 1983; Tambussi, 1995), Phorusrhacidae (*Palaeopsilopterus*; Alvarenga and Höfling, 2003), and a tiny-sized taxon with possible affinities to the early Eocene ?piciform Gracilitarsidae (*Eutreptodactylus*; Baird and Vickers-Rich, 1997; Mayr, 2005b). Paleocene stem group Sphenisciformes were described from New Zealand (Slack et al., 2006).

Surprisingly, the largest and best-preserved collection of Paleocene birds remained undescribed for nearly 70 years. These fossils stem from the Walbeck fissure filling in Sachsen-Anhalt, Germany, and were collected in 1939 (Weigelt, 1939, 1940, 1942). Several tons of sediment were then processed and revealed hundreds of avian bones, which were first mentioned by Weigelt (1939:525) who noted that a “relatively extensive material of bird bones is fairly well preserved. Most distinctive are unguis phalanges and vertebrae of the ostrich-sized Gastornis and the upper beak of a bird of prey. The remainder are limb bones, coracoids, and sacral regions of diverse size” [my translation].

So far, however, only 2 specimens that were separated from the main collection, a large tarsometatarsus and the beak mentioned by Weigelt (1939), were described (Mayr, 2002). The present study for the first time surveys the entire avian material from Walbeck, more than 450 disarticulated bones. One species is represented by a great number of bones that makes it possible to reliably assign to it different skeletal elements.

It has proven difficult to correlate the Walbeck fauna with the stratigraphically better documented North American Paleocene (Russell, 1964); its exact age is thus uncertain but probably upper Middle Paleocene (Biochron’97, 1997).

MATERIAL AND METHODS

Institutional Abbreviations—IGWuG, Institut für Geologische Wissenschaften und Geiseltalmuseum of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany.

Osteological terminology follows Baumel and Witmer (1993), if not indicated otherwise. Measurements are in millimeters.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
cf. LITHORNITHIDAE Houde, 1988
FISSURAVIS, gen. nov.

Type Species—*Fissuravis weigelti* sp. nov.

Diagnosis—Coracoid with (1) very large, deeply excavated cotyla scapularis and (2) unusually short and small processus acrocoracoideus (measuring only about 1.5 times the diameter of the cotyla scapularis).

Differential Diagnosis—*Fissuravis* gen. nov. differs from the lithornithid genera *Lithornis* Owen, 1840, *Pseudocrypturus* Houde, 1988, and *Paracathartes* Harrison, 1979 in the smaller tuberculum brachiale, shallower impressio ligamenti acrocoracohumeralis, and the shape of the cotyla scapularis which in contrast to the aforementioned taxa has its greatest extension in mediolateral direction.

Etymology—From fissura (Latin): fissure and avis (Latin): bird, in reference to the fact that the specimen comes from a fissure filling.

FISSURAVIS WEIGELTI, sp. nov.
(Fig. 1A, B)

Holotype—Incomplete left coracoid, lacking extremitas sternalis: WAL346.2007 (Fig. 1A, B); deposited in IGWuG.

Diagnosis—As for genus.

Type Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements—Length as preserved, 22.8; maximum diameter of cotyla scapularis, 4.7; minimum width of shaft, 4.2.

Etymology—The species is dedicated to Johannes Weigelt, without whom the Walbeck fauna would not have been unearthed.

Description and Comparison—This coracoid exhibits a peculiar morphology and resembles the corresponding bone of the Lithornithidae in that the cotyla scapularis is very large and deeply excavated, and the processus acrocoracoideus unusually short. The surface of the sulcus musculi supracoracoidei is convex, rather than concave as in most neornithine taxa. The impressio ligamenti acrocoracohumeralis is very shallow. The tuberculum brachiale, whose central portion is broken, is small. The processus procoracoideus is short but compact, the sulcus musculi supracoracoidei does not excavate its ventral surface which is thus not concave and hardly separated from the medial surface of the shaft. A small, elongate foramen nervi supracoracoidei is situated close to the cotyla scapularis, at the medial margin of the shaft. The bone has its greatest dorsoventral depth across the cotyla scapularis.

Discussion—In the previous features and except for the differences mentioned in the differential diagnosis, the coracoid of *Fissuravis weigelti* gen. et sp. nov. resembles that of the Lithornithidae (Houde, 1988:figs. 12 and 13), especially *Lithornis plebius* Houde, 1988. If assignment to the Lithornithidae can be confirmed by additional specimens, it would be the earliest European fossil record of this taxon (Houde, 1988; Leonard et al., 2005).

A large cotyla scapularis and even shorter processus acrocoracoideus are characteristic for the coracoid of the Mesozoic ornithurines *Yixianornis* (Zhou and Zhang, 2006:fig. 2) and *Ichthyornis* (Clarke, 2004:fig. 47), which are stem lineage representatives of Ornithurae and Neornithes respectively (Clarke et al., 2006), and may be plesiomorphic for neornithine birds.

ANSERIMORPHAE sensu Andors (1992)
GASTORNITHIDAE Fürbringer, 1888
?GASTORNIS Hébert, 1855 sp.
(Fig. 2A–D)

Referred Specimen—Right coracoid: WAL347.2007 (Fig. 2A–D); deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements—Maximum length along longitudinal axis, 70.5; maximum diameter of cotyla scapularis, 19.0; minimum width of shaft, 23.7; width of extremitas sternalis, 65.2.

Description and Comparison—This massive and solid bone is from a large flightless bird and lacks a processus acrocoracoideus. In its shape the specimen matches well with the coracoid of *Diatryma* as figured by Matthew and Granger (1917). Contrary to *Diatryma steini* (Matthew and Granger, 1917), *D. geiselensis* (Fischer, 1962), and *Gastornis parisiensis* (Martin, 1992), however, it is not fused with the scapula and does not exhibit a foramen nervi supracoracoidei. The cotyla scapularis is shallow and, as in the flightless Phorusrhacidae, its main plane is oriented almost perpendicular to the longitudinal axis of the bone. The facies articularis humeralis is small and elongate. The processus procoracoideus is very short. On the ventral surface of the bone there is a distinct longitudinal sulcus, between the processus procoracoideus and a ventral projection on the lateral side of the bone. This latter projection proceeds as a distinct ridge towards the extremitas sternalis. The extremitas sternalis itself is wide and symmetrical, with equally protruding angulus medialis and processus lateralis; its dorsal surface is markedly concave and bears some muscle striae.

Discussion—Weigelt (1939) mentioned the presence of unequal phalanges and vertebrae of *Gastornis* in the Walbeck material (see introduction and Weigelt, 1939:pl. 7, fig. 4), but I could not locate the specimens in the collection of IGWuG. WAL347.2007 was stored in a box with a label saying that it is the scapula of an “archaeocete cf. *Zeuglodon*” (= *Basilosaurus*) and the voucher specimen of a publication of “[Oscar] Kuhn”. Without reference to a particular specimen, a scapula of ‘*Zeuglodon*’ was also mentioned by Weigelt (1940:621). WAL347.2007, however, certainly is not a mammalian scapula but the coracoid of a large flightless bird. Because I could not identify a publication of Kuhn on the specimen, it is unknown whether there simply was a mismatch of labels or whether WAL347.2007 indeed has been misidentified.

The coracoid of *Gastornis parisiensis* is poorly known and was figured by Martin (1992:fig. 3), who noted that the supposed coracoid illustrated by Lemoine (1881) is a non-avian bone. The specimen figured by Martin (1992) apparently lacks most of the extremitas sternalis and is depicted from its lateral (Martin, 1992:fig. 3D) and medial sides (Martin, 1992:fig. 3E) respectively. According to Martin (1992) it is fused with the scapula to form a scapulocoracoid and there was a foramen nervi supracoracoidei. As noted above, both features distinguish it from the Walbeck specimen. However, WAL347.2007 is the earliest fossil record of the Gastornithidae (Andors, 1992), and the lack of fusion between coracoid and scapula is likely to be a primitive feature within this taxon.

WAL347.2007 resembles the coracoid which Lemoine (1881:pl. 9, fig. 13) assigned to *Remiornis*, another large Paleocene flightless bird (see introduction), but Martin (1992:103) noted that this specimen “probably belongs to *Gastornis*”, too.

cf. CHARADRIIFORMES and MESSELORNITHIDAE
sensu Mourer-Chauviré (1995)
WALBECKORNIS, gen. nov.

Type Species—*Walbeckornis creber*, sp. nov.

Diagnosis—(1) Coracoid with foramen nervi supracoracoidei and well-developed processus procoracoideus, processus acro-

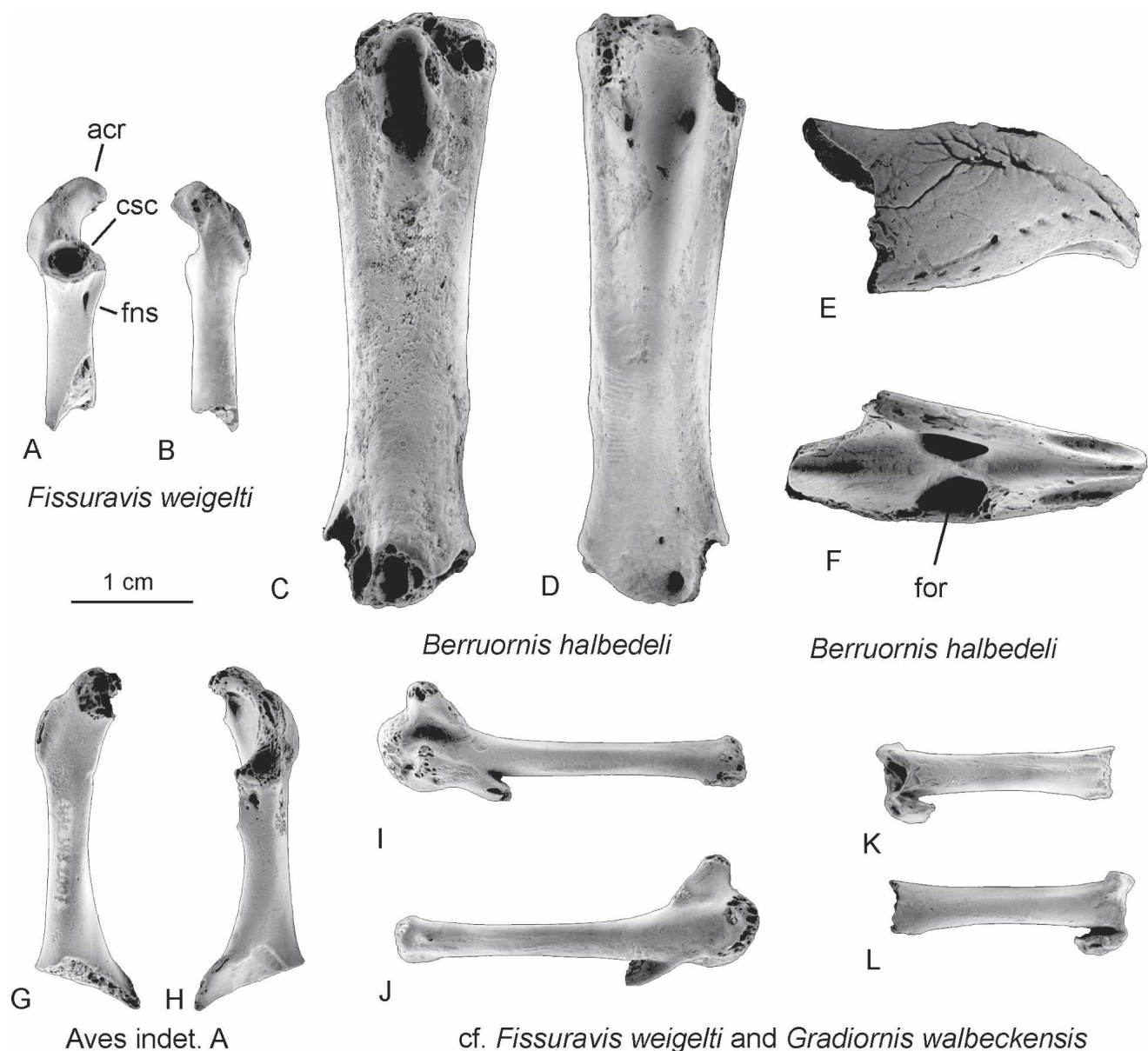


FIGURE 1. *Fissuravis weigelti*, gen. et sp. nov. (cf. Lithornithidae Houde, 1988), incomplete left coracoid, holotype (WAL346.2007) in **A**, dorsal and **B**, ventral view. *Berruornis halbedeli*, sp. nov., incomplete right tarsometatarsus, holotype (WAL01.2001) in **C**, dorsal and **D**, plantar view; tentatively referred praemaxilla (WAL02.2001) in **E**, lateral and **F**, ventral view. Aves indet., species A, incomplete right coracoid (WAL348.2007) in **G**, ventral and **H**, dorsal view. Aves indet., cf. *Fissuravis weigelti*, gen. et sp. nov. and *Gradiornis walbeckensis*, gen. et sp. nov., incomplete left carpometacarpus (WAL357.2007) in **I**, dorsal and **J**, ventral view; Aves indet., cf. *Fissuravis weigelti* gen. et sp. nov. and *Gradiornis walbeckensis* gen. et sp. nov., incomplete right carpometacarpus (WAL367.2007) in **K**, dorsal and **L**, ventral view. **Abbreviations:** **acr**, processus acroracoroideus; **csc**, cotyla scapularis; **fns**, foramen nervi supracoracoidei; **for**, oval opening inside tip of rostrum. Coated with ammonium chloride to enhance contrast.

coracoideus hook-like, sulcus musculi supracoracoidei exhibiting distinct bulge at base of processus procoracoideus; (2) sternum with small spina externi; (3) fossa pneumotricipitalis of humerus without pneumatic foramen; (4) ulna not exceeding humerus in length, strongly curved in cranio-caudal direction, proximal end with very low tuberculum ligamenti collateralis ventralis, cotyla ventralis reaching much farther distally than cotyla dorsalis and with rounded proximoventral portion; (5) carpometacarpus with very deep fovea carpalis cranialis and depressio muscularis externa (terminology after Ballmann, 1969); (6) synsacrum with 12 fused vertebrae, the cranialmost of which bears marked ovate depressions on its corpus; (7) tarsometatarsus short, without

crista medianoplantaris, block-like hypotarsus which bears a distinct medial sulcus but does not enclose bony canals. Character (5) is considered an autapomorphy of the new taxon.

Differential Diagnosis—*Walbeckornis* differs from:

crown group Charadriiformes in, e.g.: extremitas sternalis of coracoid without pointed angulus lateralis; humerus without distinct sulcus nervi coracobrachialis cranialis (Ballmann, 1979), more protruding processus flexorius, and less pronounced fossa musculi brachialis; ulna not exceeding humerus in length; hypotarsus without pronounced cristae and with single sulcus only.

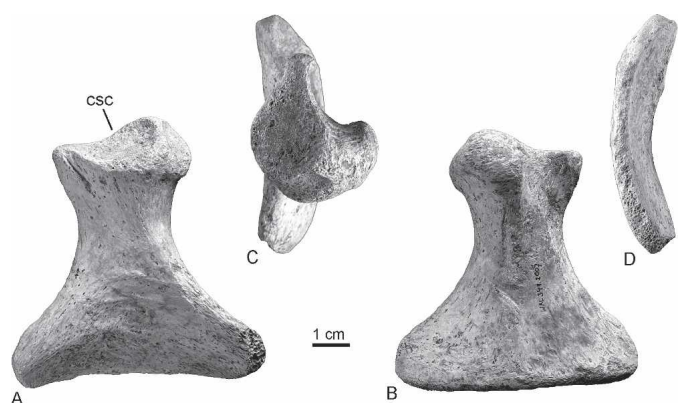


FIGURE 2. ?*Gastornis* sp. (?Gastornithidae), right coracoid (WAL347.2007) in **A**, dorsal and **B**, ventral view; view on **C**, extremitas omalis, and **D**, extremitas sternalis. Abbreviation: csc—cotyla scapularis.

Graculavus Marsh, 1872, the type genus of Graculavidae Fürbringer, 1888: humerus without elongate muscle attachment scar for musculus scapulohumeralis cranialis,

Telmabates Marsh, 1870 ('Graculavidae'): humerus with more protruding processus flexorius, shallower fossa musculi brachialis, and small fossa olecrani.

Messelornithidae sensu Mourer-Chauviré (1995) in, e.g.: carpometacarpus with much deeper fovea carpalis cranialis and less protruding processus extensorius; carpometacarpus and phalanx proximalis digiti majoris less elongated (unknown for *Itardiornis*); tarsometatarsus proportionally much shorter (much shorter than ulna versus about 1.5 times of the length of the ulna in *Messelornis cristata*) and without ossified arcus extensorius, hypotarsus with sulcus for musculus flexor digitorum longus (canal in Messelornithidae).

the Paleocene *Tshulia* Nessov, 1988 (Nessov, 1995:fig. 5L-N): tarsometatarsus with narrower shaft; foramina vascularia proximalia smaller; trochlea metatarsi II shorter and more plantarly deflected, with convex dorsal surface.

the Late Cretaceous *Palintropus* Brodkorb, 1970 (Hope, 2002:fig. 15.3) in: coracoid with well-developed processus procoracoideus; tuberculum coracoideum of scapula smaller.

Etymology—From ornis (Greek): bird and the name of the type locality.

WALBECKORNIS CREBER, sp. nov.

(Figs. 3, 4)

Holotype—Right tarsometatarsus, almost complete: WAL472.2007 (Fig. 4L-N); deposited in IGWuG.

Diagnosis—Coracoid with medial margin of extremitas sternalis dorsoventrally broadened which is here considered an autapomorphy of the new taxon.

Type Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements of Holotype—Length, 30.5; width of proximal end, 5.2; width of distal end, 5.4.

Etymology—From creber (Latin): abundant, because this species is represented by a great number of bones.

Referred Specimens—Right coracoid, largely complete: WAL01.2007—WAL04.2007, WAL12.2007, WAL17.2007, WAL39.2007 (Fig. 3A, B), WAL45.2007 (Fig. 3C), WAL48.2007; right coracoid, incomplete: WAL05.2007—WAL11.2007, WAL13.2007—WAL16.2007, WAL18.2007—WAL30.2007, WAL32.2007—WAL36.2007, WAL38.2007, WAL42.2007—WAL44.2007, WAL47.2007; right coracoid extremitas omalis:

WAL29.2007, WAL31.2007, WAL41.2007, WAL46.2007, WAL49.2007; right coracoid, extremitas sternalis: WAL37.2007, WAL40.2007; left coracoid, largely complete: WAL57.2007, WAL58.2007, WAL61.2007, WAL62.2007, WAL75.2007; left coracoid, incomplete: WAL50.2007—WAL56.2007, WAL59.2007, WAL60.2007, WAL63.2007—WAL66.2007, WAL69.2007, WAL70.2007, WAL72.2007—WAL74.2007, WAL76.2007, WAL77.2007, WAL79.2007—WAL81.2007, WAL83.2007—WAL85.2007, WAL90.2007, WAL92.2007, WAL95.2007, WAL97.2007, WAL99.2007; left coracoid, extremitas omalis: WAL67.2007, WAL68.2007, WAL71.2007, WAL78.2007, WAL82.2007, WAL86.2007, WAL87.2007, WAL91.2007, WAL93.2007, WAL94.2007, WAL96.2007; left coracoid, extremitas sternalis: WAL88.2007, WAL89.2007, WAL98.2007. Right scapula, largely complete: WAL306.2007 (Fig. 3F, G); right scapula, lacking caudal end: WAL302.2007—WAL305.2007, WAL307.2007—WAL323.2007, WAL382.2007; left scapula, lacking caudal end: WAL324.2007 (Fig. 3E)—WAL345.2007, WAL475.2007. Extremitas sternalis furculae: WAL430.2007—WAL445.2007, WAL449.2007. Sternum, cranial portion: WAL409.2007 (Fig. 3I, J)—WAL414.2007. Right humerus, largely complete: WAL102.2007 (Fig. 3K, L), WAL107.2007, WAL109.2007, WAL111.2007; right humerus, incomplete: WAL104.2007, WAL105.2007, WAL108.2007, WAL109.2007, WAL112.2007—WAL114.2007, WAL116.2007, WAL117.2007, WAL124.2007—WAL128.2007, WAL131.2007, WAL132.2007, WAL137.2007, WAL477.2007, WAL478.2007; proximal right humerus: WAL103.2007, WAL115.2007, WAL118.2007, WAL120.2007—WAL124.2007, WAL130.2007, WAL134.2007, WAL142.2007, WAL143.2007, WAL146.2007—WAL149.2007; distal right humerus: WAL110.2007, WAL119.2007, WAL120.2007, WAL135.2007, WAL136.2007, WAL138.2007—WAL141.2007, WAL144.2007, WAL145.2007; left humerus, largely complete: WAL150.2007, WAL151.2007, WAL153.2007, WAL156.2007, WAL158.2007; left humerus, incomplete: WAL152.2007, WAL154.2007, WAL155.2007, WAL157.2007, WAL159.2007, WAL160.2007, WAL165.2007, WAL167.2007, WAL168.2007, WAL170.2007, WAL172.2007—WAL175.2007, WAL178.2007, WAL179.2007, WAL181.2007—WAL183.2007, WAL185.2007—WAL189.2007, WAL192.2007, WAL193.2007; proximal left humerus: WAL163.2007 (Fig. 3M-O), WAL164.2007, WAL166.2007, WAL171.2007, WAL177.2007, WAL180.2007, WAL184.2007, WAL191.2007, WAL195.2007; distal left humerus: WAL162.2007 (Fig. 3P-R), WAL169.2007, WAL176.2007, WAL181.2007, WAL190.2007, WAL194.2007. Right ulna, largely complete: WAL198.2007 (Fig. 3T); right ulna, incomplete: WAL196.2007, WAL210.2007, WAL214.2007, WAL480.2007; proximal right ulna: WAL212.2007, WAL451.2007; distal right ulna: WAL201.2007, WAL209.2007; left ulna, largely complete: WAL199.2007; left ulna, incomplete: WAL197.2007, WAL200.2007, WAL203.2007, WAL204.2007, WAL207.2007, WAL459.2007, WAL479.2007; proximal left ulna: WAL202.2007, WAL205.2007, WAL208.2007, WAL211.2007 (Fig. 3U, V), WAL213.2007; distal left ulna: WAL206.2007, WAL474.2007. Right radius, complete: WAL466.2007; right radius, shaft: WAL471.2007; proximal right radius: WAL467.2007; distal right radius: WAL468.2007; left radius, complete: WAL461.2007; proximal left radius: WAL462.2007, WAL463.2007, WAL465.2007, WAL469.2007, WAL470.2007; distal left radius: WAL464.2007. Right carpometacarpus, largely complete: WAL238.2007, WAL239.2007; right carpometacarpus, incomplete: WAL240.2007—WAL244.2007, WAL246.2007—WAL249.2007, WAL254.2007—WAL257.2007, WAL260.2007; proximal right carpometacarpus: WAL245.2007 (Fig. 3Y-AA), WAL250.2007, WAL259.2007, WAL261.2007—WAL264.2007; distal right carpometacarpus: WAL251.2007—WAL253.2007, WAL258.2007; left carpometacarpus, largely complete: WAL221.2007 (Fig. 3W, X); left car-

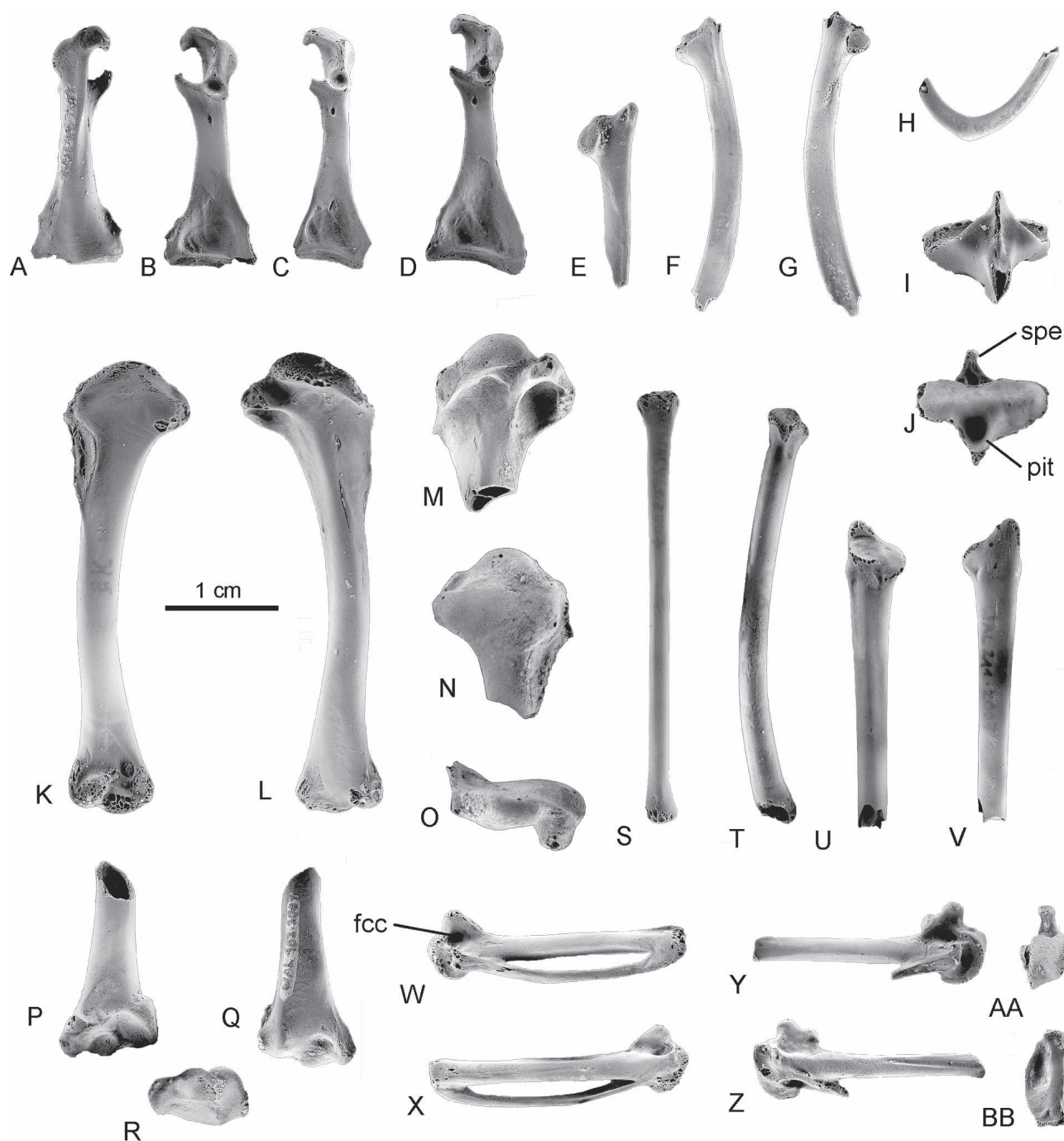


FIGURE 3. *Walbeckornis creber*, gen. et sp. nov., wing and pectoral girdle elements: right coracoid (WAL39.2007) in **A**, ventral and **B**, dorsal view; **C**, right coracoid (WAL45.2007) in dorsal view; **D**, right coracoid (WAL02.2007) in dorsal view; **E**, left scapula, extremitas cranialis (WAL324.2007) in lateral view; right scapula (WAL306.2007) in **F**, medial and **G**, lateral view; **H**, furcula, extremitas sternalis (WAL444.2007) in cranial view; sternum, cranial end (WAL409.2007) in **I**, ventral and **J**, dorsal view; right humerus (WAL102.2007) in **K**, cranial and **L**, caudal view; proximal end of left humerus (WAL163.2007) in **M**, cranial, **N**, caudal, and **O**, proximal view; distal end of left humerus (WAL162.2007) in **P**, cranial, **Q**, caudal, and **R**, distal view; **T**, right ulna (WAL198.2007) in ventral view; left ulna, proximal end (WAL211.2007) in **U**, cranial and **V**, caudal view; left carpometacarpus (WAL221.2007) in **W**, ventral and **X**, dorsal view; right carpometacarpus (WAL245.2007) in **Y**, ventral, **Z**, dorsal, and **AA**, proximal view; **BB**, left phalanx proximalis digiti majoris (WAL418.2007) in ventral view. **Abbreviations:** **fcc**, fovea carpalis cranialis; **pit**, pit dorsal on surface of corpus sterni; **spe**, spina externa. Coated with ammonium chloride to enhance contrast.

metacarpus, incomplete: WAL215.2007—WAL220.2007, WAL222.2007—WAL228.2007, WAL232.2007; proximal left carpometacarpus: WAL229.2007, WAL230.2007, WAL233.2007, WAL234.2007, WAL236.2007; distal left carpometacarpus: WAL231.2007, WAL235.2007, WAL237.2007. Right phalanx

proximalis digiti majoris: WAL415.2007; left phalanx proximalis digiti majoris: WAL416.2007—WAL419.2007. Synsacrum: WAL420.2007—WAL429.2007, WAL452.2007 (Fig. 4A, B)—WAL454.2007. Right femur, largely complete: WAL369.2007, WAL370.2007, WAL372.2007 (Fig. 4C, D), WAL377.2007; right

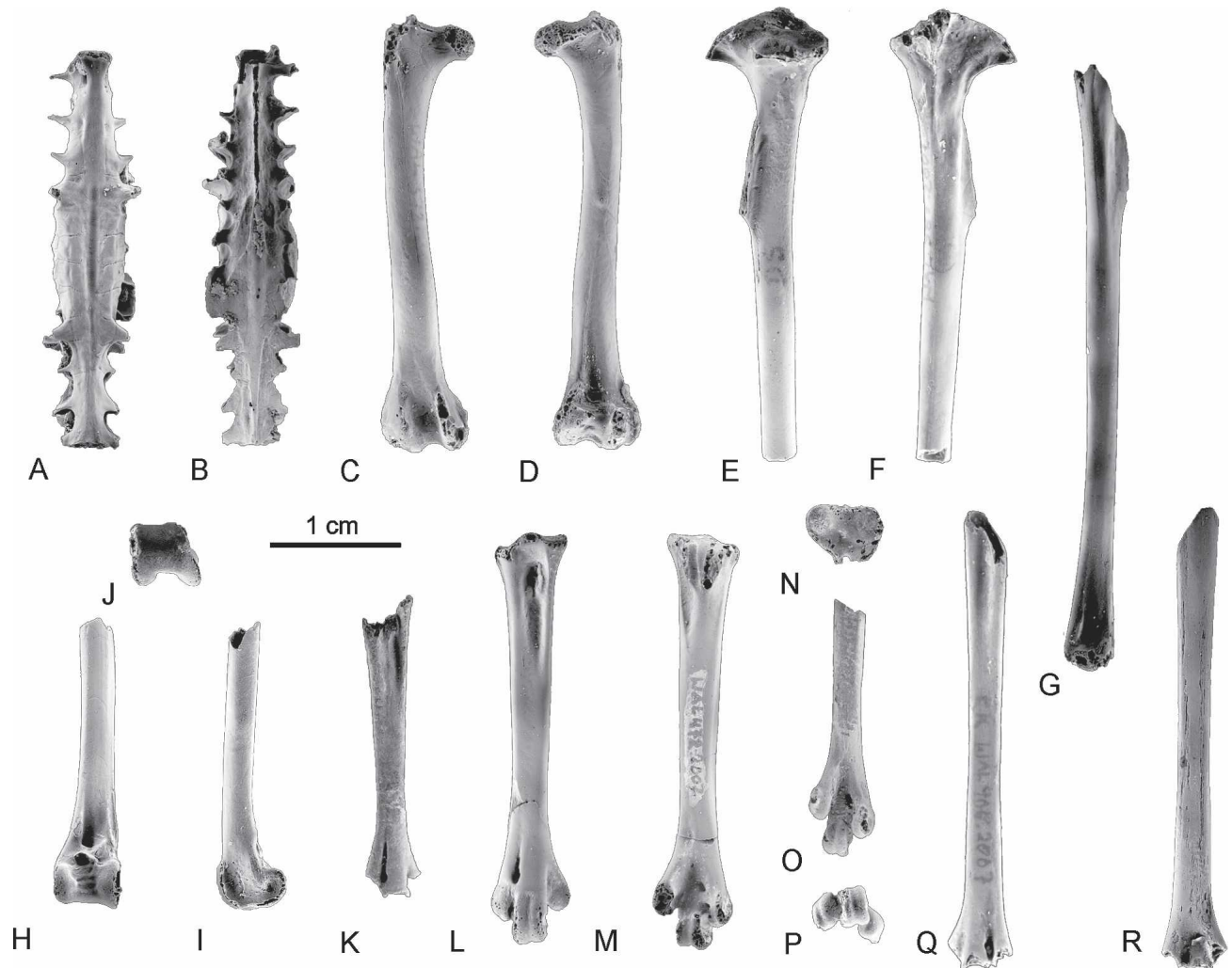


FIGURE 4. *Walbeckornis creber*, gen. et sp. nov., synsacrum and hind limb elements: synsacrum (WAL452.2007) in **A**, ventral and **B**, dorsal view; right femur (WAL372.2007) in **C**, cranial and **D**, caudal view; left tibiotarsus, proximal end (WAL383.2007) in **E**, caudal and **F**, cranial view; **G**, left tibiotarsus (WAL385.2007) in cranial view; left tibiotarsus, distal end (WAL 390.2007) in **H**, cranial, **I**, medial, and **J**, distal view; **K**, incomplete right tarsometatarsus (WAL276.2007) in dorsal view; right tarsometatarsus (WAL472.2007, holotype) in **L**, dorsal, **M**, plantar, and **N**, proximal view; right tarsometatarsus, distal end (WAL267.2007) in **O**, plantar and **P**, distal view. ?*Walbeckornis*, sp. indet. **A**, incomplete left tarsometatarsus (WAL406.2007) in **Q**, dorsal and **R**, plantar view. Coated with ammonium chloride to enhance contrast.

femur, lacking extremitas proximalis: WAL375.2007; right femur, shaft: WAL476.2007, WAL482.2007; proximal right femur: WAL371.2007, WAL483.2007; distal right femur: WAL374.2007, WAL376.2007; left femur, largely complete: WAL379.2007; proximal left femur: WAL378.2007, WAL472.2007; distal left femur: WAL381.2007, WAL473.2007; left femur, shaft: WAL380.2007. Proximal right tibiotarsus: WAL396.2007, WAL399.2007, WAL400.2007; right tibiotarsus, shaft: WAL460.2007; distal right tibiotarsus: WAL397.2007, WAL401.2007—WAL405.2007; proximal left tibiotarsus: WAL383.2007 (Fig. 4E, F), WAL386.2007, WAL388.2007, WAL395.2007, WAL458.2007, WAL481.2007; left tibiotarsus, shaft: WAL385.2007 (Fig. 4G), WAL387.2007; distal left tibiotarsus: WAL389.2007—WAL393.2007. Right tarsometatarsus, largely complete: WAL273.2007—WAL275.2007; right tarsometatarsus, incomplete: WAL266.2007, WAL272.2007, WAL276.2007 (Fig. 4K)—WAL278.2007, WAL280.2007; proximal right tarsometatarsus: WAL282.2007; distal right tarsometatarsus: WAL267.2007—WAL271.2007, WAL279.2007, WAL281.2007, WAL283.2007; left tarsometatarsus, largely complete: WAL284.2007, WAL287.2007, WAL290.2007—

WAL292.2007, WAL294.2007; left tarsometatarsus, incomplete: WAL285.2007, WAL288.2007, WAL293.2007, WAL300.2007, WAL407.2007; distal left tarsometatarsus: WAL286.2007, WAL289.2007, WAL295.2007—WAL299.2007, WAL301.2007. All specimens are deposited in IGWuG.

Measurements of Referred Specimens—See Table 1.

Description and Comparison—The coracoid (Fig. 3A–D) resembles the corresponding bone of *Messelornis cristata* (Messelornithidae; Hesse, 1990; Mayr, 2004:text-fig. 4). The well-developed tuberculum brachiale overhangs the sulcus musculi supracoracoidei, so that the processus acroracoideus has a hooked outline. The articular surface of the short processus glenoidalis slants towards the dorsal surface of the bone. The cotyla scapularis is cup-like and subcircular. The well-developed processus procoracoideus is directed towards the processus acroracoideus and continues as a short crest on the medial side of the shaft. As in, e.g., *Scolopax rusticola* (Charadriiformes, Scolopacidae), the sulcus musculi supracoracoidei bears a distinct bulge in its dorsal portion, at the base of the processus procoracoideus. The small foramen nervi supracoracoidei is situated in the center of the shaft (in two specimens, WAL48.2007

TABLE 1. Dimensions of the main skeletal elements of *Walbeckornis creber*, gen. et sp. nov. (in mm).

Skeletal element	Mean	Range	s	n
Coracoid				
Maximum length	20.8	19.0–22.4	0.9	9
Humerus				
Maximum length	38.8	36.8–40.3	1.1	9
Width proximal end	11.3	10.7–12.1	0.5	5
Width distal end	7.4	6.6–8.1	0.4	12
Ulna				
Maximum length		–37–37.5		2
Radius				
Maximum length	35.0	33.0–37.0		2
Carpometacarpus				
Maximum length	21.8	21.3–22.0	0.3	4
Femur				
Maximum length	32.4	31.3–33.0	0.8	3
Width distal end	6.0	5.3–6.6	0.5	3
Tibiotarsus				
Length as preserved		45.5		1
Estimated length		~48		1
Width distal end	4.8	4.7–4.9	0.1	4
Tarsometatarsus				
Maximum length	29.4	27.4–31.5	1.7	3
Width distal end	5.4	5.0–5.6	0.3	3

and WAL49.2007, there is no foramen but a marked, oblique furrow on the medial margin of the shaft). The dorsal surface of the extremitas sternalis lacks pneumatic openings but exhibits muscle striae (e.g., WAL50.2007). The angulus medialis is pointed. The processus lateralis is not completely preserved in any of the specimens but apparently did not form a pointed angulus lateralis. The medial margin of the sternal end is dorsoventrally broadened (WAL52.2007, WAL99.2007), WAL99.2007 also exhibits a small medial projection.

The scapula (Fig. 3E–G) is smoothly curved, without a distinctly angled caudal end. The well-developed acromion is simple and of average size, it bears a shallow fossa on its costal surface. There is a small tuberculum coracoideum.

Only extremitates sternaes of the U-shaped furcula are preserved (Fig. 3H) that lack an apophysis furculae and are fairly wide.

The sternum (Fig. 3I, J) exhibits a small, elongate, and not bifurcated spina externa of similar shape to that of extant Eurypygidae and *Anas* spp. (Anatidae) (WAL409.2007); a spina interna is absent. On the dorsal surface of the corpus sterni, there is a deep pit which does however not bear a pneumatic foramen. The sulci articulares coracoidei slightly overlap.

The humerus (Fig. 3K–R) is of similar proportions to the corresponding bone of the Messelornithidae; its shaft is sigmoidally curved in craniocaudal direction, with a subtriangular cross section in its proximal part. The proximal end of the bone slants caudally, accordingly the margo caudalis of the shaft distal to caput humeri and tuberculum dorsale is markedly concave. The tuberculum dorsale itself is well developed and merges into the caput humeri. There is no foramen pneumaticum within the fossa pneumotricipitalis. The sulcus transversus on the cranial surface of the proximal end is a shallow pit. The crista deltopectoralis is not completely preserved in any of the specimens; it is fairly long and extends to the beginning of the distal two thirds of the humerus, on the cranial surface a curved bulge extends along its base. The margo caudalis exhibits a small attachment scar, presumably for musculus latissimus dorsi. The distal end of the bone is best preserved in WAL161.2007 and WAL162.2007. The narrow, crescent-shaped fossa musculi brachialis is shallow and oriented obliquely to the longitudinal axis of the bone. The tuberculum supracondylare ventrale is small. The tuberculum supracondylare dorsale is also small and elongate, similar to the same structure of extant *Eurypyga helias* (Eurypygidae). The sulcus

scapulotricipitalis is shallow, as is the wide sulcus humerotricipitalis which bears a small fossa olecrani. Although the ventrodistally protruding processus flexorius is well developed, it does not reach farther distally than the condylus ventralis.

The ulna (Fig. 3T–V) is slightly shorter than or subequal to the humerus in length, as far as this can be judged from the disarticulated material and the low number of largely complete ulnae. Its shaft is strongly curved in cranio-caudal direction and the proximal part has a subtriangular cross-section. The proximal end of the bone resembles the proximal ulna of extant Anatidae and Threskiornithidae. The tuberculum ligamenti collateralis ventralis is very low. The cotyla ventralis reaches much farther distally than the shallow cotyla dorsalis and its proximoven-tral portion is rounded. The well-developed olecranon is compact and stout. The fossa musculi brachialis is elongate and shallow. The papillae remigales are indistinct and low. The tuberculum carpale on the distal end of the bone is small, the condylus dorsalis short and not very protruding. A small and shallow depressio radialis is situated near the dorsal margin of the bone.

The radius (Fig. 3S) is only slightly bowed and resembles the corresponding bone of *Eurypyga helias* except that the shaft has an ovate cross section (subtriangular in *E. helias*).

The carpometacarpus (Fig. 3W–AA) is a slender bone with a moderately wide spatium intermetacarpale. Its most distinctive features are a very marked fovea carpalis cranialis and depressio muscularis externa (terminology after Ballmann, 1969), as in extant *Eurypyga helias* (Fig. 3W). The processus extensorius projects perpendicular to the longitudinal axis of the bone and is rather short. The caudal portion of the trochlea carpalis is small and its ventral rim reaches distally only slightly beyond the processus pisiformis. The os metacarpale minus is fairly straight and does not exceed the os metacarpale majus in length; it is dorsoventrally wide and strap-like in its proximal part but becomes narrow towards the distal end of the bone. Distally, the os metacarpale minus further bends towards the ventral surface of the carpometacarpus and in distal view the distal end of the carpometacarpus thus has its greatest extension not in craniocaudal but dorsoventral direction. Proximally, the os metacarpale minus proceeds as a ridge to the processus pisiformis. The os metacarpale majus has a subrectangular cross-section with a flat cranial surface. The sulcus tendineus is distinct.

The phalanx proximalis digiti majoris (Fig. 3BB) resembles the corresponding bone of, e.g., early Eocene stem group Galliformes (e.g., Mayr, 2000; Mayr and Weidig, 2004). As in the latter, it bears a deep, oval fossa ventralis.

In the completely preserved synsacrum WAL452.2007 (Fig. 4A, B) only 12 vertebrae are fused. An equally low number of synsacral vertebrae is found in some Mesozoic non-neornithines, Cuculidae, Falconidae, Spheniscidae, Phaethontidae, and some taxa of the 'higher land birds' (Mayr and Clarke, 2003); Eurypygidae have 13 fused synsacral vertebrae. As in, e.g., extant Anatidae, Charadriiformes, and Eurypygidae there was a row of distinct foramina intertransversaria along the entire length of the pelvis. As in some charadriiform birds (e.g., *Pluvianus aegyptius*, Glareolidae), the most cranial synsacral vertebra bears a pair of deep oval depressions on the lateral surfaces of its corpus.

The femur (Fig. 4C, D) is a long and slender bone which is curved in craniocaudal direction and similar to the corresponding bone of extant *Scolopax rusticola* (Scolopacidae, Charadriiformes). There is no pneumatic foramen on the cranial surface of its proximal end. The crista trochanteris is broken in the specimens but appears to have been low. On the distal end, there is a marked sulcus patellaris. The fossa poplitea is of average depth, the crista supracondylaris medialis marked.

The tibiotarsus (Fig. 4E–J) is the longest limb element and similar to the corresponding bone of *Scolopax rusticola* and the

Messelornithidae. Proximally, the cristae cnemiales are protruding slightly beyond the proximal articulation facets. The crista cnemialis lateralis is well developed, with a triangular outline and a pointed tip, whereas the crista cnemialis cranialis is not completely preserved in the specimens. The sulcus extensorius on the distal end is medially situated and bridged by a proximodistally narrow pons supratendineus; the distal opening of the canalis extensorius is small. Both, lateral and medial tuberositates retinaculi extensoris are well developed, the medial tuberosity is situated farther proximally than the lateral one. The condyli are narrow and diverge in cranial direction. The condylus medialis protrudes farther cranially than the slightly larger condylus lateralis, and in distal view the bone resembles the tibiotarsus of the putative rail *Palaeorallus troxelli* (Cracraft, 1973:fig. 1). The distal rim of the condylus medialis exhibits a small notch. The trochlea cartilaginosa tibialis is proximo-distally high and bears only a shallow sulcus.

The tarsometatarsus (Fig. K–P) resembles the corresponding bone of some charadriiform birds (e.g., *Scolopax rusticola*) in which, however, the hypotarsus is more complex; it is much shorter than the tarsometatarsus of the Messelornithidae and also differs in several morphological details. The shaft is narrowest at the beginning of the distal third of the bone and gradually widens towards its proximal end. The cotyla medialis is situated farther proximally than the cotyla lateralis, the eminentia intercondylaris is low. There is a well-developed fossa infracotyloidea dorsalis which extends over more than one third of the length of the tarsometatarsus. The foramina vascularia proximalia are small, the tuberositas musculi tibialis cranialis is bipartite, with a larger and farther proximally situated medial tubercle. The hypotarsus (WAL266.2007, WAL284.2007) resembles that of extant Eurypygidae (sunbittern). In contrast to the Messelornithidae, it does not enclose bony canals but bears a distinct medial sulcus, presumably for the tendon of musculus flexor digitorum longus; lateral thereof it appears to have been block-like without distinct grooves (this part of the bone is not completely preserved in the specimens). There is a distinct fossa parahypotarsalis medialis, but no fossa parahypotarsalis lateralis. The cross-section of the midshaft is subrectangular, with a flat plantar surface. A crista medianoplantaris is absent, but there are low cristae plantares medialis et lateralis. The distinct fossa metatarsi I is located at the medial margin of the shaft. The foramen vasculare distale is situated at the distal end of a short sulcus extensorius. The trochlea metatarsi III is elongate and about twice as long as wide; it is slightly medially inflected and asymmetric in plantar view, with the medial rim being slightly shorter than the lateral rim. The trochlea metatarsi II reaches distally only to the middle of the trochlea metatarsi IV and has a convex dorsal surface with no furrow; it is plantarily deflected. The trochlea metatarsi IV bears only a weak furrow, the incisura intertrochlearis lateralis is wide. A small canalis interosseus distalis is present.

?*WALBECKORNIS* sp. indet. A
(Fig. 4Q, R)

Referred Specimen—Left tarsometatarsus, lacking proximal and distal ends: WAL406.2007 (Fig. Q, R); deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements—Length as preserved, 35.5.

Remarks—The tarsometatarsus of this species is much more elongated than the corresponding bone of *Walbeckornis creber*. Its shaft is further of equal width in its distal half. Otherwise, however, the preserved parts of the bone are similar to *W. creber*; as in the latter, the plantar surface is flat.

Assignment of this species to *Walbeckornis* is tentative owing to the fragmentary fossil material.

?*WALBECKORNIS* sp. indet. B
(Fig. 5)

Referred Specimens—Right coracoid: WAL100.2007 (Fig. 5A), WAL101.2007 (Fig. 5B, C); deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements—Length as preserved, 26.0.

Tentatively Referred Specimens—Right scapula, cranial end: WAL450.2007 (Fig. 5D). Left humerus, lacking proximal end: WAL408.2007 (Fig. 5E). Right tarsometatarsus, distal end: WAL415.2007 (Fig. 5F–H); deposited in IGWuG.

Measurements of Tentatively Referred Specimens—Humerus, length as preserved (WAL408.2007), 39.0 (estimated total length ca. 47 mm, versus ca. 52 mm in '*Messelornis russelli*'; after Mourer-Chauviré, 1995); distal width as preserved, 7.5 (9.2 in '*Messelornis russelli*'; after Mourer-Chauviré, 1995). Tarsometatarsus, distal width (WAL425.2007), 7.8.

Remarks—This species is much larger than *Walbeckornis creber*. However, the coracoid exhibits a similar morphology except that there is a marked longitudinal bulge on the dorsal surface of the extremitas sternalis, starting from the medial end of the facies interna of the crista articularis sternalis. The cotyla scapularis is further ovate and not circular as in *W. creber*. The tuberculum brachiale and processus procoracoideus are broken in both specimens.

The tentatively referred cranial end of the scapula also resembles that of *W. creber*. The tentatively referred humerus, however, differs from that of *W. creber* in that the tuberculum supracondylare dorsale is smaller and the fossa musculi brachialis is less narrow, less elongate and situated more centrally. The tentatively referred distal end of the tarsometatarsus differs from that of *W. creber* in that the trochlea metatarsi II reaches farther distally.

Again, assignment of this species to *Walbeckornis* is tentative owing to the incomplete fossil material.

Discussion—The specimens assigned to *Walbeckornis creber* gen. et sp. nov. differ considerably in size (compare, e.g., Figs. 4K and 4L). However, as there are no obvious morphological differences between the bones and as there is a continuous transition in size, I prefer classification into a single, possibly sexually dimorphic species.

Hypotarsus structure, i.e. the presence of a distinct sulcus for the tendon of musculus flexor digitorum longus, supports classification of *Walbeckornis creber* into Neognathae. However, although the species is represented by all major skeletal elements, its plesiomorphic morphology offers little clues for a further phylogenetic assignment to any neognathous subclade. Inclusion of *W. creber* in the Mayr and Clarke (2003) character matrix, the hitherto most comprehensive published morphological data set concerning the higher-level phylogeny of extant birds, and subsequent analysis with NONA 2.0 (Goloboff, 1993), did also not conclusively resolve its phylogenetic affinities within Neognathae.

In overall morphology, *W. creber* most closely resembles Charadriiformes and the 'gruiform' Messelornithidae (Hesse, 1990; Mourer-Chauviré, 1995). Especially the humerus and the coracoid are very similar to the corresponding bones of the Messelornithidae (compare Fig. 3 with Mourer-Chauviré, 1995:pls. I and II), but these similarities may well be plesiomorphic for a more inclusive clade of neognathous birds. Of the three characters listed by Mayr (2004) as apomorphies of a taxon including Messelornithidae, Rallidae, and Heliornithidae, two are present in *W. creber* (processus procoracoideus continuous with sharp crest along medial margin of coracoidal shaft, absence of pneumatic foramen on humerus). These two characters also occur in charadriiform birds which further agree with *Walbeckornis* in the

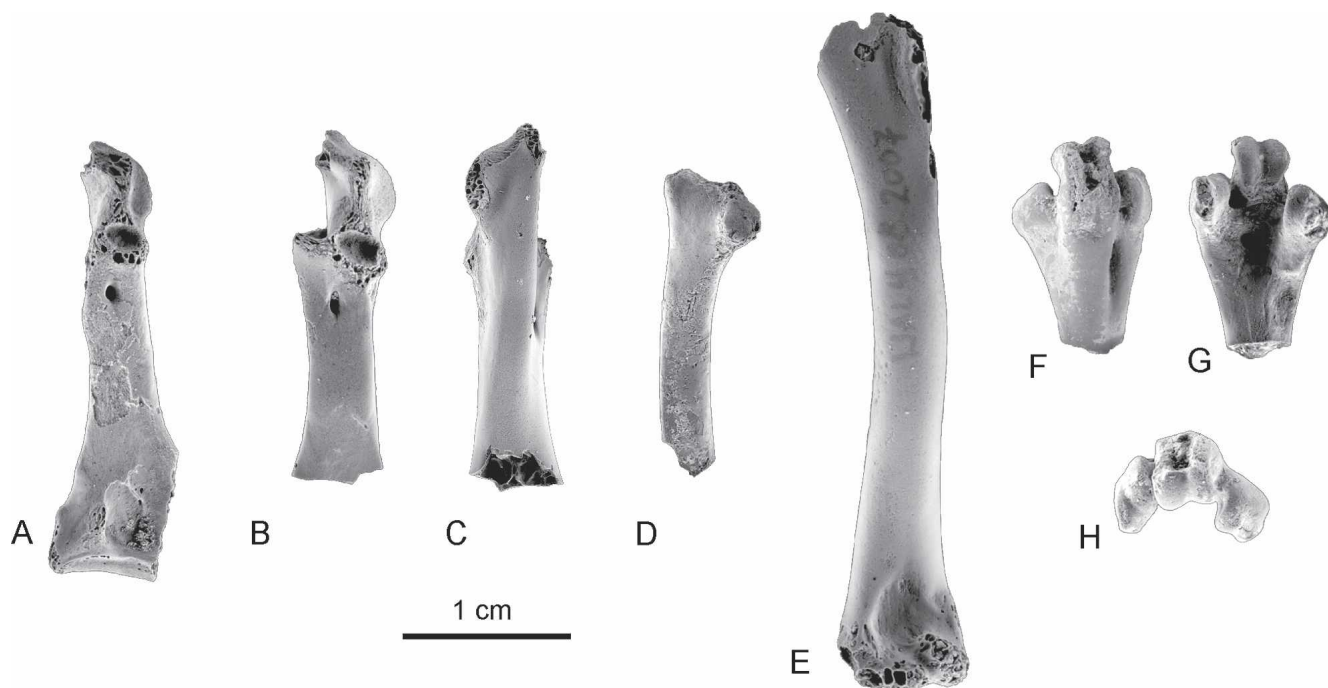


FIGURE 5. ?*Walbeckornis*, sp. indet. B, right coracoid (WAL100.2007) in A, dorsal view; right coracoid (WAL101.2007) in B, dorsal and C, ventral view; tentatively referred specimens: D, right scapula, extremitas cranialis (WAL450.2007) in lateral view; E, incomplete left humerus (WAL408.2007) in cranial view; right tarsometatarsus, distal end (WAL415.2007) in F, dorsal, G, plantar and H, distal view. Coated with ammonium chloride to enhance contrast.

presence of foramina intertransversaria (pelvis) and deep lateral excavations on the cranialmost synsacral vertebra.

A 'charadriiform' morphology was also noted for most taxa from the early Paleocene of New Jersey, which were classified in the 'transitional Charadriiformes' as 'form family Graculavidae' by Olson and Parris (1987). Only few skeletal elements of the 'Graculavidae' are known, and *Walbeckornis* resembles 'graculavids' in the shape of the proximal humerus that also lacks a pneumatic foramen in 'Graculavidae'. The holotypic fragmentary humerus of *Graculavus*, the type genus of 'Graculavidae', is however also hardly distinguishable from that of the anseriform *Presbyornis*, and as indicated by Olson and Parris (1987:4) *Presbyornithidae* Wetmore, 1926 may even be a junior synonym of 'Graculavidae' Fürbringer, 1888. Because anseriform and galliform birds form a clade which is the sister taxon of all other neognathous birds (e.g., Cracraft et al., 2004), the 'charadriiform' characters shared by *Presbyornithidae*, *Walbeckornis*, and *Charadriiformes* in humerus morphology are probably plesiomorphic for neognathous birds.

There are no derived characters which convincingly support assignment of *W. creber* to the stem lineage of any modern higher-level taxon, and unless the basal divergences within neognathous birds are better understood, a phylogenetic assignment seems hardly possible.

According to its limb proportions, which are similar to those of the extant *Scolopax rusticola* (Scolopacidae) and many galliform birds, *Walbeckornis creber* most likely was a terrestrial species which predominantly foraged on the ground.

cf. CARIAMAE sensu Olson (1985)
GRADIORNIS, gen. nov.

Type Species—*Gradiornis walbeckensis* sp. nov.

Diagnosis—Coracoid with (1) cotyla scapularis circular and very deep; (2) dorsal surface of processus acrocoracoideus with triangular facet above cotyla scapularis, whose plane forms an

angle of about 120° with that of the sulcus muscoli supracoracoidei; (3) short, triangular processus procoracoideus projecting perpendicular to longitudinal axis of shaft; (4) foramen nervi supracoracoidei absent; (5) shaft unusually straight and column-like; (6) distinct depression on ventral surface of processus lateralis; (7) lateral margin of extremitas sternalis unusually thick and with furrow; (8) humerus with elongate muscle attachment scar for musculus scapulohumeralis cranialis. Characters (2), (6), and (7) are considered autapomorphies of the new taxon.

Differential Diagnosis—*Gradiornis* gen. nov. differs from:

the early Eocene *Palaeophasianus* Shufeldt, 1913 (?Geranoididae Wetmore, 1933; Cracraft, 1969) in: dorsal surface of trochlea metatarsi IV less laterally slanting in distal view; hypotarsus without enclosed canal.

the early Oligocene to early Miocene *Bathornithidae* Wetmore, 1933 in: hypotarsus not block-like (contra *Bathornis veredus* and *B. fax*) and without hypotarsal canal (contra '*Bathornis celeripes*' and '*B. geographicus*'); dorsal surface of trochlea metatarsi IV less laterally slanting in distal view.

the Middle Eocene to Miocene *Idiornithidae* Brodkorb, 1965 in: coracoid with very deep, circular cotyla scapularis, proportionally shorter processus procoracoideus, and distinct depression on ventral surface of processus lateralis; humerus with crus dorsale fossae extending farther distally and with marked muscle attachment scar for musculus scapulohumeralis cranialis; hypotarsus not block-like.

Etymology—The genus name derives from gradere (Latin): to pace and ornis (Greek): bird, and refers to the presumably terrestrial way of living of this taxon.

GRADIORNIS WALBECKENSIS, sp. nov.
(Fig. 6)

Holotype—Left coracoid, lacking tuberculum brachiale and medial portion of extremitas sternalis: WAL349.2007 (Fig. 6A-C); deposited in IGWuG.

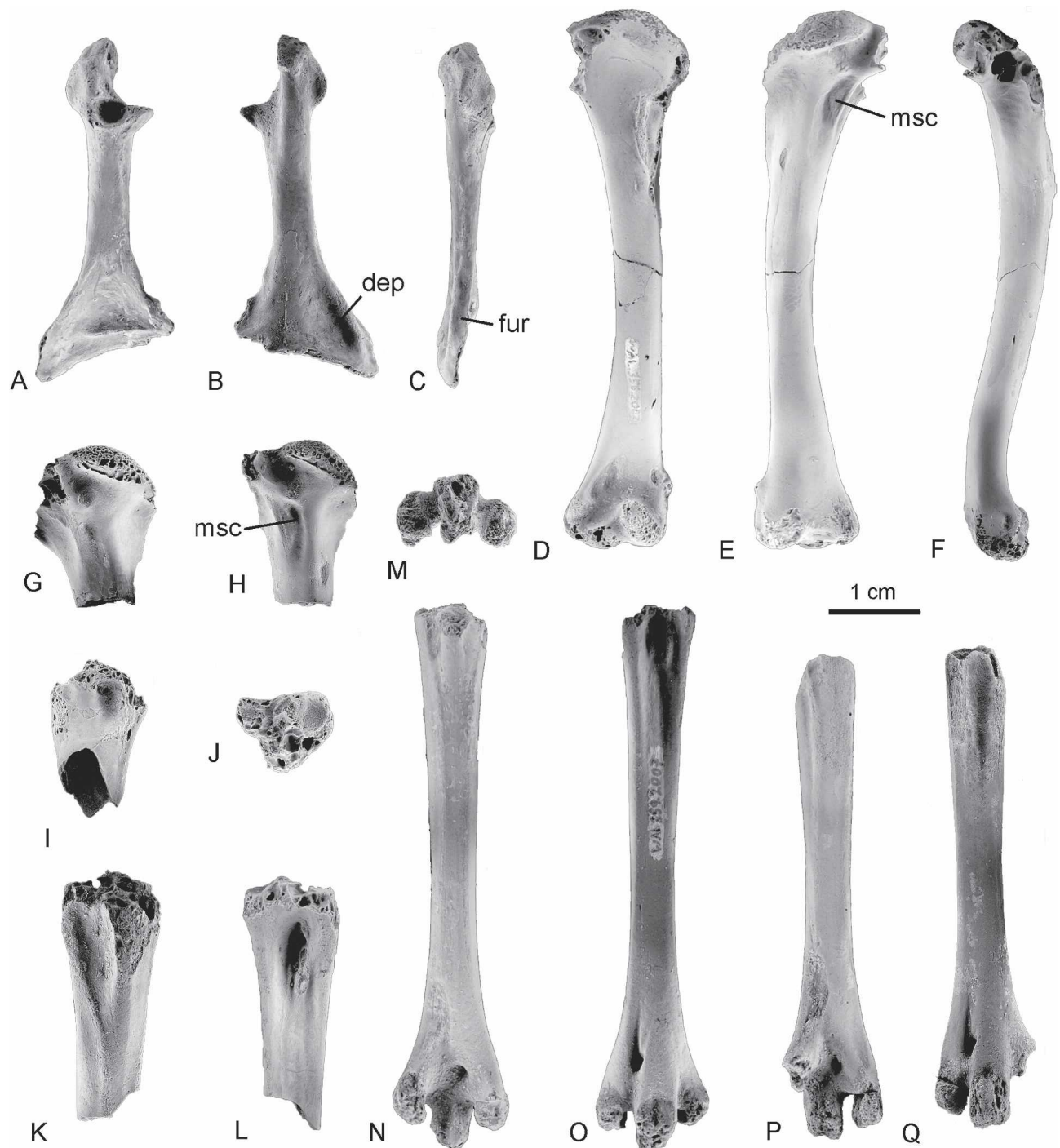


FIGURE 6. *Gradiornis walbeckensis*, gen. et sp. nov., incomplete left coracoid, holotype (WAL349.2007) in **A**, dorsal, **B**, ventral, and **C**, lateral view; referred specimens: left humerus (WAL356.2007) in **D**, cranial, **E**, caudal, and **F**, ventral view; right humerus, proximal end (WAL353.2007) in **G**, caudal view; right humerus, proximal end (WAL354.2007) in **H**, caudal view; **I**, tentatively referred right femur, distal end (WAL366.2007) in caudal view; right tarsometatarsus, proximal end (WAL360.2007) in **J**, proximal, **K**, plantar, and **L**, dorsal view; right tarsometatarsus (WAL359.2007) in **M**, distal, **N**, plantar and **O**, dorsal view; right tarsometatarsus (WAL358.2007), in **P**, plantar, and **Q**, dorsal view. Abbreviations: dep—depression on ventral surface of processus lateralis; fur—furrow along lateral margin of extremitas sternalis; msc—muscle attachment scar for musculus scapulohumeralis cranialis. Coated with ammonium chloride to enhance contrast.

Diagnosis—As for genus.

Type Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, Biochrom'97, 1997).

Measurements of Holotype—Coracoid (WAL349.2007), maximum length as preserved, 35.9; diameter of cotyla scapularis, 3.5.

Etymology—The species is named after the type locality.

Referred Specimens—Left coracoid, incomplete: WAL350.2007, WAL351.2007. Proximal right humerus: WAL353.2007 (Fig. 6G)—WAL355.2007; left humerus, largely complete: WAL356.2007 (Fig. 6D-F); left humerus, incomplete: WAL352.2007. Right tarsometatarsus, nearly complete:

WAL359.2007 (Fig. 6M-O); right tarsometatarsus, lacking extremis proximalis: WAL358.2007 (Fig. 6P, Q); right tarsometatarsus, shaft: WAL361.2007, WAL364.2007; right tarsometatarsus, shaft (juvenile): WAL365.2007; proximal right tarsometatarsus: WAL360.2007 (Fig. 6J-L); left tarsometatarsus, fragmentary shaft: WAL362.2007, WAL363.2007. All specimens are deposited in IGWuG.

Measurements of Referred Specimens—Humerus (WAL356.2007), maximum length, 59.0; width of distal end, 11.0. Tarsometatarsus (WAL359.2007), length as preserved, 58.0; width of distal end, 11.9.

Tentatively Referred Specimens—Synsacrum: WAL455.2007. Notarium: WAL456.2007. Distal right femur (Fig. 6I): WAL366.2007.

Remarks—After *Walbeckornis creber*, this is the second-most abundant species in the Walbeck material. I could identify three coracoids of *Gradiornis walbeckensis* gen. et sp. nov., whereas the two other types of coracoid of corresponding size are represented by a single bone each (see below). For this reason I also assigned the most common humeri (five specimens) and tarsometatarsi (eight specimens) of appropriate size to *G. walbeckensis*. This approach was straightforward for these two skeletal elements because only a single type of humerus and tarsometatarsus of matching size is preserved in the material. However, in the case of the carpometacarpus there are two types of similar size to *G. walbeckensis* and it was not possible to reliably assign one of these to *G. walbeckensis*; these specimens are classified ‘incertae sedis’ and described below. Assignment of skeletal elements which are only known by single bones is tentative.

Description and Comparison—The coracoid of *Gradiornis* gen. nov. exhibits a very distinctive morphology which is not matched by any other avian taxon (Fig. 6A, B). Most notably, the cotyla scapularis is circular and deeply excavated, and the short, triangular processus procoracoideus projects perpendicular to the longitudinal axis of the shaft. On the dorsal surface of the processus acroracoideus, medial of the facies articularis humeralis and directly adjacent to the cotyla scapularis, there is a triangular facet whose plane forms an angle of about 120° with that of the sulcus musculi supracoracoidei. The shaft of the bone is unusually straight and column-like, a foramen nervi supracoracoidei is absent. The processus lateralis is not completely preserved but appears to have been long and narrow as in, e.g., the Lithornithidae (Houde, 1988:fig. 13). There is a distinct depression on its ventral surface which is laterally bordered by a marked bulge, owing to which the lateral margin of the extremis sternalis is unusually thick and bears a marked furrow. The facies interna of the crista articularis sternalis is well developed.

The humerus assigned to *Gradiornis* (Fig. 6D-H) resembles that of the enigmatic and probably flightless *Strigogyps* (*Aenigmavis*) *sapea* (Cariamae) from the Middle Eocene of Messel (Peters, 1987; Mayr, 2005c:fig. 3), whereas in the Oligocene *Strigogyps* [*Ameghinornis*] *minor* the proximal end of the humerus is more strongly reduced (Mourer-Chauviré, 1983:pl. 5). The shaft of the bone is markedly sigmoidally curved in cranio-caudal direction and the caput humeri oriented more obliquely to the longitudinal axis of the humerus than in most other avian taxa. As in *Walbeckornis*, the proximal end of the humerus slants caudally and the margo caudalis of the shaft distal to caput humeri and tuberculum dorsale is concave. The crus dorsale fossae extends farther distally than the crus ventrale fossae, dorsal of it there is an elongate muscle attachment scar for musculus scapulohumeralis cranialis which also occurs in the Paleogene Presbyornithidae and some ‘Graculavidae’ (Olson and Parris, 1987) but is absent in *Strigogyps* and other Cariamae; among extant birds this scar is found in, e.g., some Ardeidae, Phoenicopteridae, and Podicipedidae (it is absent in WAL355.2007, which is somewhat smaller than the other humeri assigned to *G. walbeckensis* but

otherwise identical in morphology). There is a small pneumatic opening at the base of the fossa pneumotricipitalis. As in, e.g., extant Scolopacidae a low ridge transverses the beginning of the incisura capitis (this ridge is also present, albeit much more pronounced, in extant Tinamidae and galliform birds). The crista deltopectoralis measures about one third of the length of the humerus. There is a muscle attachment scar, presumably for musculus latissimus dorsi, in the proximal fourth of the margo dorsalis. The somewhat abraded distal end of the bone is preserved in one specimen only (WAL356.2007). The shallow fossa musculi brachialis is situated at the ventral margin of the shaft, the tuberculum supracondylare ventrale of average size. The area of the sulcus scapulotricipitalis is damaged and it cannot be discerned whether such a sulcus was present; as in *Walbeckornis*, the sulcus humerotricipitalis exhibits a small fossa olecrani. The condylus ventralis is elongate, the incisura intercondylaris shallow. The processus flexorius is moderately developed and protrudes about as far distally as the condylus ventralis. There is a small tuberculum supracondylare dorsale.

The notarium which is tentatively assigned to this species consists of two fused vertebrae, the caudal one of which exhibits a small ovate depression on each side of the corpus. The synsacrum is too incomplete preserved for a meaningful description. Likewise the distal end of the femur is too fragmentary for a detailed description, its most distinctive feature is a marked fossa poplitea.

The tarsometatarsus (Fig. 6I–Q) is an elongated bone which reaches the length of the humerus. Except for the structure of the hypotarsus, it resembles the tarsometatarsus of some Cariamae, most notably the Bathornithidae and their Paleogene European relatives, the Idiornithidae. The shaft has an asymmetric trapezoid cross-section, with a medially slanting plantar surface; it is narrowest in its midsection and widens towards the proximal and distal ends. The small foramina vascularia proximalia are situated close together. A damaged hypotarsus is preserved in one specimen only (WAL360.2007) and forms a ‘roof-like’ protrusion whose medial surface is perpendicular to the plantar surface of the shaft, and whose lateral surface is oriented at an angle of about 45° against the plantar surface of the shaft; distally, it passes gradually into the shaft, via a very short crista mediano-plantaris. The hypotarsus of *Gradiornis* does not enclose bony canals; whether there were any sulci cannot be discerned, as the plantar surface is damaged. The hypotarsus of most Cariamae is short and block-like, and although that of some Bathornithidae (*Bathornis celeripes*) and the Paleogene ‘gruiform’ *Palaephasianus* (?Geranoididae; Cracraft, 1969) exhibits a similar shape, it encloses a bony canal in these taxa. There is a distinct fossa parahypotarsalis medialis but no fossa parahypotarsalis lateralis. The large fossa metatarsi I is situated on the plantar surface of the bone, at the medial margin of the shaft. The foramen vasculare distale is situated farther proximally than in *Walbeckornis*. The trochlea metatarsi II is only slightly shorter than the trochlea metatarsi IV and only slightly plantarily deflected. The trochleae are separated by wide incisurae intertrochleares, a small canalis interosseus distalis is present. In distal view the arrangement of the trochleae is similar to that of *Strigogyps sapea*, except that the trochlea metatarsi III is deeper in dorso-plantar direction.

Discussion—Phylogenetic assignment of *Gradiornis* gen. nov. is difficult as this taxon is represented by few more or less damaged bones only.

As detailed above, the referred humerus and tarsometatarsus most closely resembles the corresponding bones of some fossil species assigned to the Cariamae, a taxon which includes the Idiornithidae, Bathornithidae, Phorusrhacidae, and extant Cariamidae (Olson, 1985). The holotypic coracoid does not contribute much to a phylogenetic assignment of *Gradiornis*, although it agrees with that of the Cariamae in the presumably derived ab-

sence of a foramen nervi supracoracoidei; the deeply excavated cotyla scapularis is plesiomorphic for neornithine birds (e.g., Mourer-Chauviré, 1992).

Cariamae are among the most abundant medium-sized, long-legged birds in the Eocene and Oligocene of Europe (e.g., Mourer-Chauviré, 1983; Mayr, 2005a), but so far only the Phorusrhacidae are known from Paleocene deposits (see introduction).

However, because *Gradiornis* lacks the derived, block-like hypotarsus of the Cariamae (e.g., Mourer-Chauviré, 1983; Olson, 1985) and sister group relationship between *Gradiornis* and the Cariamae cannot be established with derived similarities, the phylogenetic affinities of the new taxon have to remain uncertain.

Judging from its elongate and robust tarsometatarsus, *Gradiornis walbeckensis* also was a terrestrial bird, and the similarities to *Strigogyps* in humerus morphology suggest weak flight capabilities (see Mourer-Chauviré, 1983; Peters, 1987). The juvenile tarsometatarsus WAL365.2007 indicates that the species was breeding in the Walbeck paleoenvironment.

STRIGIFORMES Wagler, 1830
BERRUORNIS Mourer-Chauviré, 1994
BERRUORNIS HALBEDELI, sp. nov.
(Fig. 1C–F)

Holotype—Right tarsometatarsus, lacking articular ends: WAL01.2001 (Fig. 1C, D); deposited in IGWuG.

Differential Diagnosis—Smaller than *Berruornis orbisantiqvi* Mourer-Chauviré, 1994 (estimated total length 56–57 mm versus ~69 mm in *B. orbisantiqvi*) from which it further differs in: (1) proportionally larger foramina vascularia proximalia, and (2) shaft most narrow at level of fossa metatarsi I and becoming gradually wider towards its proximal end (of nearly equal width in *B. orbisantiqvi*).

Measurements—Length as preserved, 53.1; minimum width of shaft, 10.3.

Etymology—The species is named after Mr. Halbedel, a quarryman who was among the first to recognize the Walbeck vertebrate remains (Weigelt, 1939).

Type Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, Biochrom'97, 1997).

Tentatively Referred Specimen—Praemaxilla, lacking the tip: WAL02.2001, deposited in IGWuG (Fig. 1E, F).

Measurements of Tentatively Referred Specimen—Maximum length as preserved, 31.1; medio-lateral width at caudal end of praemaxillary symphysis, 8.1; dorso-ventral depth at caudal end of praemaxillary symphysis, 12.9.

Remarks—WAL01.2001 was described in detail by Mayr (2002) who substantiated its assignment to *Berruornis* Mourer-Chauviré, 1994, an apomorphy of which is the presence of a perforation in the crista medialis hypotarsi. Assignment of *Berruornis* to the Strigiformes can be established with the presumably derived absence of a pons supratendineus on the distal tibiotarsus, the morphology of the hypotarsus, and the configuration of the tarsometatarsal trochleae (see Mourer-Chauviré, 1994). Its classification into the Sophiornithidae (Mourer-Chauviré, 1994), however, is largely based on overall similarity and needs to be substantiated with derived characters. As detailed by Mourer-Chauviré (1994), *Berruornis* and *Sophiornis* Mourer-Chauviré, 1987, the type genus of the Sophiornithidae, differ in numerous features, of which at least the less plantarly deflected trochleae metatarsorum II et IV may indicate a sister group relationship between *Berruornis* and other strigiform birds.

WAL02.2001 is the “upper beak of a bird of prey” mentioned by Weigelt (1939; see introduction) and was also described by

Mayr (2002). It comes from a species of similar size to *Berruornis halbedeli* to which it is here tentatively assigned. As detailed by Mayr (2002), the specimen differs significantly from the beak of crown group Strigiformes, with which it however shares the presence of two large oval openings inside the tip of the rostrum, at the caudal end of the praemaxillary symphysis (Fig. 1F). There are no other similar-sized birds in the Walbeck material.

Incertae sedis
Gen. et sp. indet. A
(Fig. 1G, H)

Referred Specimen—Right coracoid, lacking most of the extremities sternalis: WAL348.2007 (Fig. 1G, H); deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, Biochrom'97, 1997).

Measurements—Length as preserved, 29.6.

Description and Comparison—This coracoid differs from the corresponding bone of the above taxa in the proportionally longer processus acrocoracoideus. Although most of the tuberculum brachiale is broken, it can be discerned that the tip of the processus acrocoracoideus is excavated by the sulcus musculi supracoracoidei. The cotyla scapularis is only moderately excavated. The processus procoracoideus is broken but, judging from its insertion on the bone, appears to have been wide, extending distally beyond the foramen nervi supracoracoidei. The ventral opening of the foramen nervi supracoracoidei is situated farther towards the sternal end of the coracoid than the dorsal opening. There are distinct muscle striae on the dorsal surface of extremities sternalis, at the beginning of the impressio musculi sternocoracoidei.

Remarks—A phylogenetic assignment of this specimen is not possible owing to its fragmentary preservation; in its proportions it exhibits some similarity to the coracoid of extant Accipitridae from which it however differs in morphological details (e.g., processus acrocoracoideus without articulation facet for facies articularis acrocoracoidea of furcula, position of foramen nervi supracoracoidei).

Gen. et sp. indet. B
(not figured)

Referred Specimens—Proximal left femur: WAL373.2007. Right tibiotarsus, shaft: WAL398.2007; distal left tibiotarsus: WAL394.2007; left tibiotarsus, shaft: WAL384.2007, WAL457.2007. All specimens are deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, Biochrom'97, 1997).

Measurements—Tibiotarsus (WAL394.2007), distal width, 3.6 (on average 4.8 in *W. creber*, see Tab. 1); minimum width of shaft, 2.1. Tibiotarsus (WAL398.2007), length as preserved, 37.1; minimum width of shaft, 1.9.

Remarks—The specimens assigned to this species are distinctly smaller than the corresponding bones of *W. creber*, even taking into account that these exhibit a wide size range. The proximal end of the femur closely resembles that of *W. creber*, the tibiotarsi are too poorly preserved for detailed comparisons.

Gen. et sp. indet. C
(not figured)

Referred Specimens—Left tibiotarsus, shaft: WAL484.2007; deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, Biochrom'97, 1997).

Measurements—Length as preserved, 28.9; minimum width of shaft, 1.4.

Remarks—This tibiotarsus represents the smallest avian species in the Walbeck material. It is a long and slender bone but otherwise too fragmentary for a meaningful description.

cf. *FISSURAVIS WEIGELTI* gen. et sp. nov. and
GRADIORNIS WALBECKENSIS, gen. et sp. nov.
(Fig. 1I–L)

Referred Specimens—Left carpometacarpus, lacking os metacarpale minus: WAL357.2007 (Fig. 1I, J). Right carpometacarpus, lacking os metacarpale minus as well as proximal and distal ends: WAL367.2007 (Fig. 1K, L), WAL368.2007. All deposited in IGWuG.

Locality and Horizon—Walbeck near Helmstedt, Germany; ?upper Middle Paleocene (?MP 5, BiochroM'97, 1997).

Measurements—WAL357.2007, length, 31.8. WAL368.2007, length as preserved, 21.8.

Remarks—In the Walbeck material there are two types of carpometacarpi which come from a species of similar size to *Fissuravis weigelti* and *Gradiornis walbeckensis*. One of these is represented by two right ossa metacarpalia majores (WAL367.2007 and WAL368.2007; Fig. 1K, L), which exhibit a very peculiar morphology in being very short and stout, and apparently are from a flightless, or nearly so, species. What remains from the os metacarpale minus indicates that it was straight and the spatium intermetacarpale narrow; its distal insertion is on the caudal surface of the os metacarpale majus. The distal section of the cranial surface of the unusually thin-walled os metacarpale majus slants ventrally, the sulcus tendineus is hardly visible.

The other type of carpometacarpus (WAL357.2007; Fig. 1I, J) resembles the corresponding bone of the Psophiidae and some Cariamae in its shape. The processus extensorius is well developed and the fovea carpalis cranialis much shallower than in *Walbeckornis*. The shaft of the os metacarpale minus has a subrectangular cross-section. The os metacarpale minus is broken but appears to have been bowed, delimiting a wide spatium intermetacarpale; its distal insertion is on the ventrocaudal surface of the os metacarpale majus and the ossa metacarpalia did thus not run parallel. The sulcus tendineus is indistinct.

A reliable assignment of one of these specimens to either *Fissuravis* or *Gradiornis* is not possible, and none of the specimens resembles the carpometacarpus of the Lithornithidae to which *Fissuravis* is tentatively assigned in the present study.

CONCLUSIONS

Russell (1964) noted that the mammalian fauna of Walbeck is comparatively taxon-low compared with that from the Upper Paleocene of the Reims area in France, and includes several archaic forms not found in the French sites. Unfortunately, the avifauna of the French Paleocene is still too poorly known for meaningful comparisons with that of Walbeck. Of the taxa described in the present study Berruornithidae and Gastornithidae also occur in the Reims deposits. As noted above, the humerus of *Walbeckornis* is further very similar to that of the Messelornithidae, which makes it necessary to substantiate generic identification of the French '*Messelornis russelli*' (Mourer-Chauviré, 1995) with additional bones.

By the curious dominance of one species (*Walbeckornis creber*) and its species poorness, the Walbeck avifauna sharply contrasts with the very diverse avifaunas known from the earliest Eocene of Europe (e.g., Kristoffersen, 2002; Mayr, 2005a). Moreover, all of the sufficiently well preserved avian taxa from Walbeck belong to terrestrial forms whereas small arboreal birds appear to be completely absent. Because the Walbeck material was screen-washed and includes numerous small bones, it is unlikely that there was a collecting bias, and its composition either

reflects properties of the Walbeck paleoenvironment or is of taphonomic origin (as detailed by Weigelt, 1939, many specimens seem to constitute prey remains).

Controversial hypotheses exist on the timing of the origin of neornithine birds and the effect of a possible mass extinction event at the K/T boundary on the avian diversity (e.g., Feduccia, 1995, 2003; Cooper and Penny, 1997). In particular, it is often assumed that non-neornithine birds became extinct at the end of the Cretaceous (e.g., Feduccia, 2003; Dyke and van Tuinen, 2004). The evidence therefore is, however, very weak because the fossil record of birds in the Late Cretaceous and around the K/T boundary is extremely scanty and largely restricted to North America. By the incomplete fusion of the metatarsalia, the tarsometatarsus of *Qinornis paleocenica* from the early Paleocene of China corresponds well with that of the Late Cretaceous non-neornithine *Apsaravis* (Clarke and Norell, 2002:fig. 21), and *Qinornis* thus suggests survival of some basal ornithurines across the K/T boundary. It is unlikely that the presence of incompletely fused metatarsalia in *Q. paleocenica* indicate a juvenile condition of the specimen (contra Xue, 1995), because the distal tarsalia are completely fused with the metatarsalia and the articular ends of the tarsometatarsus do not exhibit the blurred surfaces characteristic for the growing bones of juvenile neornithine birds.

Most of the species described in the present study cannot be reliably assigned to a modern higher-level taxon which is not unexpected, because recent calibrations of molecular data indicate diversification of most neoavian lineages around or shortly after the K/T boundary (Slack et al., 2006; Ericson et al., 2006). Paleocene avian taxa are thus likely to represent the earliest divergences within neognathous birds and to be sister taxa of clades including several modern 'orders'. A phylogenetic assignment of most of these taxa seems hardly possible unless the basal divergences within extant birds are better understood (e.g., Cracraft et al. 2004; Fain and Houde 2004; Ericson et al. 2006).

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