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We report on a new species of basal ornithuromorph bird, *Piscivoravis lii* **gen.** et **sp. nov.**, based on a well-preserved and nearly complete specimen from the Lower Cretaceous Jiufotang Formation in western Liaoning Province, northeastern China. The new specimen preserves several unique anatomical features previously unreported in Early Cretaceous ornithuromorphs, such as a robust furcula with strongly tapered omal tips, a broad sternum without craniocaudal elongation and large and strongly curved manual unguals. Phylogenetic analysis indicates that *Piscivoravis* is more derived than *Archaeorynchus*, but in a basal polytomy with *Jianchangornis*, *Patagopteryx*, and the clade including all more derived ornithuromorphs. The preserved wing and tail feathers provide new information on feather diversity and evolution in Early Cretaceous ornithuromorphs. The preservation of fish bones ventral to the dentary and in the stomach provides direct evidence that the new species was piscivorous – previously only reported in *Yanornis*, and as in some living birds, was capable of moving food bidirectionally through the alimentary canal.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:92F23126-9E89-4E51-9700-C6608E0D66EB

Keywords: Early Cretaceous; Jiufotang Formation; Ornithuromorpha; diet; Xiaotaizi

Introduction

The Lower Cretaceous Jehol Group in northeastern China, consisting of the Dabeigou, Yixian and Jiufotang Formations, has yielded the world's greatest wealth of exceptionally well-preserved early birds, feathered dinosaurs, mammals, angiosperms and pterosaurs (Wang and Zhou 2003a). Over the past decade, more than 30 bird taxa have been reported from the Jehol Group – approximately one-third of the known global diversity of Mesozoic birds (Zhou and Wang 2010). These discoveries include the long-tailed jeholornithiform birds, the oldest known pygostylians Sapeornithiformes and Confuciusornithiformes and a huge diversity of the cosmopolitan enantiornithines and ornithuromorphs (Zhou et al. 2010). Ornithuromorpha, the clade that includes living birds, is the most derived group in the Lower Cretaceous (Zhou et al. 2009). The global record of basal ornithuromorphs during the Early Cretaceous is otherwise limited to isolated, fragmentary specimens, such as the holotype specimens of *Ambiortus dementjevi* (Kurochkin 1985) and *Enaliornis baretti* (Galton and Martin 2002), which provide limited anatomical information. Several well-preserved specimens of *Gansus yumenensis* have been collected from the Xiagou Formation in Gansu Province, western China; however, they are all incomplete and no skull material has been reported (Hou and Liu 1984; You et al. 2006). Benefiting from the sequence of alternating lacustrine and volcanic deposits, the well-preserved specimens from the Jehol Biota have greatly improved our knowledge of the early history and evolution of Ornithuromorpha (Wang and Zhou 2003b; O'Connor et al. 2010).

Here, we describe a new specimen (IVPP V 17078) preserving food remains recently collected from the Lower Cretaceous Jiufotang Formation near Xiaotaizi village, Jianchang, Liaoning Province. The new specimen preserves numerous characters that indicate it is an ornithuromorph bird (Figure 1), and several features suggest the new taxon is a basal member of this clade. The presence of several autapomorphies indicates the specimen represents a new taxon. We discuss the implications of this new species on our understanding of the early diversification of Ornithuromorpha with respect to character evolution and diet.

Institutional abbreviations

FRDC, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development, Lanzhou, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

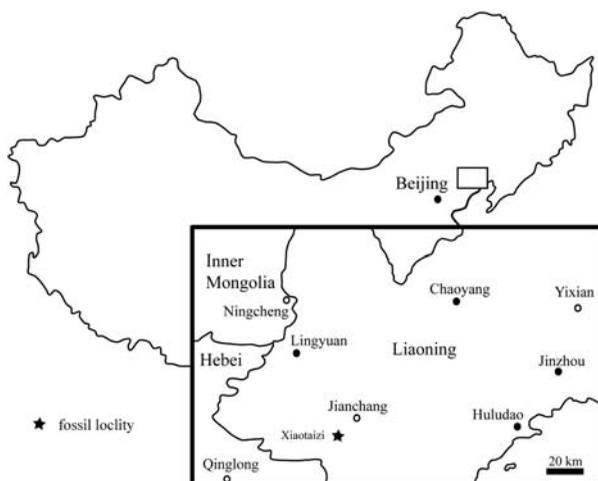*Corresponding author. Email: zhoushuang_ivpp@163.com

Figure 1.   Map showing the localities of *Piscivoravis lii* **gen.** et **sp. nov.** in Liaoning, northeast China. Scale bar equals 20 km. Modified from Zhou et al. (2013) (planned for single column width).

Systematic paleontology

Aves Linnaeus, 1758

Ornithuromorpha Chiappe, 2002

Ord. and Fam. Indet

Piscivoravis lii **gen.** et **sp. nov.**

Holotype

IVPP collection number V17078; a subadult individual represented by a nearly complete, articulated skeleton missing the cranium, preserving an organic outline of the body, food remains preserved in the abdominal area and ventral to the dentary and impressions of the wing and tail feathers (Figures 2, 3).

Figure 2.   Photo of the holotype of *Piscivoravis lii* **gen.** et **sp. nov.** (IVPP V 17078). Scale bar equals 1 cm (planned for double column width).
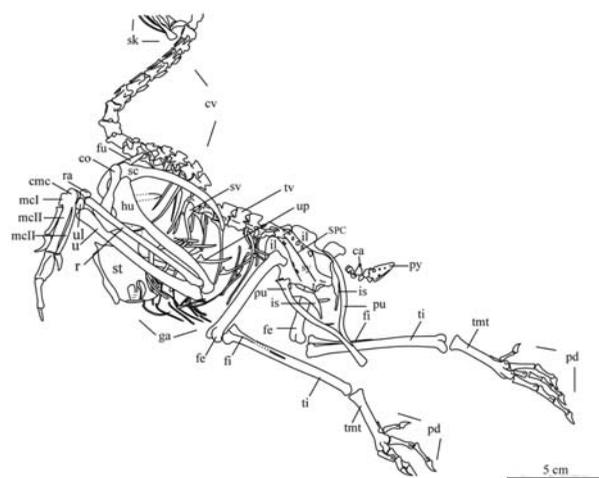

Figure 3.   Line drawing of the holotype of *Piscivoravis lii* **gen.** et **sp. nov.** (IVPP V 17078). Abbreviations: al, alula; ca, caudal vertebra; cmc, carpometacarpus; co, coracoid; cv, cervical vertebra; fe, femur; fi, fibula; fu, furcula; ga, gastralia; hu, humerus; il, ilium; is, ischium; md, manul digits; mcI, alular metacarpal; mcII, major metacarpal; mcIII, minor metacarpal; mt, metatarsus; pd, pedal digits; pm, primaries; pu, pubis; py, pygostyle; r, radius; ra, radiale; sc, scapula; se, semilunate carpal; sk, skull; spc, spinal crest; sr, sternal rib; st, sternum; sy, synsacrum; ti, tibia; tmt, tarsometatarsus; tr, thoracic rib; u, ulna; ul, ulnare. Scale bar equals 1 cm (planned for single column width).

Etymology

Piscivoravis, Latin for 'fish-eating bird', referring to the food remains associated with the specimen; the species name is dedicated to Mr Li Yutong (IVPP), who patiently prepared many important fossil birds and feathered dinosaurs.

Locality and horizon

Near the village Xiaotaizi, Liaoning Province; Jiufotang Formation. Lower Cretaceous, Aptian; approximately 120 Ma (He et al. 2004).

Diagnosis

A relatively large basal ornithuromorph bird, with an autapomorphic character: cranial 1/3–1/2 of pubis dorsomedially excavated by a deep groove; and has a unique combination of the following features: synsacrum with tall spinous crest that diminishes caudally; furcula with strongly tapered omal tips; sternum broad, width greater than length; scapula long, tapered and distally constricted; deltopectoral crest cranially deflected; large and strongly curved manual claws; intermembral index (humerus + ulna + major metacarpal/femur + tibiotarsus + metatarsal III) is approximately 1.14 (Table 1) and two well-developed cnemial crests on the proximal tibiotarsus.

Table 1. Measurements of some skeletal elements of *Piscivoravis lii* **gen.** et **sp. nov.** (IVPP V 17078).

Elements		Measurements (mm)
Scapula	L	61
Coracoid	L	35
Humerous	L	74
Ulna	L	77
Radius	L	75
Alular metacarpal	L	7
Alular metacarpal	W	3
Major metacarpal	L	34
Major metacarpal	W	4
Minor metacarpal	L	34
Minor metacarpal	W	2
Alular digit I	L	17
Alular digit II	L	10
Major digit I	L	15
Major digit II	L	15
Major digit III	L	6
Minor digit I	L	9
Pubis	L	63[a]
Pubic symphysis	L	14[a]
Femur	L	56
Fibular	L	33
Tibiotarsus	L	71
Tarsometatarsus	L	35
Metatarsal I	L	6
Pedal digit I-1	L	8
Pedal digit I-2	L	5
Pedal digit II-1	L	12
Pedal digit II-2	L	11
Pedal digit II-3	L	7
Pedal digit III-1	L	13
Pedal digit III-2	L	10
Pedal digit III-3	L	10
Pedal digit III-4	L	7
Pedal digit IV-1	L	10
Pedal digit IV-2	L	8
Pedal digit IV-3	L	6
Pedal digit IV-4	L	7
Pedal digit IV-5	L	6
Forelimb/Hindlimb		1.14

Abbreviations: L, length; W, width.
[a] Estimated value.

Description

Skull

Most of the skull is not preserved except for the caudal portions of the mandibular bones, which provide only limited information (Figure 4). The quadrate is in caudolateral view, in articulation with the lower jaw, thus obscuring some details of its morphology. The caudal margin is perforated by a foramen, just proximal to the mandibular articulation, interpreted as a pneumatopore, also documented in some enantiornithines (e.g. *Shenqiornis*, *Pengornis*) (O'Connor and Chiappe 2011). The elongate otic process is covered so it cannot be determined how many articular facets were present. The orbital process appears long and tapered, as in neornithines, but the rostral margin is unclear. Two
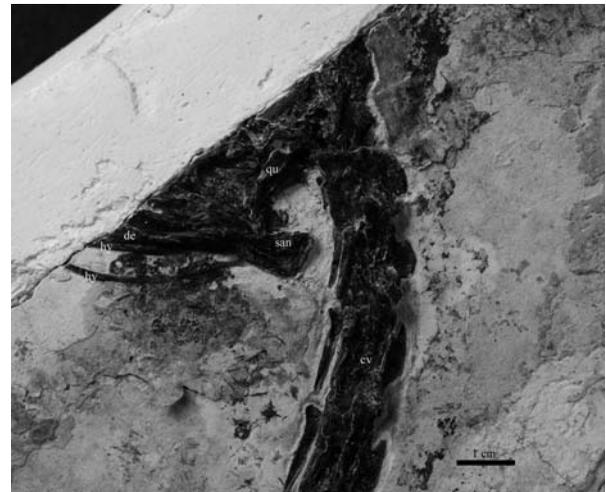

Figure 4. Photo of the skull of the holotype of *Piscivoravis lii* **gen.** et **sp. nov.** (IVPP V 17078). Abbreviations: an, angular; cv, cervical vertebra; de, dentary; hy, hyoid bone; qu, quadrate; san, surangular. Scale bar equals 1 cm (planned for single column width).

well-developed condyles are preserved at the mandibular articulation but due to abrasion it cannot be determined if a third condyle was also present. Only the distal ventrally tapering end of the dentary is preserved and it cannot be determined if a small dorsal wing was also present. Only the proximal ends of the surangular and articular are not preserved; these two bones are subequal. A small cotyla for the quadrate is present on the articular, near where the quadrate makes contact. A pair of slender and rod-shaped bones preserved ventral to the mandible are interpreted as hyoid bones.

Axial skeleton

The complete vertebral series is preserved in articulation with the exception of several proximal caudal vertebrae (Figures 2, 3). Twenty-two presacral vertebrae are present, the same as *Yixianornis* (Clarke et al. 2006). There are approximately 10 cervical vertebrae with well-developed costal processes. The atlas is broken; the axis preserves a prominent ventral process. The cranial cervical vertebrae are more elongate than the caudal ones, with the length approximately twice the width. The mid-series cervicals have short but robust prezygopophyses and short neural spines with concave cranial surfaces. No obvious epipophyses can be observed. Although the entire series is in articulation, the anterior vertebrae seem to be heterocoelous. The last cervical vertebra is much shorter, nearly equal in length and width, and preserves a well-developed ventral process.

The 12 thoracic vertebrae are all much shorter than the cervicals (slightly shorter than the last cervical), with broad fossae excavating their lateral surfaces as in other ornithuromorphs (Clarke et al. 2006). The second through

fourth vertebrae have prominent ventral process, not previously reported in any Early Cretaceous specimen. The parapophyses are located on the craniodorsal margin of the fossa (not centrally located as in enantiornithines). The thoracic centra are twice as long as they are wide, with flat amphyplatous articular surfaces.

The synsacrum is nearly fully fused and preserved in dorsal view with a prominent spinal crest that tapers to vanish distally (the preserved maximum height of the proximal end is about 3 mm). The exact number of sacrals is difficult to determine due to poor preservation of some of the transverse processes; we estimate 9–10 vertebrae that formed the synsacrum. The transverse processes of the sacrals are expanded and appear fused to the ilia. The caudal-most pair of processes is caudally directed.

Only three free caudal vertebrae are preserved, followed by a nearly completely co-ossified, roughly triangular pygostyle. A fourth caudal can be identified but appears to be fused to the pygostyle despite the presence of a well-developed transverse process, suggesting fusion was incomplete and that the specimen is a subadult. In the proximal free caudals, the transverse processes are equal to the centrum in length and appear to be laterally directed; in the last two caudals, the transverse processes are caudally directed. This process is longest in the fourth preserved caudal. Although the centra are fused, neural spines can be distinguished indicating at least four vertebrae that formed the pygostyle in this taxon.

Approximately 13 partial or complete delicate thoracic ribs are preserved roughly *in situ* (Figures 2, 3). Several gastralia are preserved. As in *Yixianornis*, the elongate, slender uncinate processes cross two ribs (Clarke et al. 2006). The proximal ends of these processes are expanded where they contact the ribs, similar to *Chaoyangia* (O'Connor and Zhou 2012), and were unfused with the ribs.

Pectoral girdle

Only the left side of the pectoral girdle is preserved (Figures 2, 3). The scapula is curved, tapered distally and nearly the same length as the humerus. Approximately 10% from the distal end the scapular blade constricts, as in *Yixianornis*. The coracoid is exposed in ventrolateral view; it is strut-like and elongate. The procoracoid process is not visible. The total omal-sternal length of the coracoid is approximately twice than that of the sternal margin, which is greater than that in *Yixianornis*, *Yanornis*, *Jianchangornis* and *Archaeorhynchus*, but nearly equal to *Hongshanornis* and *Longicrusavis*. The robust lateral process may have possessed a delicate omal projection like that in *Gansus* (the omal margin of the lateral process is concave), but it is obscured by overlap with the radius. The furcula is partially overlain by the coracoid and broken, obscuring its precise morphology. The bone is U-shaped, with a narrow
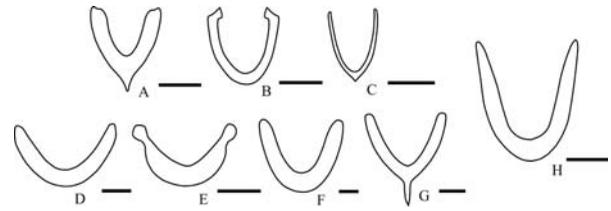

Figure 5.   Comparison of the furcula of Piscivoravis lii (H) and the other Early Cretaceous ornithuromorphs. A, Schizooura lii; B, Archaeorhynchus spathula; C, Hongshanornis longicresta; D, Archaeopteryx lithographica; E, Confuciusornis sanctus; F, Jeholornis prima; G, Pengornis houi. Scale bar equals 10 mm. Modified from Zhou et al. (2012) (planned for single column width).

interclavicular angle of approximately 60°, similar to other known ornithuromorphs (Figure 5). The clavicular rami are long and the omal tips are tapered strongly resembling *Yanornis*, not expanded into well-developed articular surfaces for the scapula as in *Archaeorhynchus*.

The sternum is exposed in ventral view with only the left side preserved (Figures 2, 3). Overall, the sternum is proportionately very wide, although it is possible that the rostral margin may be incomplete. A piece of bone overlain by the ulna may be the craniolateral corner of the sternum, which could also be the underlying right coracoid. The well-developed keel appears to extend the full length of the sternal body (caudally it is abraded); the apex projects cranially beyond the rostral margin. The sternum appears broader than other known ornithuromorphs; the estimated width is slightly greater than the preserved length. Caudally, the sternum bears a pair of incisures that extend for less than one-third the sternal length. The lateral trabeculae are short and robust, but extend beyond the caudal margin of the sternum; distally they end into a fan-shaped expansion. The intermediate trabecula is broken but it appears to be thin and medially curved, enclosing a large lachriform fenestra, similar to *Yixianornis*, *Yanornis*, *Songlingornis* and *Gansus*. The caudal margin of each half of the sternum is convex so that the midline bears a short cleft; potentially this is an ontogenetic artefact.

Forelimbs

Only the left wing is visible in the new specimen (Figures 2, 3). The humerus is preserved in caudodorsal view; a well-developed ventral tubercle is visible. The deltopectoral crest is broken making the exact shape hard to determine; however, it appears the crest was cranially deflected as in modern birds – this has not been previously reported in an Early Cretaceous bird. The crest extends for slightly less than one-third the length of the humerus. Distally, the humerus is abraded revealing no anatomical information. The left ulna is primarily in dorsal aspect; it is slightly longer than the radius, and both the

ulna and radius are longer than the humerus. The ulna is only slightly bowed near the proximal end; the olecranon is not developed. Both ends of the ulna are rather blunt, and slightly expanded relative to the midpoint of the shaft. The radius is straight and slightly expanded at the distal end. Well-developed intermuscular lines are visible on the ventral surface. The mid-shaft width of the radius is greater than half that of the ulna. The ulnare does not appear developed into distinct rami, although potentially one ramus is not in view.

The hand is in dorsal view. Proximally, the carpometacarpus is completely fused. The alular metacarpal is slender, approximately half the width of the major metacarpal, and an extensor process is absent. The major metacarpal is robust and straight; an intermetacarpal process is absent. The minor metacarpal is shorter than the major metacarpal, with lesser proximal extent, less than half of the major metacarpal width, and slightly curved near the proximal end. The major and minor metacarpals also appear fused distally enclosing a narrow intermetacarpal space. The first alular phalanx is long, more than twice as long as the alular metacarpal. The ungual phalanx is well developed, more than half the length of the first phalanx, and very curved compared to other known ornithuromorphs. Together, the digit extends beyond the distal margin of the major metacarpal, as in the hongshanornithids. The first phalanx of the major digit possesses a well-developed cranial pila and is dorsoventrally compressed and caudally expanded, as in other ornithuromorph birds; the second phalanx is of nearly equal length but is much more slender. The small ungual phalanx is preserved in cranial view. The first phalanx in the minor digit is approximately half the size of the second phalanx in the major digit and tapered to the distal end; the second phalanx is extremely reduced, as in other ornithothoracines.

Pelvic girdle

The pelvic girdle is dorsally preserved and fully articulated; although unclear in the preserved aspect, the pelvic bones appear well fused at the level of the acetabulum (Figures 2, 3). The preacetabular wing of the ilium is slightly broader than the postacetabular wing. The ventrolateral margin of the preacetabular ilium is rostrally convex but strongly concave proximal to the acetabulum. The pubic pedicel appears narrower than the ischiadic pedicel and a well-developed pectineal process is absent. The ischium is much shorter than the pubis with a short triangular dorsal process developed at approximately the midpoint of the bone, as in some other ornithuromorphs (e.g. *Yixianornis*). The ischium is broad proximally and sharply tapered along its distal half. The ventral margin is concave and the entire bone appears curved medially (medial surface also concave). The pubes are

robust, elongate and caudally directed; the proximal half appears to be excavated dorsomedially by a deep groove (autapomorphy) that may be exaggerated by preservation. The pubic symphysis is long, extending more than one-third of the total length of the pubis. The pubis is laterally very concave, as the two pubes approach each other and run parallel before they contact. The distal ends are only slightly expanded, lacking a prominent pubic foot and laterally compressed where they articulate. The pubes are preserved tightly ankylosed, but fusion remains incomplete.

Pelvic limb

The left femur is preserved in caudal view, whereas the right femur, overlain by the pelvic girdle, is preserved in craniomedial view (Figures 2, 3); a distinct femoral head separated by a slight neck is visible on both sides. The femur appears slightly bowed craniocaudally. It is slightly shorter than the tibiotarsus with a femur to tibiotarsus ratio of approximately 0.79. On the left femur, the distal condyles are abraded revealling no anatomical information; however, a faint caudal intermuscular line is visible along the caudomedial margin of the shaft proximal to the condyles. On the right side, a patellar groove is visible but may be exaggerated by preservation.

The tibiotarsus is completely fused and is more than twice the length of the tarsometatarsus. Two cnemial crests are present; the cranial crest has a greater proximodistal length, but the lateral crest projects slightly further proximally, beyond the proximal articular surface of the tibiotarsus, while in most other ornithuromorphs (e.g. *Chaoyangia*, *Gansus*, *Yanornis*, *Yixianornis*) the cnemial crests that can be observed always project cranially but not proximally. The fibular crest, visible on the left side, is poorly preserved but appears to have extended for less than one-quarter the length of the bone. On the proximocaudal surface, the lateral articular surface appears to be developed as a slight caudal projection defining a primitive flexor fossa. The distal ends of both tibiotarsi reveal no information, although the distal articular surface appears to be mediolaterally expanded (right tibiotarsus). The fibula is just over half the length of the tibiotarsus. Its proximal end is fat and robust, but it tapers quickly, and the distal half is thin and delicate. The left tarsometatarsus is preserved in plantar view, whereas the right is in dorsal view. The relatively short tarsometatarsus is well fused, as in other ornithuromorphs. Proximally the third metatarsal is plantarly displaced with respect to metatarsals II and IV, as in other ornithuromorphs (e.g. *Yanornis*, *Yixianornis*). The cranial surface of metatarsal II is strongly convex along its proximal third. A well-developed tubercle for the attachment of the m. tibialis cranialis muscle is not preserved; however, a difference in texture on the lateral surface of metatarsal II

where it contacts the medial surface of metatarsal III may represent this insertion point. A proximal vascular foramen perforates the tarsometatarsus between metatarsals III and IV. In plantar view, the region of the hypotarsus has been abraded revealling no information. The plantar surface of the tarsometatarsus is excavated, enclosed by the medial and lateral plantar crests most developed at the midpoint of metatarsals II and IV, respectively. Metatarsal V is absent. Metatarsal III is the longest; metatarsal IV extends to the proximal margin of the metatarsal III trochlea and metatarsal II is slightly shorter. The distal trochleae of metatarsals II and III are roughly subequal in width and wider than that of metatarsal IV; all three trochlea appear ginglymous (lateral condyle abraded in metatarsal IV). Similar to *Gansus* but to a lesser degree, the trochlea are not arranged in the same plane: metatarsal IV is plantarly displaced, as is metatarsal II but to a lesser degree. The distal margin of metatarsal II is angled proximomedially and laterodistally; this also appears present in metatarsal III. A dorsal trochlear depression is present on metatarsal II only. The first metatarsal is small, compressed laterally, and tapers proximally with the expanded distal end. It is placed fairly high on the metatarsus, not reaching the proximal margin of the metatarsal II trochlea. A distal vascular foramen perforates the tarsometatarsus between metatarsals III and IV; on the cranial surface it lies in a groove defined by metatarsals III and IV that extend the entire length of the bone.

The pedal digits are long and robust, with a pedal phalangeal formula of $2-3-4-5-x$; the phalanges have well-formed distal ginglymous trochleae and distinct pits for the attachment of the collateral ligaments. The proximal phalanges are longer than the distal ones, and the unguals are subequal in size, short and not strongly curved, as in other Early Cretaceous ornithurmorphs. The most slender phalanx and the shortest claw in the foot belong to the hallux. The second digit is shorter than the fourth digit and has the largest claw in the foot. The third digit is the longest and most robust in the foot; the first phalanx of this digit is the largest in the foot. The fourth digit ends in a small claw, approximately equal to that of digit III. All the pedal unguals are smaller and less curved than that of the alular digit.

Integument

The holotype of Piscivoravis possesses extensive feather impressions, preserved as carbonised traces or imprints (Figure 2). Carbonised feather impressions are preserved along the dorsal and ventral surfaces of the body. The feathers are assumed to be in a natural articulation and reach the bones (Hone et al. 2010). The wing feathers (remiges) are preserved as impressions. There are at least five elongate primary feathers preserved with the left

wing; they are long and asymmetric. Several feathers appear to attach to the alular phalanx, interpreted as an alula or bastard wing. The tail feathers in the holotype are similar to those preserved in other ornithuromorphs (e.g. *Yixianornis*, *Hongshanornis*, *Archaeorhynchus*): they are long, approximately equal to body length (measured as the distance from the sternum to the pygostyle), and appear to form a large, graded fan. The distal ends of the feathers are preserved as carbonised remains and indicate at least six elongate tail feathers were present. Linear impressions of the individual feather barbs can be recognised.

Food remains

The new specimen preserves the macerated remains of fish in two places of the body (Figure 2). A small cluster of fish bones is present near the dentary; approximately four to five vertebrae and a few ribs are visible (Figure 4). The fish bones are not in articulation but form an oval cluster measuring 13 mm by 8 mm. A much larger cluster of fish bones is located in the abdomen, laterally overlain by the thoracic ribs and uncinate processes; some fin rays and some larger fragments can also be recognised (Figure 6). The fish bones have tentatively been identified as belonging to a primitive teleost fish.

Discussion

Phylogenetic analysis

A phylogenetic analysis was conducted basing on the Zhou and Zhang (2008) data matrix, adding some new taxa (*Jianchangornis*, *Schizooura*, *Zhongjianornis* and *Piscivoravis*). The clade Dromaeosauridae was scored as the outgroup. A total of 205 characters (195 parsimony-informative, 40 ordered and all equally weighted) were evaluated for 33 taxa, conducting a heuristic search using Paup 4.0 (Swofford 2003). The analysis produced six most parsimonious trees (MPTs) of equal length (length = 571 steps). The results support our interpretations that *Piscivoravis lii* is a basal ornithuromorph; however, its position varies in the six MPTs with respect to *Jianchangornis* and *Patagopteryx*. This may be due to the lack of cranial material in the *Piscivoravis* holotype. The relative placement of *Cathayornis yandica* and *Concornis lacustris* within Enantiornithes also varied in the MPTs. Here we present the strict consensus of the six MPTs (Figure 7).

Piscivoravis shares with other ornithuromorphs a very short, plough-shaped pygostyle (ch 69. 0); a synsacrum composed of more than eight vertebrae (ch 62. 3/4); a keel extending along the full length of the sternum (ch 73. 1); fused manus with a robust, craniocaudally expanded first phalanx in the major digit and reduced minor digit (ch 152. 2); two large cnemial crests on the tibiotarsus
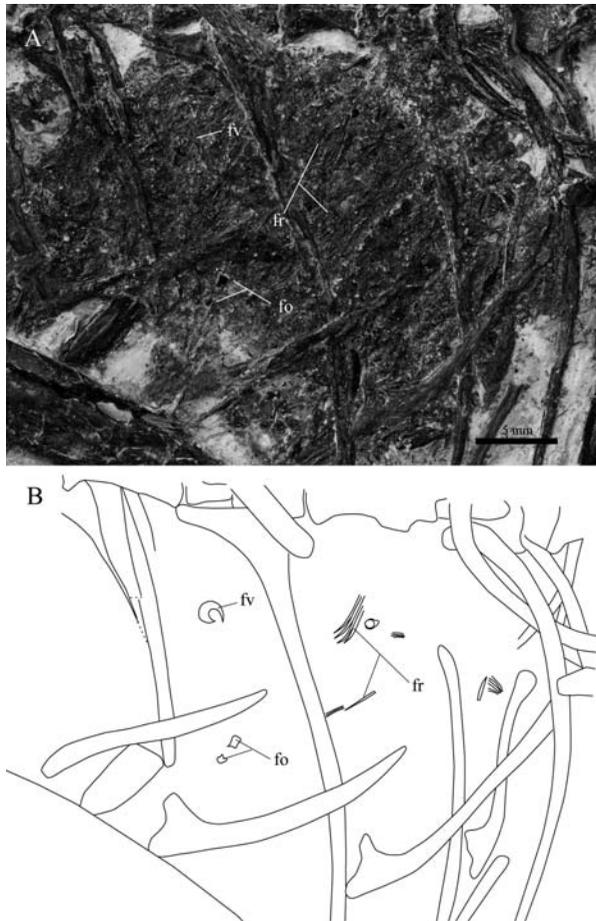
Figure 6. Detail photograph (A) and line drawing (B) of the food remains preserved in the abdominal cavity of *Piscivoravis lii* **gen.** et **sp. nov.** IVPP V17078. Abbreviations: fv, fish vertebra; fr, fin rays; fo, fish opercular fragments. Scale bar equals 5 mm (planned for single column width).

(ch 181. 1) and a well-fused tarsometatarsus (ch 191. 2). The autapomorphic feature and the unique morphological combination preserved in *Piscivoravis* reveal new information regarding the morphology of basal ornithurines.

Piscivoravis is comparable to *Jianchangornis*, *Schizooura* and *Yanornis* in body size, but larger than *Yixianornis*, the hongshanornithids and *Archaeorhynchus*. The length ratio of the forelimb to the hindlimb is approximately 1.14 (Table 1), which is similar to *Yanornis* (1.12) and *Jianchangornis* (1.1), but greater than that of *Yixianornis* (0.98), *Schizooura* (1.01) and the hongshanornithids (*Hongshanornis*: 0.79; *Parahongshanornis*: 0.63; *Longicrusavis*: 0.85). *Piscivoravis* is most similar to *Yanornis* but differs in that it has a proportionately longer femur relative to the tibiotarsus (*Piscivoravis*: 0.79; *Yanornis*: 0.67).

With the exception of the most basal taxa (e.g. *Archaeorhynchus*), the ornithuromorph sternum shares at least one common feature: the imperforate region is
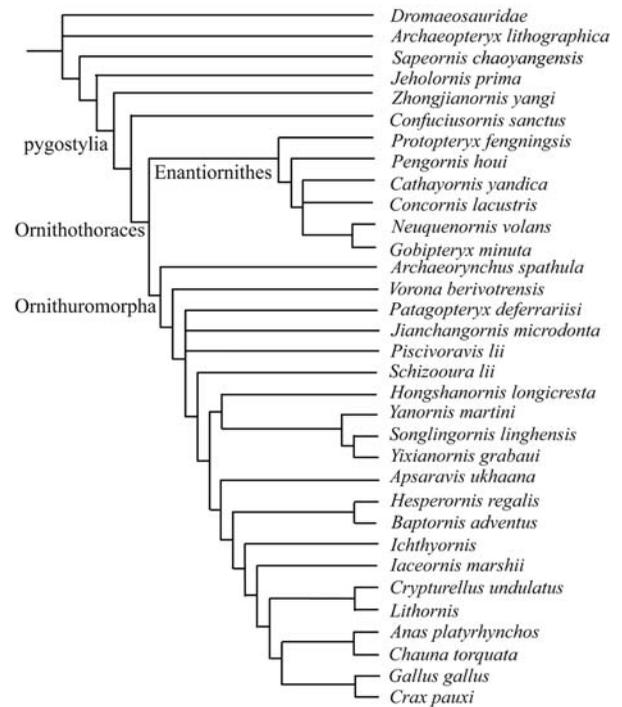

Figure 7. Strict consensus cladogram of the six MPTs (length 571) illustrating the hypothetical phylogenetic position of *Piscivoravis lii* **gen.** et **sp. nov.** CI: 0.4694, RI: 0.7432 (planned for single column width).

craniocaudally elongate (e.g. *Songlingornis* [Hou 1997]; *Yanornis*, *Yixianornis* [Zhou and Zhang 2001; Clarke et al. 2006]; *Jianchangornis* [Zhou et al. 2009]; hongshanornithids [Zhou and Zhang 2005; O'Connor et al. 2010; Li et al. 2011]; *Schizooura* [Zhou et al. 2012]) (Figure 8). Although the sternum in *Piscivoravis* is not entirely clear, it appears more quadrangular than in other taxa. New

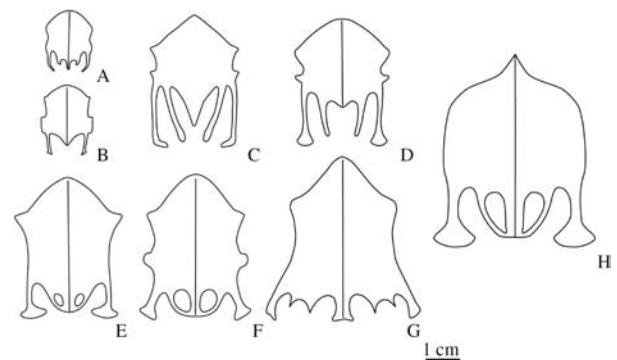

Figure 8. Comparison of the sternum of Early Cretaceous ornithuromorphs. A, Hongshanornis longicresta; B, Longicrusavis houi; C, FRDC − 05 − CM − 02; D, Archaeorhynchus spathula; E, Yixianornis grabaui; F, Yanornis martini; G, Jianchangornis microdonta; H, Piscivoravis lii. Modified from Zhou et al. (2013). Scale bar equals 1 cm (planned for single column width).

specimens of *Archaeorhynchus* reveal that in this basal taxon the length of the sternum was slightly shorter than the width (Zhou et al. 2013). Both taxa, like most ornithothoracines, preserve two pairs of equal length caudal trabeculae, the lateral pair with fan-like distal expansions. However, like enantiornithines, in *Archaeorhynchus*, the imperforate region of the sternum is short and the intermediate trabeculae are free (also as in hongshanornithids). The intermediate trabeculae in *Piscivoravis* contact the xiphial region, as in *Yixianornis*, *Yanornis*, *Gansus* and *Songlingornis*, distally enclosing a pair of fenestrae, and the lateral trabeculae extend caudally beyond the level of the xiphial region (Figure 8). Sterna with short bodies and long trabeculae bordering deep incisures (closed *in vivo* by fibrous membranes) convergently occur in the terrestrial, largely cursorial galliforms (You et al. 2010). Although in *Piscivoravis*, the trabeculae are not long and border only shallow incisures, the relatively extreme breadth of the sternum compared to other Early Cretaceous ornithuromorphs may hint at more limited flight capabilities.

Relative to other ornithuromorphs, *Piscivoravis* has comparatively more primitive hand with both the alular digit and the major digit having well-developed unguals. The alular ungual is large, more than half the length of the first phalanx, and strongly curved, having a needle-like point. The morphology of the major digit ungual is unclear but it appears only slightly smaller than that of the alular digit. In most ornithuromorphs, the manual claws are small and weakly curved. Furthermore, the digit is fairly long, comparable only to hongshanornithids within Ornithuromorpha. The morphology of the manus in *Piscivoravis* is much more similar to the basal pygostylian *Sapeornis* (Figure 9). Despite the primitive appearance of the hand due to the well-developed claws, the first phalanx of the major digit is specialised for flight (expanded caudally and dorsoventrally compressed), a feature restricted to Ornithuromorpha.

Integument

The alula is an essential structure in modern birds for low-speed flight and maneuverability (Zhang and Zhou 2000). An 'alula' (also called bastard wing, spurious wing; is the group of three to six small, rather stiff feathers growing on the first digit, pollex or thumb of a bird's wing) has been reported in several enantiornithines: *Eoalulavis* and *Eoenantiornis* both preserve an alula with a reduced alular digit; *Protopteryx* preserves an alula with an unreduced alular digit, although the claw is relatively small (Zhang and Zhou 2000). Within Ornithuromorpha, an alula has only been clearly identified in *Archaeorhynchus* and *Piscivoravis*, despite the remarkably unreduced alular digit and well-developed claw in the latter (Figure 2). This
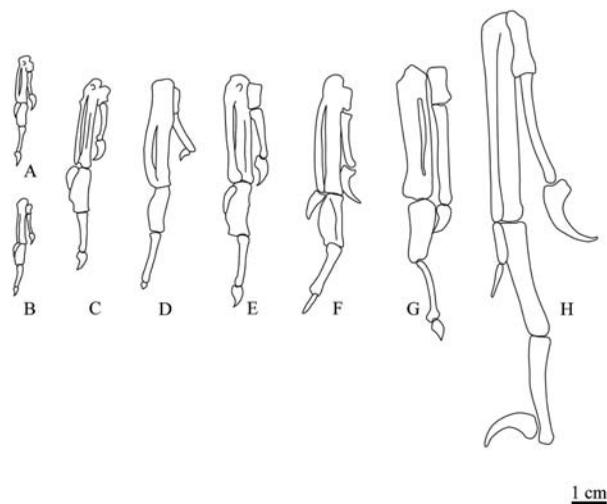

Figure 9.   Comparison of the manus of Piscivoravis lii (F) with the other Early Cretaceous ornithuromorphs and Sapeornis chaoyangensis. A, Longicrusavis houi; B, Hongshanornis longicresta; C, Yanornis martini; D, Schizooura lii; E, Yixianornis grabaui; G, Jianchang microdonta; H, Sapeornis chaoyangensis [modified from Zhou and Zhang (2003) and O'Connor et al. (2010)]. Scale bar equals 1 cm (planned for single column width).

discovery supports the argument that the alula appeared before the reduction of the alular digit in Ornithuromorpha, and suggests the feature is plesiomorphic to Ornithothoraces, as indicated by its presence in *Protopteryx* and in other enantiornithines (O'Connor 2009).

Tail impressions are rarely preserved among ornithuromorphs relative to the diversity of feather patterns recognised for Enantiornithes (O'Connor et al. 2009). Only two tail shapes have been reported among ornithuromorphs. *Yixianornis* and *Hongshanornis* both preserved large, elongate, graded, fan-shaped tails (Clarke et al. 2006; O'Connor et al. 2010). A minimum of eight long rectrices are preserved in the holotype of *Yixianornis*, with lengths ranging from 7.2 to 9.5 cm, whereas in *Hongshanornis*, there are at least four feathers, approximately 5 cm in length, preserved distal to the pygostyle (Clarke et al. 2006; O'Connor et al. 2010). Another basal ornithuromorph, *Schizooura*, preserves a forked tail composed of elongate rectrices medially separated by a deep notch (Zhou et al. 2012). The holotype of *Piscivoravis* also preserves a fan of caudal rectrices associated with the plough-shaped pygostyle (Figure 10). The exact number of feathers forming the tail is unclear due to overlap; however, we estimate a minimum of six feathers were present. The rectrices are broad and rounded at their distal ends. The central two feathers are slightly longer than the feathers on either side, suggesting the feathers were graded to form a fan-shaped tail. The overlap between the feathers indicates they would have formed a cohesive aerodynamic surface. The absence of diversity

Figure 10. Photo of the tail feather of the holotype of *Piscivoravis lii* (IVPP V 17078). Scale bar equals 1 cm (planned for single column width).

among ornithurine rectricial patterns, together with the morphological disparity between ornithothoracine pygostyles (large and robust pygostyle in Enantiornithes), and the derived phylogenetic position of *Shanweiniao*, the only enantiornithine that potentially preserves an aerodynamic rectricial pattern (O'Connor et al. 2009), suggest that the fan-shaped tail morphology evolved independently within each clade and support the hypothesis that the rectricial bulb may have co-evolved with the osteologically modern pygostyle within the ornithuromorph clade (*Yixianornis* [Clarke et al. 2006]; *Hongshanornis* [O'Connor et al. 2010]). Based on the previous research done by Thomas, the lift generated by the tail is proportional to the square of its maximum continuous span. Lift is unaffected by substantial variations in tail shape provided that the tail initially expands in width along the direction of flow. Behind the point of maximum width of the tail, the flow is dominated by the wake of the forward section. Any area behind this point therefore causes only drag, not lift (Thomas 1997). In other words, large fan-shaped tails were only aerodynamically beneficial when advanced musculature was in place to manipulate the shape of the fan during flight. This is supported by aerodynamics studies that for optimal high-speed flight, a tail is not necessary; if the fan cannot be folded during rapid flight, it would induce too much drag to be beneficial for flight (Thomas 1997).

Ecology
The Jehol Group not only represents a taphonomic window into early bird anatomy but also reveals the aspects of their biology, especially regarding dietary adaptations (Zhou et al. 2004; Zheng et al. 2011). A large number of specimens preserve the evidence of diet, especially common within Ornithuromorpha (O'Connor 2009; O'Connor et al. 2013). The direct evidence of diet, stomach contents, is reported in several taxa: seeds have been reported in the basal avian *Jeholornis* (Zhou and Zhang 2002), the ornithuromorph

Hongshanornis and the basal pygostylian *Sapeornis* (Zheng et al. 2011). Seed masses have also been reported preserved in the crop of specimens of the latter two taxa, strongly suggesting these species were seed-eating birds (Zheng et al. 2011). This is consistent with the robust morphology of the rostrum in *Sapeornis*. True gizzard stone geo-gastroliths have been reported in *Sapeornis* (Zhou and Zhang 2003), *Archaeorhynchus* (Zhou and Zhang 2006) and *Yanornis* (Zhou et al. 2004). However, another specimen of *Yanornis*, rather than preserving gastroliths, preserves the macerated remains of fish in its abdomen (Zhou et al. 2002). Although small amounts of sediment may get into the gizzards of living birds by accidental ingestion or intake within prey, these interpretations are inconsistent with the large quantity of evenly sized preserved stones. A large number of stones of equal size and suitable lithology in the gizzard is indicative of grinding gizzard adapted for an herbivorous diet (Zhou et al. 2004). Considering the morphology of the teeth of *Yanornis* (large, recurved and laterally compressed), the distribution of gastroliths and macerated fish remains among *Yanornis* specimens is interpreted as evidence for intermittent changes in diet, from the one high in non-digestible fibre, such as seed eating, to a fish-based diet (Zhou et al. 2004). Two Jehol ornithuromorphs are known to have fed on fish. With only a single specimen of *Piscivoravis* available, we are unable to determine if similar seasonal changes in diet occurred in this taxon.

One of the most notable aspects of the holotype of *Piscivoravis* is the preservation of food remains in two places. One small cluster of bones is preserved ventral to the dentary, which is considered too rostrally located to be in the crop (Figure 4). One specimen of *Confuciusornis* preserves a similar cluster of fish bones underlying the ventral region of the seventh and eighth cervical vertebrae, interpreted as a pellet about to be regurgitated (Dalsätt et al. 2005). The fragmentary nature of the fish bones in *Piscivoravis* resembles that of *Confuciusornis*, except they are more scattered. Though this cluster of bones seems to referable to a single species (a kind of teleost), the state of preservation of the remains and their location suggest that this cluster may have been a pellet that had already been regurgitated. Although there is considerable direct evidence of diet preserved among Jehol ornithuromorphs (e.g. *Yanornis*, *Hongshangornis*, *Archaeorhynchus*), this is the first observation of a pellet. A pellet, in ornithology, is the mass of undigested parts remaining from a meal that some bird species occasionally regurgitate, especially birds of prey (e.g. Hawk, owl) (Zheng 1995). The passing of pellets allows a bird to remove indigestible material from its proventriculus, the glandular stomach. In the Neornithes, the regurgitated items may help to lighten body weight for flight (Zheng 1995).

A second larger aggregate of macerated fish remains is preserved in the abdomen, where some fin rays and some

bigger fragments can be recognised (Figure 6). The fish bones are tentatively identified as belong to a primitive teleost.

After *Yanornis*, this is only the second direct documentation of an ornithuromorph bird eating fish. The cranium is missing and there are no teeth preserved in the new specimen so the presence of dental or rostral specialisations cannot be used to confirm dietary inferences in the new taxon. Similar to other Early Cretaceous Jehol ornithuromorphs, several morphologies suggest that *Piscivoravis* had a predominantly terrestrial ecology: metatarsal III longest; and its distally trochlea in a single plane with II and IV; proximal pedal phalanges longer than the distal ones and pedal unguals weakly curved (Hopson 2001). We propose that *Piscivoravis* may have lived in a terrestrial, near lakeshore environment and primarily fed on fish.

Acknowledgements

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