A New Specimen of the Fossil Palaeognath *Lithornis* from the Lower Eocene of Denmark

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''Buy preparations?! [but] we have not enough money left to buy gunpowder''—comment of the British Prime Minister William Pitt during the Napoleonic Wars (recorded by Flower, 1898). The original holotype of *Lithornis vulturinus* was purchased by the British government in 1799 as part of a collection to ''be maintained in its integrity to serve the education of the citizens''.

ABSTRACT

Palaeognathous birds (Aves, Palaeognathae) are uncontroversially the most basal clade among modern birds (Neornithes), having been defined for more than 100 years on the basis of their palatal morphology. However, because many fossil specimens that have been described to date lack detailed skull material (especially in association with postcrania), aspects of the early evolutionary history of these birds remain unclear, and their relationships on the basis of anatomical characters are as yet unresolved. In this paper we present a new and exceptionally well-preserved specimen of the Lower Eocene fossil palaeognath *Lithornis* that has a remarkable three-dimensionally preserved and complete skull. New anatomical information provided by this Danish fossil leads us to suggest that a number of cranial characters previously considered diagnostic for ratites may in fact be primitive among palaeognaths. The presence of members of Lithornithidae in the Lower Eocene (earliest Tertiary) is consistent with the hypothesis that basal divergences within Palaeognathae occurred at an earlier geological time, perhaps prior to the Cretaceous–Tertiary (K–T) boundary, as has been proposed based on evidence from much less well-preserved fossil material.

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INTRODUCTION

For more than a century, avian taxonomists have agreed on the presence of a broad subdivision within modern birds (Neornithes) into two basal clades: the flighted Neognathae and the largely terrestrial Palaeognathae. Historically, this classification has been based on the morphology of the palate, which is far more complex and robust in the flightless group (Huxley, 1867). Despite a seemingly clear distinction between these taxa, however, a definitive phylogeny *within* palaeognaths—including morphology and a wide range of extinct taxa—has so far proved elusive. Still, these birds are commonly further subdivided into the ratites and the tinamous on the basis of their anatomy (McDowell, 1948; Bledsoe, 1988; Lee et al., 1997). Ratites are the group that comprises the large, flightless ostrich, rheas, emu, cassowaries, and kiwis, along with the extinct moas and elephant birds. Tinamous are a diverse group of birds that share palatal similarities but have retained the ability to fly (Feduccia, 1996; Bertelli et al., 2002). Overall, the relationships of palaeognaths remain inadequately resolved by use of anatomical characters. Morphological analyses have either incompletely sampled the skeletons of these birds (Cracraft, 1974) or have not considered fossil taxa (Lee et al., 1997), and markedly different results have been recovered when phylogenies have been founded on molecular characters (Lee et al., 1997; van Tuinen et al., 1998; Haddrath and Baker, 2001; Cooper et al., 2001). However, since it is universally accepted that palaeognaths occupy the basal-most position in the neornithine tree (Groth and Barrowclough, 1999; van Tuinen et al. 1998, 2000; Livezey and Zusi, 2001; Mayr and Clarke, 2003), resolving their evolutionary history is of paramount importance. Recent biogeographic hypotheses to explain the modern-day distributions of these birds in Africa (ostrich), South America (rheas, tinamous), and Australasia (kiwis, emu, cassowaries, moas) have been developed on the basis of molecular phylogenies that have not included any fossil evidence (Cooper et al., 2001; Cracraft, 2001; Haddrath and Baker, 2001; but see van Tuinen et al., 1998).

One key fossil group in particular that has long been thought to have bearing on the problem of palaeognath relationships comprises *Lithornis* and its kin (Lithornithidae). Lithornithidae are an assemblage of chicken-size flighted birds that were initially recognized in the 1980s (Houde and Olson, 1981; Houde, 1986, 1988) from fossil material described much earlier (Owen, 1840, 1841; see Harrison and Walker, 1977). These birds are known from some very good fossil material, including largely complete skeletons, from the Lower-Middle Eocene of Europe and North America (Houde and Olson, 1981; Houde, 1988) and have previously been placed on the lineage leading to tinamous after the ratite–tinamou divergence (Houde and Olson, 1981). This tree shape, combined with the fact that tinamous retain the ability to fly, would suggest that all palaeognaths, including the flightless ratites, are descended from volant ancestors and have secondarily lost the power of flight. The basal divergence of the group therefore (tinamous–ratites) is likely to have occurred in the Northern Hemisphere (Houde and Olson, 1981; Houde, 1986, 1988). The phylogenetic relationships of Lithornithidae, however, remain controversial, on the one hand, because little well-preserved cranial material of these birds is known—it is in the skull that the majority of diagnostic palaeognath characters occur (Cracraft, 1974; Houde and Olson, 1981; Houde, 1988; Lee et al., 1997)—and on the other, because the characters of these birds have never been tested by cladistic analysis (see fig. 1). Descriptions of new fossils are badly needed to resolve the issue of the relationships of these birds.

In this paper, we present descriptions of a new and exceptionally well-preserved specimen of the lithornithid *Lithornis* that includes a complete skull, vertebral series (including the synsacrum), pelvis, shoulder girdle (right coracoid and both scapulae), and forelimb. Articulation of the skull with the postcranial skeleton allows unambiguous identification of the fossil as *Lithornis*—features of its cranial and vertebral anatomy that bear on the relationships of these birds are highlighted.

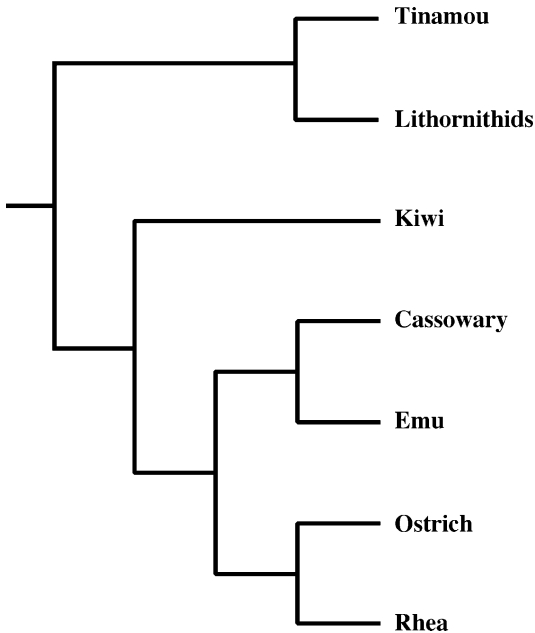INSTITUTIONAL ABBREVIATIONS: **AMNH,** American Museum of Natural History, New

Fig. 1.   Phylogenetic tree redrawn from Lee et al. (1997) that shows the interrelationships of living palaeognaths (based on molecular and morphological data). We have added the position of the lithornithids based on Dyke (2003).

York; **BMNH,** Department of Palaeontology, The Natural History Museum, London; **GM,** Geiseltal Museum, Halle; **MGUH,** Geologisk Museum of the University of Copenhagen, Dankræ Fossil Collection, Copenhagen; **NMING,** National Museum of Ireland, Division of Natural History (Geology), Dublin; **PU,** Princeton University collections (Peabody Museum of Natural History, Yale University), New Haven, CT; **UM,** Museum of Palaeontology, University of Michigan, Ann Arbor; **USNM,** United States National Museum of Natural History, Washington, DC.

We have used anatomical terminology modified following Howard (1929) from the standard avian nomenclature of Baumel and Witmer (1993).

SYSTEMATIC PALEONTOLOGY

PALAEOGNATHAE PYCRAFT, 1900

LITHORNITHIDAE HOUDE, 1988

Lithornis vulturinus (Owen, 1840)

NEOTYPE: BMNH A 5204, partial specimen (see Houde, 1988: 25–26) originally referred to the musophagid (turaco) *Promusophaga magnifica* (Harrison and Walker, 1977) (see below).

REFERRED SPECIMEN: MGUH 26770, articulated skeleton (fig. 2) from the Lower Eocene (ca. 55 Mya) Fur Formation of Denmark (Kristoffersen, 2001). This specimen is the first known member of the Lithornithidae in which the skull is completely preserved in three dimensions and is articulated with the postcranial skeleton (fig. 2A).

COMMENTS AND EMENDED DIAGNOSIS: The fossil genus *Lithornis* was named by Owen (1840) on the basis of a specimen purchased by the Royal College of Surgeons in 1798 from the collection of the English anatomist John Hunter following his death in 1793. Because the original holotype was destroyed in the bombing of London during World War II, a suitable neotype was erected by Houde (1988). However, because the original diagnosis of *Lithornis* was based on postcranial anatomy (Owen, 1840) and differentiation with respect to the other known genera of Lithornithidae, *Pseudocrypterus* and *Paracathartes* (Houde, 1988), relevant emendations are given here on the basis of MGUH 26770. *Lithornis* can thus be diagnosed on the basis of the presence of the following characters (all of which are preserved in MGUH 26770): small pterygoid fossa, caudal processes of palatines absent, palatines hooked rostrally, quadrate not pneumatized, orbital process of quadrate large and rounded, marked and well-developed pectoral crest of humerus, 13 cervical and 9 free thoracic vertebrae, incisura arcus caudalis of atlas narrow, rostral pneumatic foramina present on cervical vertebrae.

DESCRIPTION OF MGUH 26770

We compared MGUH 26770 with representative specimens already referred to the genus *Lithornis* (Houde, 1988), as well as with skeletons of other extant and fossil palaeognaths. In addition to its exceptionally well-preserved skull (fig. 2A), much of the remainder of the postcranial skeleton of this specimen is intact and articulated (although notably lacking hind limbs). The cervical and thoracic vertebral series are complete, as is one forelimb (comprising the humerus, ra-
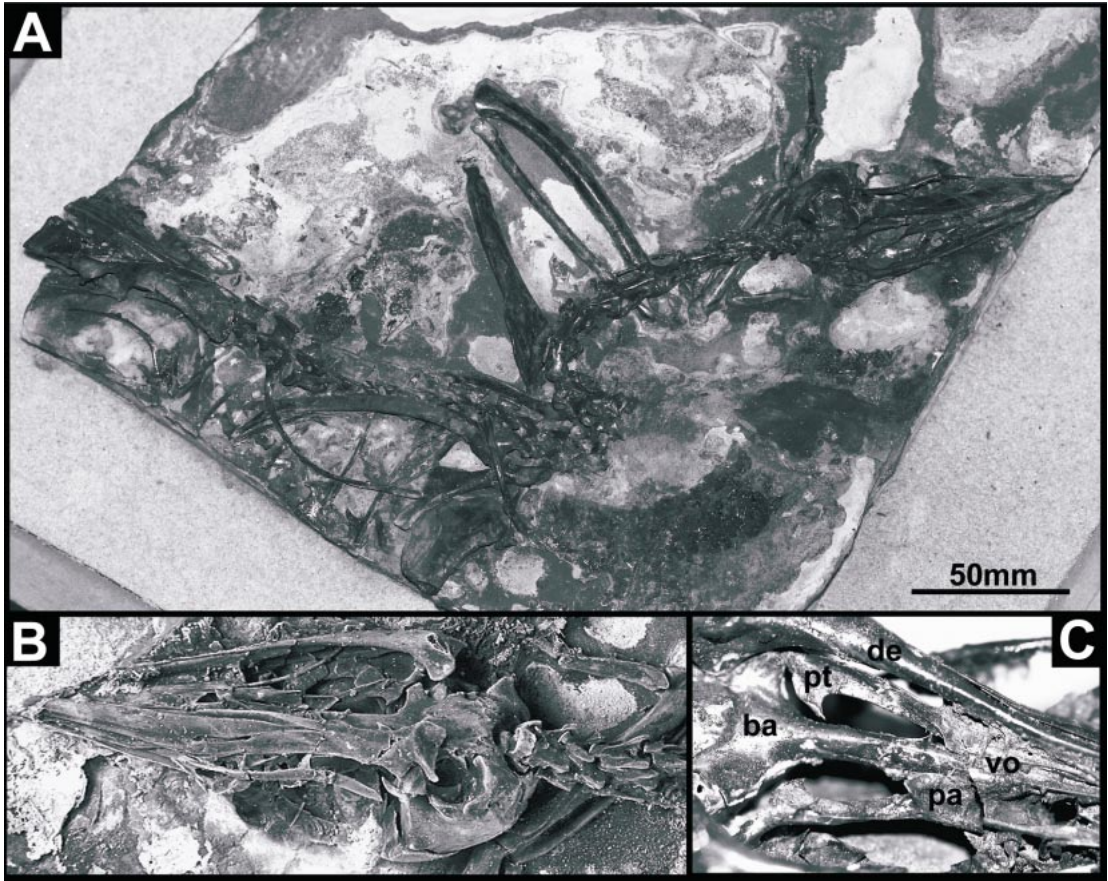
Fig. 2.   MGUH 26770, specimen referred to *Lithornis*. **A,** skull in articulation with complete post-cranial skeleton; **B,** skull preserved in oblique lateral view, exposing right side; **C,** palate of MGUH 26770 in ventral view. Anatomical abbreviations: **ba,** basitemporal plate; **de,** dentary; **pa,** palatine; **pt,** pterygoid; **vo,** vomer.

dius, ulna, carpometacarpus, and digits of the wing) (fig. 2A). The pelvis of MGUH 26770 is also present but is incomplete—just the synsacrum and seven ribs are visible and intact. Since the sternum, coracoids, and scapulae are also present and well preserved, MGUH 26770 can be referred with confidence to *Lithornis* (see above) and compared with older, previously published character codings for this taxon (Houde, 1988; Dyke, 2001, 2003).

SKULL

The skull of MGUH 26770 is preserved in oblique lateral view so that its entire right side is exposed (fig. 2B). In right ventral view, the paroccipital processes are poorly developed and flat, approaching, but not extending below, the ventral margin of the otic cavity. The basitemporal processes are rounded and raised medially, bearing distinct foraminae on their lateral sides. There do not appear to be any distinct and well-developed mammillar tuberosities on the basitemporal plate, as is the case in some other extant palaeognath taxa. Previous codings for these birds (Lee et al., 1997) indicate that such tuberosities either are absent or are poorly developed in the Tinamidae and other ratites, with the notable exception of the kiwi (*Apteryx*) and some moa (*Dinornis*; Worthy and Holdaway, 2002). The basipterygoid processes in MGUH 26770 are elongate and abut the caudal surface of the pterygoids, as

is the case in all living palaeognaths (Cracraft, 1974). There is no distinct neck to the occipital condyle in MGUH 26770; the entire occipital region of the skull is inclined caudally when viewed laterally (fig. 2). A number of distinct foramina are present underneath the lateral processes of the parasphenoid; the parasphenoid ala is not developed—a distinct notch is present between the lamina parasphenoidalis and the paroccipital process. Also in right lateral view, the temporal fossa can be seen to be well developed caudally but not deep. This fossa does not extend far over the back of the cranium, as is the case in several moa genera (Worthy and Holdaway, 2002). In MGUH 26770, the lamboidal and temporal ridges are widely separated (fig. 2B), and a prominent frontoparietal suture is present. The zygomatic process of the squamosal in this specimen is not markedly projected and does not approach the length of the otic process (fig. 2B).

The palate of MGUH 26770 is formed from the fusion of a large circular vomer and simple pterygoids and palatines (fig. 2C). This surface is typically palaeognathous in structure (Cracraft 1974; Houde, 1988)—a smooth flat surface of almost continuous bone. However, and unlike the condition seen in most other palaeognaths, the pterygoids of MGUH 26770 are clearly divided both rostrally and caudally (fig. 2C). In *Apteryx*, for example, typical of the extant condition, these bones are broad and ventrally concave (McDowell, 1948). Houde (1988) noted that lithornithids possess a number of "typical" palaeognathous characteristics seen in this region of the palate, including the bent hourglass shape of the pterygoids and a very extensive pterygoid-quadrate articulation. The caudal surfaces of the palatines in MGUH 26770 are rounded, divided, and hooked rostrally so that they articulate both laterally and dorsally with the pterygoids, similar to the condition seen in the kiwi *Apteryx* (previously referred to as saddle-shaped; Lee et al., 1997). Hence, and as previously reconstructed (Houde, 1986), there is a small "pterygoid fossa" on the medial surface of the rostral end of these bones.

The palatines of MGUH 26770 are elongate and concave in ventral view so that they overlap the vomer medially (and are contin-uous with the pterygoids, thus lacking any sutures; Houde, 1988; fig. 2C). The articulation of these elements with the maxilla is continuous (often referred to as the palaeognath maxillopalatines; Houde and Olson, 1981; Lee et al., 1997), and they are located in a much more lateral position in MGUH 26770 compared with Tinamidae and kiwis (McDowell, 1948). On the left medial side of the maxilla, a small concave depression can be seen formed between the rostral maxillopalatine and the caudal surface of the maxilla. In other palaeognaths, this has been referred to as the maxillopalatine antrum, or "pocket" (Lee et al., 1997). The left jugal of this specimen is broken and distorted so that it touches the medial side of the left maxillopalatine; this element is small, delicate, and rounded in cross-section (fig. 2C). Toward the tip of the skull, just as is the case in Tinamidae, the maxillary rostrum is formed as a flat sheet of bone that occupies about one third of the total skull length. Indeed, lithornithid bills described by Houde (1988) closely resemble those of Tinamidae. The structure of the bill in these birds is straight and quite fragile.

Both quadrates of MGUH 26770 are preserved articulated in their original positions. The medial surface is visible on the right quadrate (fig. 2B); the caudal surface is visible on the left. While the otic process is short and stocky (the articulating surface is not visible within its cotyla), the orbital process of MGUH 26770 is large, rounded, and blunt (this was described as reduced in *Paracathartes*, the other lithornithid genus for which the quadrate is known; Houde, 1988). Unlike in most neornithine birds (Mayr and Clarke, 2003), no pneumaticity is visible on the medial surface of this element. Palaeognathous non-pneumatic quadrates have also been described in *Apteryx* and *Paracathartes* (Houde, 1988). In MGUH 26770, the quadrate articulations are overlapped by an elongated lateral process of the mandible (fig. 2B).

VERTEBRAE

The atlas, axis, and 13 cervical vertebrae of MGUH 26770 are preserved in series, articulated proximally with the skull (fig. 2A).
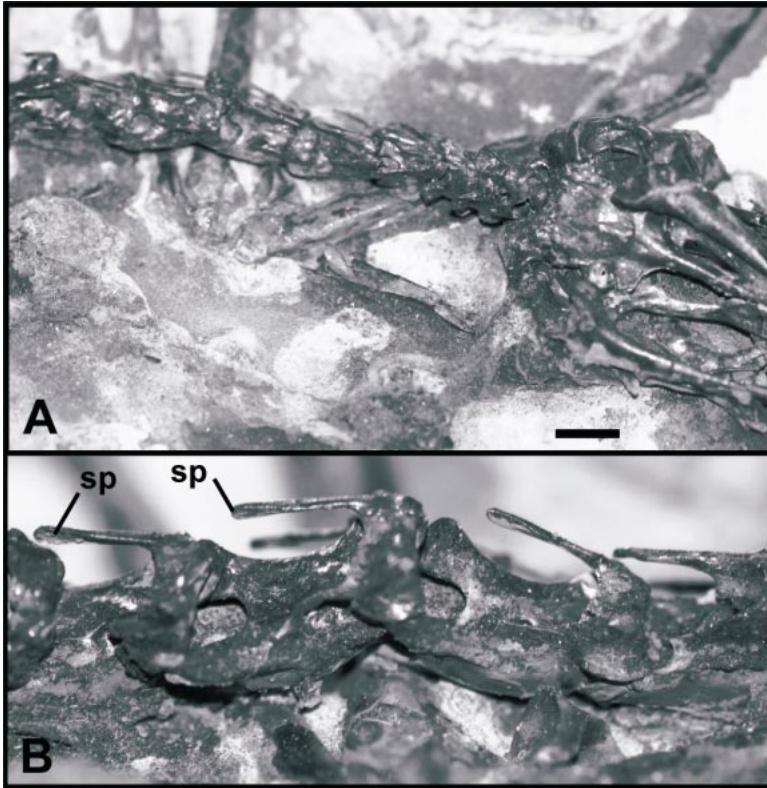
Fig. 3. MGUH 26770, close-up views of cervical vertebrae (**A, B**), lateral sides (**sp,** spinous processes). Scale bar is 10 mm.

The cervicals are articulated to one another on their ventral sides, with small spinous processes extending caudally and robust postzygopophyses on their dorsal sides (fig. 3). Although their number (13) is less than that reported for *Pseudocrypturus* (15 cervicals; Houde, 1988), in MGUH 26770 these elements are narrow-bodied with tall neural arches and wide diapophyses, resembling an intermediate state between tinamous and cassowaries.

Nine thoracic vertebrae are preserved in MGUH 26770 (again compared with the eight reported for *Pseudocrypturus*; Houde 1988). These elements are large and robust and have rectangular spinous processes on their dorsal sides. This number of vertebrae is similar to that seen in the Elephant Bird *Aepyornis*, which has eight free thoracic vertebrae. As previously reported for *Pseudocrypturus* (Houde 1988), each of these elements bears a large pneumatic foramen on

its lateral face, similar to those seen, for example, in the Late Cretaceous ornithurine bird *Ichthyornis* and in some basal Galliformes (Dyke and Gulas, 2002; Norell and Clarke, 2002). The articulating surfaces of the thoracic vertebrae are saddle-shaped and concave. Transverse processes project laterally that are prominent and club-shaped.

The obscured preservation of the caudal vertebrae in MGUH 26770 (fig. 1) makes description of these elements problematic. At least in number, however, they appear to be similar to the caudals of other extinct palaeognaths (usually seven or eight free caudals excluding the pygostyle).

FORELIMB

Both scapulae are present in MGUH 26770, but only the right element is entirely visible (figs. 1A, 4A). The left scapula remains buried; only its proximal end and a
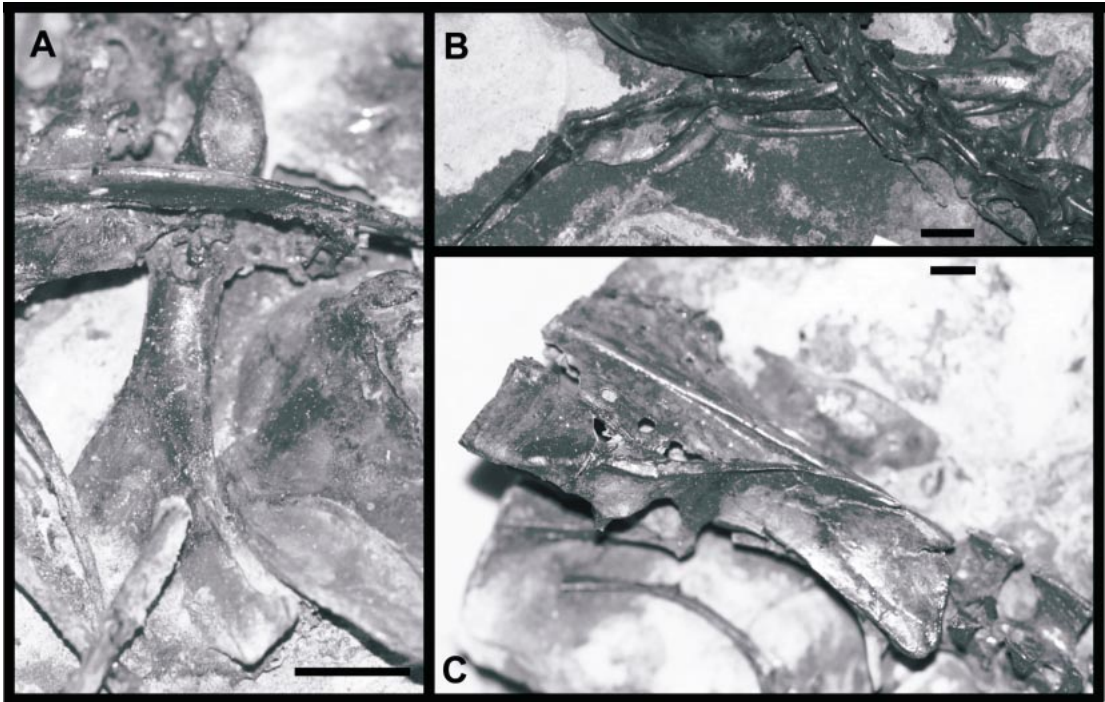
Fig. 4.   Some preserved postcranial elements of MGUH 26770. **A,** right coracoid in dorsal view; **B,** distal carpometacarpus and digit; **C,** pelvis in lateral view. Scale bars are 10 mm.

segment of its lateral side can be seen. However, the acromion of the right element is extremely prominent proximally, extending far beyond the coracoidal articulation on its medial side. Such a long, pointed acromion is a feature seen in all of the known lithornithids (Houde, 1988), as well as in the Cretaceous ornithurine *Ambiortus* (Kurochkin, 1999). The glenoid facet of the proximal scapula is turned medially where it articulates with the coracoid (itself relatively narrow in MGUH 26770 and separated from the acromion by a deep notch). The blade of this element is markedly curved along its entire length and tapers to a point proximally, similar to some of the larger specimens described by Houde (1988); curvature of the scapula is not seen in smaller Lithornithidae, which have long, straight, and narrow blades (e.g., *Lithornis celetius* [PU 23484, USNM 290554], *Lithornis promiscuus* [USNM 336535], *Lithornis plebius* [USNM 336534], *Paracathartes howardae* [USNM 361419].

Only the right coracoid is preserved in dorsal view in MGUH 26770 (fig. 4A). The proximal end of this bone has a marked ovoid depression, indicating a dorsally oriented glenoid facet, as well as pronounced extension of the coracoidal neck. Similar to the condition in MGUH 26770, the sternal facet of some specimens discussed by Houde (1988) are narrow dorsolaterally and wide mediolaterally, with the main body of the coracoid being narrow (e.g., *Lithornis celetius* [USNM 290554], *Lithornis plebius* [USNM 336534], *Lithornis promiscuus* [USNM 336535], *Paracathartes howardae* [USNM 361417]). The shaft of the coracoid in MGUH 26770 is quite slender compared with its caudal end, which articulates with the sternum (fig. 4A). The caudal half of this bone widens significantly and appears to be flattened dorsoventrally.

The length of the humerus in MGUH 26770 is approximately equal to that of the ulna. This element is flattened dorsoventrally and broadened proximally when compared with its distal end and shaft. On the palmar surface, the deltoid crest flares greatly on the lateral side of the proximal end. The humerus

is of uniform width along its entire shaft and terminates in an expansion on its distal end. Both external and internal condyles are pronounced and ovoid dorsolaterally and distally. Similarly, a small brachialis anticus depression is present directly above the external condyle.

The left radius of MGUH 26770 is slender and elongate, again approximately equal in length to the humerus, but only half its width. This differs slightly from the lithornithids described by Houde (1988): Most of the known radii of these birds are shorter than their corresponding humerus and are only marginally shorter than the ulna (e.g., *Lithornis vulturinus* [BMNH A 5204], *Lithornis promiscuus* [USNM 336535], *Lithornis plebius* [USNM 336534, AMNH 21902]). There is a slight distal expansion to this bone, terminating in a broad shallow groove. On the proximal end, where it articulates with the humerus, the tuberculum bicipitale is clearly developed as a protrusion on the lateral side of the radius (muscle scars extend along the main body of the shaft; Houde, 1988). The entire radius of MGUH 26770 curves slightly proximodistally but not to the same extent as do the humerus and ulna.

The ulna of MGUH 26770 is preserved in dorsal view. This element is longer than its articulating radius and has a curved shaft—its width remains uniform along its length—that widens only proximally and distally. This ulna is shorter than the humerus, also similar to other specimens described by Houde (1988) (e.g., *Lithornis promiscuus* [USNM 336535], *Lithornis plebius* [USNM 336534]).

The carpometacarpus of MGUH 26770 is exceptionally well preserved and displays several key features of the wing in this taxon. Metacarpal I is located on the proximal end on the lateral side of the bone; it articulates with digit I, which is slender and elongate. Metacarpal II, the minor metacarpal, is located laterally. This is a far more robust structure, and is wider and straighter, than the third metacarpal (fig. 4B). Digit II articulates with the digital facet of metacarpal II on the distal end of the carpometacarpus. This is raised medially into a rounded ridge running proximodistally and has an extension of this laterally, which is flattened dorsoventrally.

Metacarpal III is bowed, is quite slender compared with metacarpal II and is slightly curved. Digit III is shorter than the previous two but tapers to a point as in all of the digits.

PELVIS AND HIND LIMB

MGUH 26770 preserves an almost complete pelvis that includes the sacral vertebrae and synsacrum (although this is broken caudally) (fig. 4C). The preacetabular portion of the ilium is narrow dorsoventrally, narrowing to a pointed ridge along its dorsal surface, while the postacetabular portion is broad and flattens dorsoventrally toward its anterior end. An ilium of this shape is also seen in the extinct *Aepyornis* (Elephant Bird) as well as in some extant taxa such as the ostrich (*Struthio*) and rhea (*Rhea*). In ventral view, the ilium narrows dorsoventrally, but its height remains the same for most of the distance from the acetabulum to its anterior end. The ischium of MGUH 26770 is also present, possessing a slight upward curvature, but there is no distal expansion of the ischium, nor is there fusion of it to either the ilium or pubis. *Struthio* and *Rhea* all show similar states with regard to their ischia—a slight distal expansion but no fusion to the pubis and ilium (Lee et al., 1997)—but differ from *Apteryx*, which shows a distal broadening of the ischium and is fused to the pubis. Interestingly, Verheyen (1960) suggested that all ratites possess ischia that enlarge terminally and ankylose with the pubis, contrasting with the coding of Lee et al. (1997), who noted that this fusion is absent in both the ischium and the pubis.

Only the proximal end of the right femur is preserved in MGUH 26770. On its anterior end there is a prominent trochanteric ridge with an angular projection visible on its dorsolateral side. The femoral head is incomplete. As a result, it is not possible to distinguish the attachment site for the round ligament. As the proximal end of the femur grades into the shaft, it narrows slightly, as is the case in other palaeognaths (i.e., emu, rhea, ostrich). The iliac facet is also present and has a convex surface area, and there is no lip surrounding the facet.

DISCUSSION

Description of this new Danish *Lithornis* specimen is important with regard to the systematics of palaeognaths. Not only does articulation of the MGUH 26770 skull and postcranial skeleton confirm a number of aspects of the anatomy of these birds, but we will also be able to use this specimen to corroborate the early evolutionary history of modern paleognaths, particularly their historical biogeography: *Lithornis* and its kin were important constituents of Northern Hemisphere avifaunas in the earliest Tertiary. MGUH 26770 further demonstrates that a number of features of the palaeognathous palate evolved early within the group. Previous systematic treatments of these birds (Houde, 1988) suggest that the volant Lithornithidae should be considered basal among palaeognaths—intermediate between the extant tinamou, the ratites, and the kiwi. This implies a single loss of flight within the lineage. The antiquity of *Lithornis* is perhaps further corroborated by some other Cretaceous lithornithid-like fossils (Clarke and Chiappe, 2001), consistent with palaeognath origination prior to the Cretaceous–Tertiary boundary (van Tuinen et al., 1998; Cooper et al., 2001; Cracraft, 2001; Dyke, 2001) and with a monophyletic Paleognathae, Neognathae. and Galloanseres.

Description and analysis of the exceptionally well-preserved fossil birds from the Lower Eocene Fur Formation is an ongoing project. As has been discussed elsewhere (Kristoffersen, 2001), despite the marine despositional environment of this deposit, a large number of clades of neornithine (= modern) birds have been recognized and are undergoing description. For example, Kristoffersen (2001) recorded 29 individual bird specimens from this formation that may represent up to 14 of the traditional avian orders (Monroe and Sibley, 1993). In terms of broad diversity, and with respect to the groups thus far identified, the composition of birds known from the Fur Formation is extremely similar to other European deposits of Tertiary age—the London Clay Formation of England (Lower Eocene) and the Messel deposits in Germany (Middle Eocene), for example. Mounting evidence from the Lower Eocene of Denmark, combined with other Northern Hemisphere fossil material, suggests that avifaunas known from this time period were largely tropical in their composition. This may suggest that many groups (mousebirds [Coliidae], for example) currently restricted to the tropics are relics of clades that were widespread in the Eocene in areas that now form temperate zones of the Northern Hemisphere. Gradual global cooling throughout this period in Earth's history caused retraction of the global tropical zone toward the Equator and restricted some clades of birds to their present-day distributions. While it is likely that the bulk of the modern avian radiation occurred prior to the Lower Eocene (perhaps in the Cretaceous), much more well-preserved fossil information is required to firmly address this issue.

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