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New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds

Received: 11 June 2003 / Accepted: 5 November 2003 / Published online: 17 December 2003
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Abstract We report on a new Mesozoic bird, *Longirostravis hani*, from the Early Cretaceous Jehol Biota of northeastern China. The new taxon has a long, slender rostrum and mandible, and a small number of rostralmost teeth. Postcranial characters such as a furcular ramus wider ventrally than dorsally, a centrally concave proximal margin of the humeral head, and a minor metacarpal that projects distally more than the major metacarpal, support the placement of *Longirostravis* within euenantiornithine Enantiornithes, the most diverse clade of Mesozoic birds. The morphology of the skull, however, suggests that *Longirostravis* had a probing feeding behavior, a specialization previously unknown for Enantiornithes. Indeed, this discovery provides the first evidence in support of the existence of such a foraging behavior among basal lineages of Mesozoic birds.

Introduction

During the morphological and functional transformation from non-avian dinosaurs to birds, new evolutionary challenges were imposed on early avians. The evolution

of wings required novel feeding mechanisms without the involvement of forelimbs and the aerodynamic demands of flight made the development of a lightweight feeding apparatus essential. We report on the discovery of a new enantiornithine species from the Early Cretaceous of China, whose cranial morphology adds to the poorly known diversity of feeding specializations among early birds and suggests the existence of a foraging behavior previously unknown for any Mesozoic avian.

Systematic paleontology

- Aves Linnaeus 1758
- Enantiornithes Walker 1981
- Euenantiornithes Chiappe 2002
- *Longirostravis* gen. nov.
- *Longirostravis hani* sp. nov.

Etymology

Longirostravis from the Latin “*longirostravis*” meaning a bird with a long rostrum; *hani* is in honor of its discoverer, Mr. Han.

Holotype

IVPP V 11309 (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences), a quail-sized, nearly complete and articulated skeleton surrounded by much of its plumage (Fig. 1).

Locality and horizon

Yixian County, Liaoning Province, northeastern China. Middle to upper Yixian Formation, Early Cretaceous (~120 mya; see Swisher et al. 2002; Zhou et al. 2003).

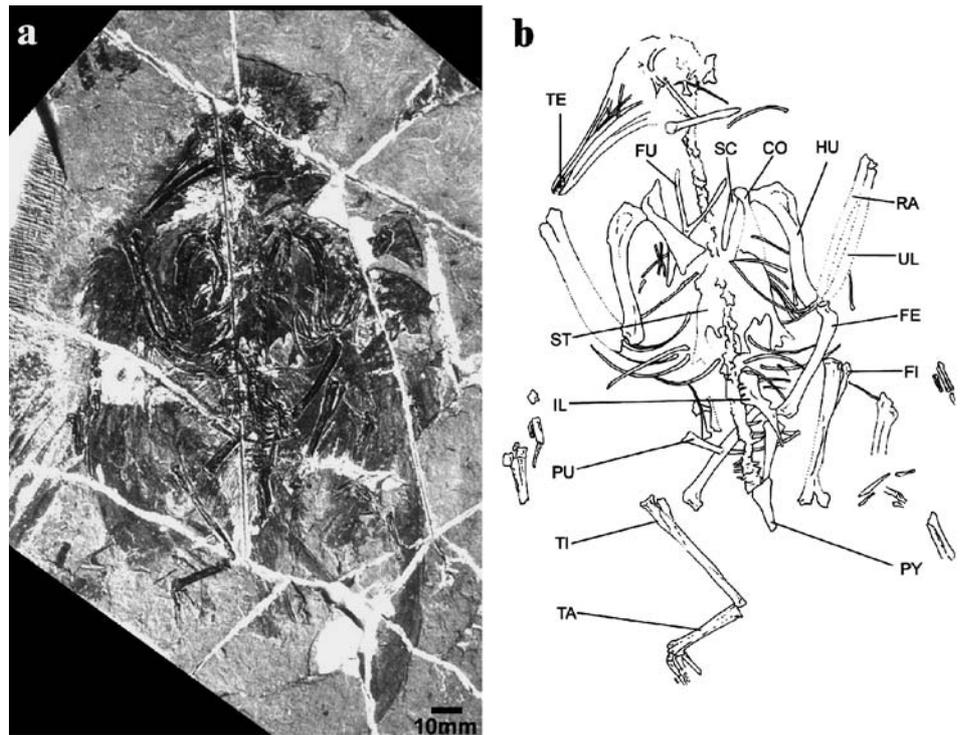
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Fig. 1 The skeleton of *Longirostravis hani* (IVPP V 11309). Abbreviations: *CO* coracoid, *FI* fibula, *FE* femur, *FU* furcula, *HU* humerus, *PU* pubis, *PY* pygostyle, *IL* ilium, *RA* radius, *SC* scapular, *ST* sternum, *TI* tibia, *TA* tarsometatarsus, *TE* teeth, *UL* ulna



Diagnosis

Small euenantiornithine bird with the following autapomorphies: long, tapering, and slightly curved rostrum and mandible; dentition restricted to cranial tip of rostrum and mandible; lateral process of sternum with three-branched, “moose-horn”-like distal expansion.

Description

The skeleton of *Longirostravis hani* is mostly exposed in dorsal view (Fig. 1; Table 1). Its most remarkable feature is the specialized nature of the skull, which has a long (35 mm) and tapering rostrum and mandible that gently curve downwards (Fig. 2A, B). Dentition is restricted to the tip of the skull, where ten small (~0.5 mm) and conical (~15°) teeth are arranged in pairs in the combined premaxillae and rostralmost portion of the dentaries. Caudally, the toothless maxilla extends for most of the length of the rostrum, whose dorsal margin is formed by the long dorsal processes of the premaxillae. The exact location of the external nares remains uncertain; nonetheless it is clear that they were retracted from the tip of the rostrum. Caudal to the dentigerous region, the lateral surface of the dentary and maxilla is pierced by a line of slit-like foramina, suggesting that these bones were covered by a rhamphotheca.

The anterior presacral vertebrae exhibit some degree of heterocoely. Seven fused vertebrae form a synsacrum that approaches the length of the ilium. Five free caudals precede a long and proximally forked pygostyle. The

Table 1 Selected measurements of *Longirostravis hani* (mm)

Selected measurements of <i>Longirostravis hani</i> (mm)	
Estimated skull length	36.0
Coracoid length (rt.)	14.0
Sternal end of coracoid width (rt.)	7.3
Scapular length (lf.)	19.2
Clavicular length (excluding hypocleideum) (lf.)	10.8
Sternal length	17.0
Sternal width (midpoint)	13.0
Humeral length (lf.)	24.0
Ulnar length (lf.)	25.5
Iliac length (rt.)	13.8
Femoral length (rt.)	20.0
Tibiotarsal length (rt.)	25.5
Tarsometatarsal length (lf.)	14.0

rt., based on right element; lf., based on left element

furcula bears a slender hypocleideum and an interclavicular angle of approximately 50°. The coracoid is strut-like and its lateral margin is slightly convex. The strong acromion of the scapula is wider costolaterally than dorsoventrally. The nearly quadrangular sternum has a parabolic cranial margin and a caudocentral portion projected into a distally expanded xiphoid process. Lateral sternal processes end in a unique three-branched, “moose-horn”-like expansion (Fig. 2C). Medial sternal processes are shorter and somewhat curved medially. A few gastral elements, laid in the typical zig-zag pattern, are preserved between the right lateral process of the sternum and the ilium.

The humerus is slightly shorter than the radius–ulna and the ratio of the shafts of the latter is approximately 1:2. The metacarpal proximal ends are fused to one

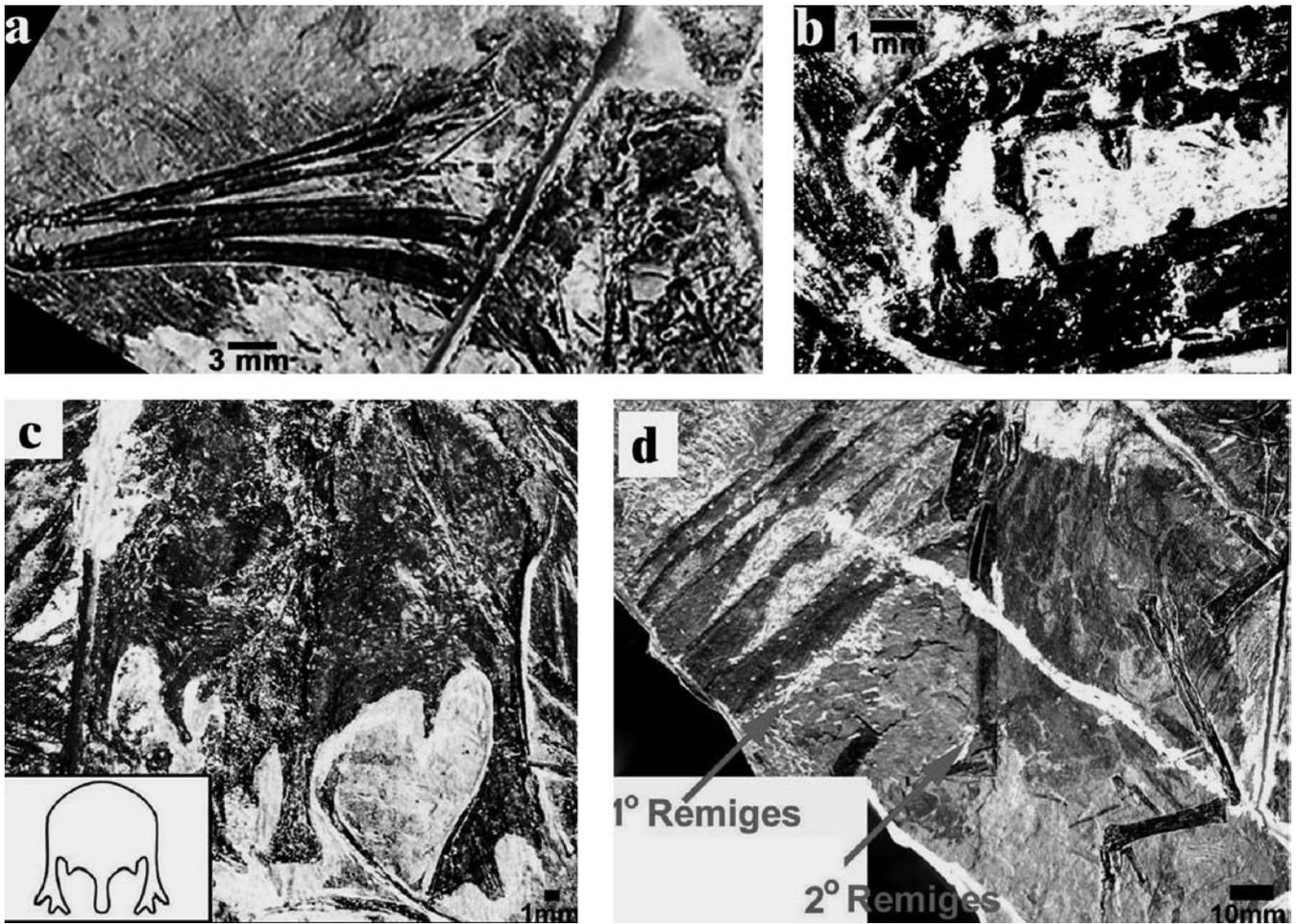


Fig. 2 Details of the skeleton of *Longirostravis hani* (IVPP V 11309): **a** skull, **b** tip of the rostrum, **c** sternum, **d** primary and secondary remiges

another and to the distal carpals, but their distal ends remain unfused. The alular metacarpal is short and semicircular. The minor metacarpal projects distally more than the major metacarpal. The ilium has a wide and cranially rounded preacetabular wing and a shorter and narrow postacetabular wing. The ischium bears a well-developed proximodorsal process. The femoral head is set on a distinct neck. The long tibiotarsus exhibits minimal development of a cnemial crest and bulbous distal condyles separated by a narrow intercondylar groove. The distal fibula extends only slightly beyond the tibia's fibular crest. The tarsometatarsus is slightly longer than half the length of the tibiotarsus. Metatarsals are fused to each other only proximally. In cranial view, metatarsal III is the widest and metatarsal IV the narrowest, although this is not as reduced as in some other enantiornithines.

Feathers, mostly preserved as carbonizations, surround the entire skeleton except for the rostrum and feet (Fig. 2D). They show regional specializations including down, covert, crown feathers as well as rectrices and primary and secondary remiges (Fig. 1A). Downy feathers around the trunk are about 5–7 mm in length. Branched barbs are best seen at the distal end of these

feathers, although no barbule structures can be differentiated. Remiges (~80 mm) are strongly asymmetrical—the medial vanes could be up to five times wider than the lateral vanes. A pair of central rectrices, similar to those of the enantiornithine *Protopteryx* (Zhang and Zhou 2000), appear to be present. These, however, are largely incomplete.

Phylogenetic position

A number of derived characters support the inclusion of *Longirostravis hani* within the euenantiornithine Enantiornithes, a clade of flying birds ubiquitous among terrestrial Cretaceous avifaunas (Chiappe and Walker 2002). Among the unambiguous synapomorphies supporting this hypothesis is the presence of a convex lateral margin of the coracoid (although in *Longirostravis* the condition is not as marked as in other euenantiornithines), a ventral margin of the furcula that is wider than its dorsal margin, a proximal margin of the humeral head that is concave in its central position, a minor metacarpal that projects distally more than the distal end of the major

metacarpal, and a very narrow and deep intercondylar sulcus of the tibiotarsus. Other derived characters shared between *Longirostravis* and euenantiornithines include the presence of a cranial fork on the pygostyle, a scapula with an acromion that is transversally wider than deep, a distinct distal expansion of the lateral process of the sternum, and a subcircular-shaped metacarpal I.

Foraging inferences

Feeding specializations are paramount throughout avian evolution (Zweers and Vanden Berge 1997; Zweers et al. 1997). Direct evidence of the diet of Mesozoic birds is limited to the presence of stomach contents indicating arthropod-based (Sanz et al. 1996), seed-based (Zhou and Zhang 2002), or fish-based diets (Zhou et al. 2002) and the possible existence of a sap-eater (Dalla Vecchia and Chiappe 2002). Inferences on the foraging habits of Mesozoic birds have also been made on the basis of the well-known correlation between the rostral morphology and the feeding behaviors of living birds (Gill 1994). The short, triangular skulls with small teeth typical of many Jurassic–Early Cretaceous birds have been assumed to indicate an insectivorous diet (Serenó and Rao 1992; Feduccia 1999; Elzanowski 2002).

We suggest that the long and slender bill of *Longirostravis* was probably best for probing in the mud. The length of the bill of *Longirostravis* falls within the range of those of extant charadriiforms, such as oystercatchers (Haematopodidae) and redshanks (Scolopacidae), whose diets are primarily based on worms, bivalves, and crustaceans (Gill 1994). The teeth in the rostralmost portion of the skull of *Longirostravis* may have facilitated securing the prey. The morphology of the bill of *Longirostravis* is unique among birds. An elongate rostrum is also known for the slightly younger Early Cretaceous enantiornithine *Longipteryx* (Zhang et al. 2001), also from northeastern China. Nonetheless, the rostrum of *Longipteryx* is proportionally much shorter and less slender than that of *Longirostravis*, and its teeth are substantially larger and more robust than those of the latter taxon. All this suggests that the skull of *Longipteryx* was probably better specialized for catching fish than for probing in soft substrates. The present discovery provides for a trophic design previously unknown for any lineage of basal, Mesozoic birds.

Acknowledgements This work was supported by grants from the NSP, Study of Jehol Biota (4982020) and the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China) to L.H. and F.Z., the National Institute of Health and the National Science Foundation to C.M.C., and the Eppley Foundation and the Discovery Channel to L.M.C. We thank Dr. Ping Wu and anonymous reviewers for comments on the manuscript, and Ms. Marijane Ramos and Ms. Fiona McCulloch for their help in preparing the manuscript.

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