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Annales de Paléontologie 94 (2008) 29–37
ANNALES DE PALÉONTOLOGIE
http://france.elsevier.com/direct/ANNPAL/

Original article

First substantial Middle Eocene record of the Lithornithidae (Aves): A postcranial skeleton from Messel (Germany)

Première preuve substantielle de la présence de Lithornithidae (Aves) de l'Éocène moyen : un squelette postcrânien de Messel (Allemagne)

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Available online 12 February 2008

Abstract

A postcranial skeleton of a representative of the palaeognathous Lithornithidae (Aves) is described from the Middle Eocene of Messel in Germany. The specimen is slightly smaller than *Lithornis plebius* from which it, however, differs in limb bone proportions. It constitutes the latest fossil record of the Lithornithidae in Europe, whose only other Middle Eocene record is a fragmentary tibiotarsus from North America.
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Résumé

Un squelette postcrânien d'un représentant des Lithornithidae (Aves, Palaeognathae) est décrit de l'Éocène moyen de Messel (Allemagne). Le spécimen est un peu plus petit que *Lithornis plebius*, dont il diffère, cependant, par les proportions des os des membres. Il constitue le dernier représentant fossile des Lithornithidae en Europe et l'unique autre spécimen datant de l'Éocène moyen est un tibiotarse fragmentaire provenant d'Amérique du Nord.
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Keywords: Fossil birds; Lithornithidae; Eocene; Messel

Mots clés : Oiseaux fossiles ; Lithornithidae ; Éocène ; Messel

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doi:10.1016/j.annpal.2007.12.004

1. Introduction

The Lithornithidae are volant palaeognathous birds of controversial composition and phylogenetic affinities, which occur in the early Eocene of Europe and North America (Houde, 1988). Eight species in three genera are currently included in this taxon: the type genus *Lithornis* Owen, 1840 is known from the Lower Eocene of Europe and the Paleocene and Lower Eocene of North America (Houde, 1988; Leonard et al., 2005). *Pseudocrypturus* Houde, 1988 was reported from the Lower Eocene of North America but also tentatively identified in the Lower Eocene of England, whereas the large *Paracathartes* Harrison, 1979 occurs in the Lower Eocene of North America only.

Most European Lithornithidae have been found in the Lower Eocene London Clay in England (Houde, 1988), but recently specimens were also reported from the Lowermost Eocene of Denmark (Kristoffersen, 1999; Leonard et al., 2005) and a tentative record comes from the Paleocene of Germany (Mayr, 2007).

Here, I report on a postcranial skeleton of a lithornithid bird from the Middle Eocene (about 47 million years ago; Mertz et al., 2004) of Messel in Germany. The specimen is the only substantial Middle Eocene fossil record of the Lithornithidae, the only other being a fragmentary tibiotarsus of an unnamed species from the Middle Eocene (Bridgerian) of Wyoming, USA (Houde, 1988: 42).

The fossil specimens are stored in the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Germany (SGPIMH), the National Museum of Natural History, Washington, USA (USNM) and the private collection of Michael Daniels, Clacton-on-Sea, Essex, UK (WN). Osteological terminology follows Baumel and Witmer (1993).

2. Systematic Paleontology

Aves Linnaeus, 1758
Palaeognathae Pycraft, 1900
Lithornithidae Houde, 1988
Gen. and sp. indet.

2.1. Referred specimen

SGPIMH MEV1a + b (slightly dissociated skeleton on two slabs, lacking skull, distal phalanges of right wing, left carpometacarpus with distal phalanges and both feet; Figs. 1–3).

2.2. Locality and horizon

Messel near Darmstadt, Hessen, Germany; lower Middle Eocene (MP 11).

2.3. Measurements

See Table 1.

2.4. Remarks

Parts of the skeleton are painted and seem to have been restored by the preparator of the specimen: in SGPIMH MEV1a this pertains to the distal portion of the shaft of the right humerus and the midsection of the shafts of left humerus, ulna and radius; in SGPIMH MEV1b to the distal

Fig. 1. Lithornithidae indet., postcranial skeleton from the Middle Eocene of Messel (SGPIMH MEV1a). Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.
Fig. 1. Lithornithidae indet., squelette post-crânien de l'Éocène moyen de Messel (SGPIMH MEV1a). Couvert de chlorure d'ammonium pour augmenter le contraste. L'échelle représente 10 mm.

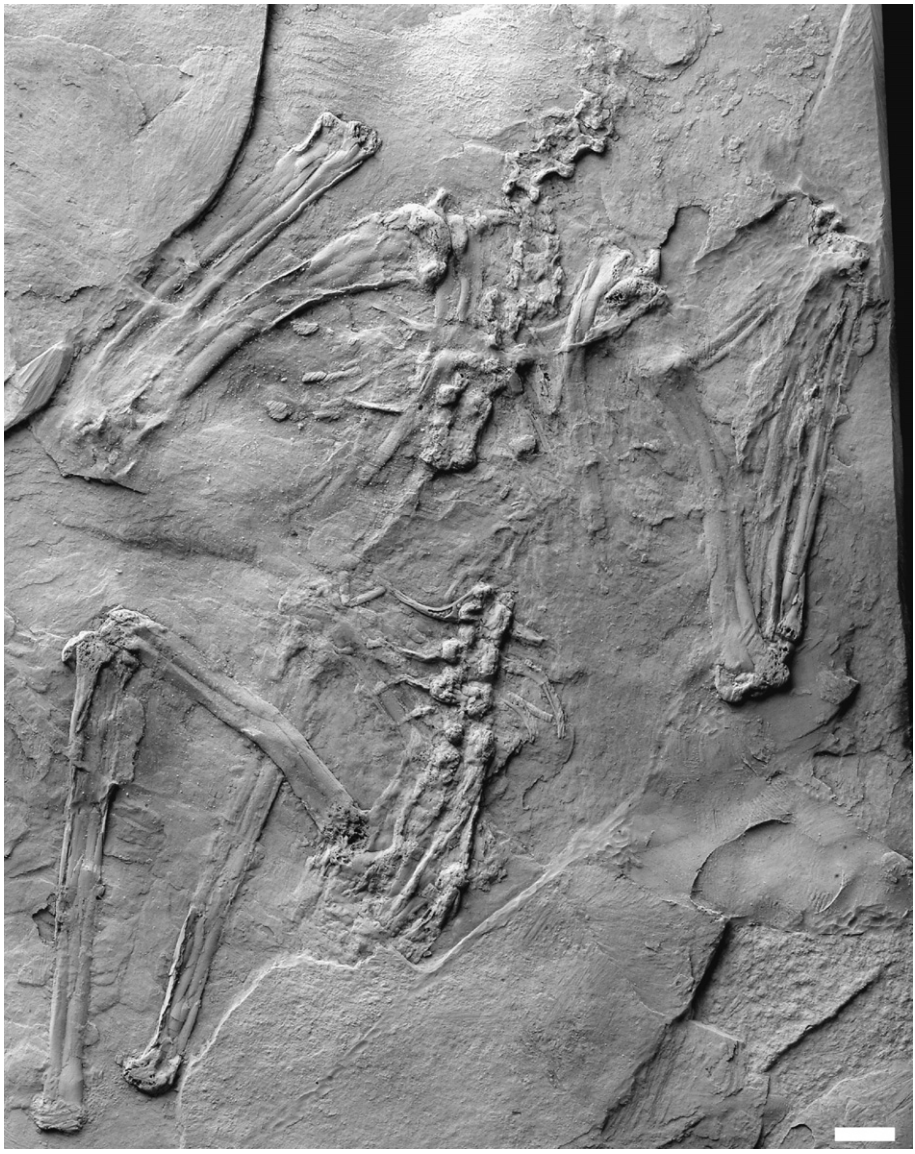

Fig. 2. Lithornithidae indet., postcranial skeleton from the Middle Eocene of Messel (SGPIMH MEV1b). Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.
Fig. 2. Lithornithidae indet., squelette postcrânien de l'Éocène moyen de Messel (SGPIMH MEV1b). Couvert de chlorure d'ammonium pour augmenter le contraste. L'échelle représente 10 mm.

end of left humerus and the proximal part of left ulna and radius, as well as the distal section of right ulna and radius.

2.5. Description and comparison

Seventeen praesacral vertebrae are preserved (according to Houde, 1988, Lithornithidae have 23 praesacral vertebrae). Except for the cranialmost one, the cervical vertebrae do not exhibit long

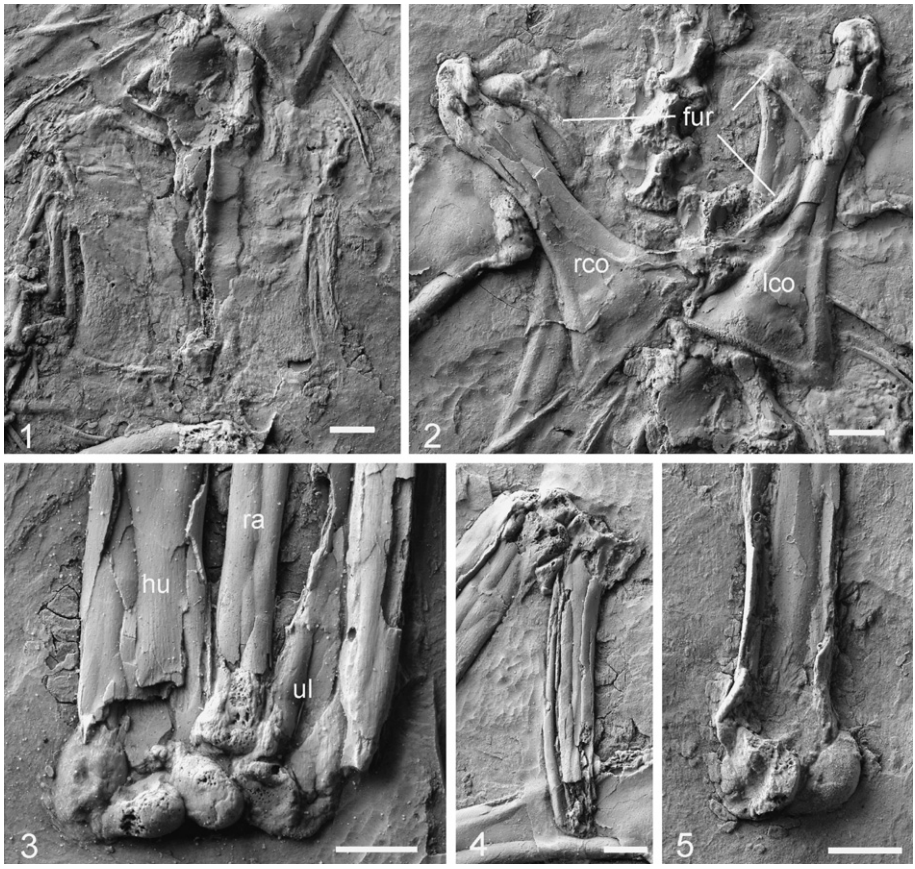

Fig. 3. Lithornithidae indet., from the Middle Eocene of Messel. **1:** SGPIMH MEV1a, sternum in ventral view; **2:** SGPIMH MEV1a, coracoids in ventral view. **3:** SGPIMH MEV1a, distal end of left humerus in cranial view; **4:** SGPIMH MEV1a, right carpometacarpus in dorsal view; **5:** SGPIMH MEV1a, distal end of left tibiotarsus in cranial view. Abbreviations: fur – furcula, hu – humerus, lco – left coracoid, ra – radius, rco – right coracoid, ul – ulna. Coated with ammonium chloride to enhance contrast. Scale bars equal 5 mm.

Fig. 3. Lithornithidae indet., de l'Éocène moyen de Messel. **1 :** SGPIMH MEV1a, sternum, face ventrale ; **2 :** SGPIMH MEV1a, coracoïdes, face ventrale ; **3 :** SGPIMH MEV1a, extrémité distale d'humérus gauche, face crânienne ; **4 :** SGPIMH MEV1a, carpométacarpe droit, face dorsale ; **5 :** SGPIMH MEV1a, extrémité distale de tibiotarse gauche, face crânienne. Abréviations : fur – furcula, hu – humérus, lco – coracoïde gauche, ra – radius, rco – coracoïde droit, ul – ulna. Couvert de chlorure d'ammonium pour augmenter le contraste. Les échelles représentent 5 mm.

processus costales, which are well-preserved in the Danish lithornithid described by Leonard et al. (2005) and in SGPIMH MEV1 may have been lost during preparation of the specimen. The corpus of at least the penultimate thoracic vertebra bears an, albeit small, pneumatic foramen; large foramina were reported to be present on the thoracic vertebrae of other Lithornithidae (Houde, 1988; Leonard et al., 2005). A notarium is absent. Five sternal ribs articulate with the sternum.

The coracoid (Fig. 3) has a slender shaft and resembles the corresponding bone of *Lithornis* and *Pseudocrypturus* in its proportions. The extremitas omalis bears a marked impressio ligamenti acrocoracohumeralis (as in *Lithornis* and *Pseudocrypturus* but in contrast to *Paracathartes*; Houde, 1988: 41), but is otherwise too incompletely preserved for detailed comparisons.

Table 1
Dimensions of major limb bones of the Messel lithornithid SGPIMH MEV1 in comparison to seven of the eight described lithornithid species (left/right, in millimetres); the species are ordered by increasing length of humerus and/or ulna. Complete bones of *Lithornis hookeri* are unknown and this species is thus not included in the table
Tableau 1
Dimensions des principaux os des membres du Lithornithidae de Messel SGPIMH MEV1 en comparaison avec sept des huit espèces décrites de Lithornithidae (gauche/droite, en millimètres) ; les espèces sont disposées selon la longueur croissante de l'humérus et/ou de l'ulna. On ne connaît pas d'os complets chez *Lithornis hookeri* et donc cette espèce n'est pas incluse dans le tableau

	Coracoid	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus
SGPIMH MEV1 (Lithornithidae indet.)	32.1/–	~68.0/~72.8	70.0/–	35.9/–	57.0/59.2	81.9/82.2
Lithornis plebius (USNM 336534)[a]	~31.1/–	78.2	76.6	41.3/41.8	64.6/65.1	97.2/95.8
Pseudocrypturus cercanaxius (Siber specimen)[a]	35.6/36.8	~84.4	–	–	~63.0/~62.7	90.3/89.0
Lithornis celetius (USNM 290554)[a]	–	–	» 85.5	> 48.5	–	–
Lithornis nasi (WN 81373)[a]	–	–	~86.0	–	–	112.5
Lithornis vulturinus (BMNH A 5204)[a]	–	» 91.3	–	–	–	–
Lithornis promiscuus (USNM 336535)[a]	42.7/42.7	112.7/–	105.5/–	–/58.5	> 83.0/–	–/129.6
Paracathartes howardae (USNM 361425)[a]	–	> 123.6	~120.0	–	–	–

[a] After Houde (1988).

The short processus procoracoideus is visible on the right coracoid of SGPIMH MEV1a. Whether there was a foramen nervi supracoracoidei cannot be discerned. The extremitas sternalis is very wide, with a strongly protruding angulus medialis and a well-developed and narrow processus lateralis.

Although the furcula (Fig. 3) is broken, it can be discerned that it was widely U-shaped. The extremitas omalis is similar to that of *Pseudocrypturus cercanaxius* (Houde, 1988: Fig. 35).

As is characteristic for lithornithid birds, the shaft of the scapula is strongly mediolaterally curved and the bone is similar to the scapula of *Lithornis promiscuus* (Houde, 1988: Fig. 14C) in its shape. Another characteristic of the lithornithid scapula, the greatly elongated, pointed acromion, however, cannot be discerned in the Messel specimen: although the acromion is elongated, it is proportionally shorter than in other Lithornithidae, which may either be an artifact of preservation or a distinctive feature of the Messel species. There seems to be a pneumatic opening between the acromion and the facies articularis humeralis (see Houde, 1988: 21). The tip of the caudal end of the bone is blunt.

The sternum (Fig. 3) exhibits the characteristic lithornithid morphology in that the subrectangular corpus sterni has concave lateral margins and lacks caudal incisions. The corpus sterni of SGPIMH MEV1 is only slighter longer than wide (width across processus craniolaterales 39.0 mm, maximum length as preserved 45.2 mm), whereas it is almost twice as long and exceeding the femur in length in *Lithornis promiscuus* (Houde, 1988: Fig. 10) and *L. celetius* (Houde, 1988: Fig. 9); its greatest width is across the short processus craniolaterales. As in other lithornithids, the midpart of the caudal margin is caudally protruding. Most of the carina sterni is broken, details of the cranial margin cannot be discerned.

The elongate humerus corresponds well with that of *Lithornis* in the size and shape of the cristae deltopectoralis and bicipitalis, the small tuberculum dorsale and the strongly curved shaft. The morphology of the distal condyles also corresponds with other Lithornithidae and, as in the latter, the sulci humerotricipitalis and scapulotricipitalis appear to have been shallow, although the corresponding area is very poorly preserved.

The ulna is as long as the humerus whereas, according to Houde (1988: Tabs. 10 and 14), it is distinctly shorter than the humerus in most lithornithid species except *Lithornis plebius* and *Paracathartes howardae* (concerning a specimen from the Lower Eocene of Denmark, the comments of Leonard et al., 2005: 8 are contradictory in that these authors note that the radius is "approximately equal in length to the humerus", whereas the ulna "is longer than its articulating radius" and "shorter than the humerus"; measurements are not provided but judging from the photograph, ulna and radius are considerably shorter than the humerus). The preservation of the bone only allows the recognition of a very short olecranon and a small and shallow cotyla ventralis. The radius exhibits a broad distal end.

As in other Lithornithidae, the carpometacarpus (Fig. 3) is slender, with a straight os metacarpale minus and a narrow spatium intermetacarpale. The articular surface of the processus alularis is concave. As in other lithornithids, there appears to have been a depression on the proximocranial surface of the trochlea carpalis (the corresponding area is, however, damaged in the specimen).

The pelvis is very poorly preserved but of similar proportions to that of other Lithornithidae. The praeacetabular portion is narrow, the alae praeacetabulares ilii have concave lateral margins. The cristae iliacae dorsales are fused with the crista spinosa synsacri (Leonard et al., 2005: Fig. 4C). The crista spinosa synsacri forms a low ridge along the caudal portion of the synsacrum. The tubercula praeacetabularia appear to have been weakly developed as in *Lithornis promiscuus* (Houde, 1988: Fig. 21), owing to the preservation of the specimen. The foramen ilioischiadicum, which is caudally open in lithornithids, cannot be discerned.

The long and slender femur is craniocaudally curved.

The tibiotarsus is the longest limb element and exceeds the humerus in length. The cristae cnemiales are low. As in other Lithornithidae, there is no ossified pons supratendineus and the margo medialis of the shaft forms a medial projection, just proximal of the condylus medialis (Fig. 3; Houde, 1988: Fig. 25). Possibly owing to the fact that the distal end of the bone is crushed, a sulcus extensorius is not visible. The condylus lateralis is slightly larger than the condylus medialis. The fibula reaches two thirds of the length of the tibiotarsus.

Remains of a single, short (~25 mm) feather are preserved next to the distal end of the left humerus.

3. Discussion

SGPIMH MEV1 is clearly distinguished from the avian taxa recorded from Messel so far and closely resembles other lithornithids in limb proportions and osteology (e.g., scapula long and curved, humerus with markedly curved shaft, ulna not exceeding humerus in length, carpometacarpus slender and elongate, and hindlimbs long). Although the diagnostic features of the skull and pelvis (Houde, 1988) are not visible in the specimen, the Messel specimen shares with other Lithornithidae firstly, a presumably derived morphology of the sternum, which exhibits markedly concave lateral margins and lacks incisions in the caudal end and, secondly, the absence of a pons suprantendineus on the distal tibiotarsus.

So far, five species of Lithornithidae have been reported from the early Eocene of Europe (Houde, 1988; Leonard et al., 2005): *Lithornis vulturinus* Owen, 1840, *L. nasi* (Harrison, 1984), ?*L. hookeri* (Harrison, 1984), *L.* cf. *plebius* Houde, 1988 and cf. *Pseudocrypturus cercanaxius* Houde, 1988. The Messel lithornithid is distinguished from *Paracathartes*, the largest lithornithid taxon, by the more slender scapula, humerus and ulna, but a well-founded assignment to either *Lithornis* or *Pseudocrypturus* is not possible.

SGPIMH MEV1 is smaller than *Lithornis plebius* Houde, 1988 (Table 1) but larger than the smallest lithornithid, ?*L. hookeri* (Harrison, 1984) (the width of the distal end of the humerus is 12.0 mm in the Messel specimen versus 10.3 in ?*L. hookeri* and 12.5–12.9 in *L. plebius*; Houde, 1988: Tab. 11). It distinctly differs from *L. plebius* in its limb proportions and whereas the coracoid is slightly longer than that of *L. plebius*, the tibiotarsus is much shorter (see Table 1; the ratio ulna: tibiotarsus is 0.85 in the Messel bird versus 0.79 in *L. plebius* [specimen USNM 336534, after Houde, 1988]). Measurements of the Danish lithornithid (Leonard et al., 2005) have not been published, but this specimen was assigned to *L. vulturinus*, which is much larger than SGPIMH MEV1 (Table 1).

In addition to the fact that it represents a previously unknown taxon of the Messel avifauna, the new specimen is of significance because it constitutes the latest and only Middle Eocene fossil record of the Lithornithidae in Europe (Mayr, 2005).

Lithornithids are considered to have been "sensitive-billed probers" (Houde, 1988: 109), which lived and foraged along shorelines and other bodies of water (Houde, 1988: 107; Kristoffersen, 1999). Similar feeding niches are today mainly occupied by scolopacid charadriiform birds, which are unknown from early Eocene deposits (Mayr, 2005). It is conceivable that ecological competition with the latter contributed to the extinction of lithornithids, although such hypotheses are difficult to test, given our scant knowledge on the exact stratigraphical distribution of Paleogene birds.

Recognition of lithornithids in Messel testifies the great similarity between the Messel avifauna and that of the Lower Eocene London Clay in England (Mayr, 2005). Probably for taphonomic

reasons, the Messel avifauna is biased towards small avian species, which may explain the fact that lithornithids are rarer in the Messel deposits than in the London Clay and the North American Willwood Formation.

Acknowledgements

I thank W. Weitschat (SGPIMH) for the loan of the fossil specimen and S. Tränkner for taking the photographs. I am also indebted to C. Mourer-Chauviré for reviewing the manuscript and correction of the French abstract.

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