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Shuang Zhou [a] [b] , Zhonghe Zhou [a] & Jingmai K. O'Connor [a]

[a] Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, People's Republic of China

[b] Graduate University of Chinese Academy of Sciences, Beijing, 100049, People's Republic of China

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ARTICLE

ANATOMY OF THE BASAL ORNITHUROMORPH BIRD *ARCHAEORHYNCHUS SPATHULA* FROM THE EARLY CRETACEOUS OF LIAONING, CHINA

SHUANG ZHOU,*[1,2] ZHONGHE ZHOU,[1] and JINGMAI K. O'CONNOR[1]
[1]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China, zhoushuang_ivpp@163.com; zhouzhonghe@ivpp.ac.cn; jingmai@usc.edu;
[2]Graduate University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

ABSTRACT—As one of the earliest-known beaked ornithuromorph birds, *Archaeorhynchus spathula* is important for understanding the early evolution of this derived avian clade. Recently, two new complete and articulated specimens of *Archaeohyrnchus spathula* were collected from Lower Cretaceous deposits of Jianchang, Liaoning, northeastern China. These specimens preserve new anatomical information, particularly in regards to the morphology of the skull (including the inner structure of the occiput), forelimbs, hind limbs, and sternum. The sternum is similar to that of an unnamed ornithuromorph from the Xiagou Formation, Gansu Province. These new specimens are subadult: together with the holotype of *Archaeorhynchus*, they constitute the entire Early Cretaceous record of subadult ornithuromorphs and reveal important information regarding the ontogeny of this group. The caudal vertebrae are complete in the two referred specimens and provide information about the development of the pygostyle in basal ornithuromorphs. At least four vertebrae form the pygostyle of *Archaeorhynchus* and fusion progresses distoproximally. The preservation of gastroliths in all known specimens of *Archaeorhynchus* signifies that it was likely herbivorous.

INTRODUCTION

The Lower Cretaceous lake deposits of the Jehol Group in western Liaoning Province are well known for producing many exceptionally preserved fossils, including feathered dinosaurs, early birds, mammals, pterosaurs, and flowering plants (Zhou et al., 2003; Zhou, 2006) (Fig. 1). In the last two decades, over 30 genera of birds have been reported from the Dabeigou, Yixian, and Jiufotang formations, including long-tailed birds, the oldest known pygostylians, enantiornithines, and ornithuromorphs (Zhou et al., 2010). Ornithuromorphs represent the most derived group of birds that coexisted with the enantiornithines and more basal avians in the Lower Cretaceous (Zhou et al., 2009). The earliest known ornithuromorph taxa from the Jehol Group, such as *Chaoyangia* (Hou and Zhang, 1993), *Liaoningornis* (Hou, 1997a), and *Songlingornis* (Hou, 1997b), are represented by fairly fragmentary specimens. More recently, several complete and articulated specimens have been discovered, such as the holotype specimens of the type species of *Yanornis*, *Yixianornis* Zhou and Zhang, 2001, *Hongshanornis* Zhou and Zhang, 2005, *Archaeorhynchus* Zhou and Zhang, 2006, *Jianchangornis* Zhou, Zhang, and Li, 2009, *Longicrusavis* O'Connor, Gao, and Chiappe, 2010, and *Parahongshanornis* Li, Wang, and Hou, 2011. These specimens have revealed a wealth of information regarding the skeletal anatomy of basal ornithuromorphs as well as their biology, with preservation of gut contents, gastroliths, and feather impressions (Zhou et al., 2004; Clarke et al., 2006). However, with the exception of *Yanornis martini*, known from at least five specimens (Zhou et al., 2004), most ornithuromorph taxa are known from single specimens.

Archaeorhynchus spathula was first reported in 2006 as a medium-sized basal ornithuromorph bird (Zhou and Zhang, 2006). It was collected from the Yixian Formation (125 Ma), in Yixian, Liaoning Province (Swisher et al., 1999, 2002) (Fig. 1). The holotype of *Archaeorhynchus* (IVPP V14287) is a subadult individual represented by a nearly complete skeleton missing only the manus and pedal digits; the skull is slightly disarticulated, although most of the postcranial bones remain in articulation. *Archaeorhynchus* is distinguishable from other Mesozoic ornithuromorphs by the unique combination of the following characters: toothless jaws; premaxillae broad with slightly rounded tips; dentary decorated with elongated foramina or grooves and a longitudinal ridge; sternum broad with a pair of long lateral trabeculae; furcula with long and pointed acromion processes; metatarsals II and IV subequal in length; and ratio of femur to tibiotarsus 0.88; ratio of forelimb (humerus + ulna + major metacarpal) to hind limb (femur + tibiotarsus + metatarsal III) about 1.35 (Zhou and Zhang, 2006). Phylogenetic analysis indicates that *Archaeorhynchus* is one of the most basal ornithuromorphs known (Zhou and Zhang, 2006).

Two new specimens (IVPP V17075 and V17091) were recently collected from the Lower Cretaceous Jiufotang Formation in Jianchang, Liaoning Province (Fig. 1). They are both almost complete and articulated skeletons, with large aggregates of gastroliths in the abdominal areas; one of them (IVPP V17091) also preserves feather impressions (Figs. 2, 3). We referred both specimens to *Archaeorhynchus spathula* based on detailed anatomical comparison with the holotype. Because the vertebrae and the extremities of many long bones are not well ossified (e.g., coracoid, humerus, and femur) or fused (e.g., carpometacarpus and tarsometatarsal bones), IVPP V17075 and IVPP V17091 are considered to be subadult.

Archaeorhynchus is the only Early Cretaceous ornithuromorph for which subadult specimens are known; it provides a rare glimpse into the ontogeny of basal ornithuromorphs and shows that they are important for understanding the early evolution of the unique modern avian growth strategy, the development of compound bones, and other derived avian features.

Institutional Abbreviations—**FRDC**, Fossil Research and Development Center, Third Geology and Mineral Resources

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*Corresponding author.

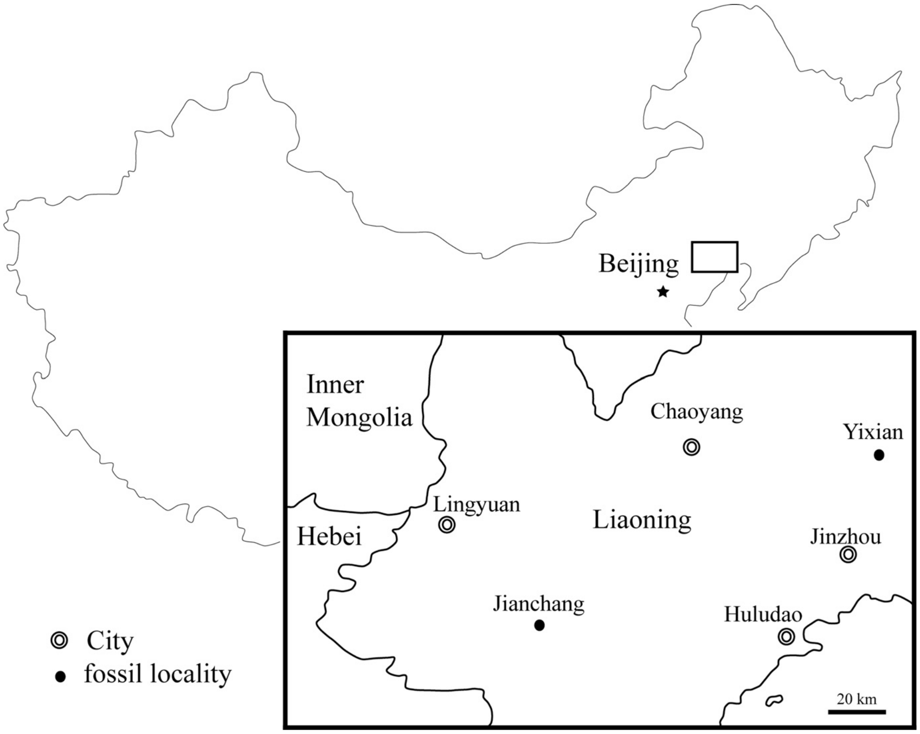

FIGURE 1. Map showing the localities of *Archaeorhynchus spathula* in Liaoning, northeast China.

Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development, Lanzhou, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

DESCRIPTION

Skull

In the holotype (IVPP V14287), the skull bones are exposed mainly in ventral view and were slightly disarticulated during decomposition. This preservation, however, made it possible to recognize many elements that are normally difficult to identify when the skull is in articulation (Zhou and Zhang, 2006). In IVPP V17075 the skull bones are preserved in dorsal view (Fig. 4), whereas in IVPP V17091 they are disarticulated and exposed mainly in left lateral view (Fig. 5). Compared with the holotype, these new specimens reveal much more anatomical information about the skull.

Both the upper and lower jaws are toothless in all three specimens. Grooves and foramina on the external surface of the dentary and the premaxilla suggest that both supported a horny rhamphotheca, although no specimen preserves it. In both the holotype and IVPP V17091, fusion of the premaxillae is limited to the proximal end (suture visible in IVPP V17075). The rostral part of each premaxilla is sharply tapered, but is not as pointed as in *Hongshanornis*. The premaxillary corpus is not rostrally restricted as in more basal birds, but is also not greatly expanded caudally as in more advanced taxa: it accounts for approximately half of the total length of the premaxilla along the rostral margin. The premaxilla has a long, slender, tapering maxillary process and a longer nasal (frontal) process. The maxillary and nasal processes of the premaxilla diverge at an angle of approximately 20°. The two nasal processes appear to be in contact with the frontals (IVPP V17075), and are in very close contact along their full length, but are not completely fused together. The nasals are broad and separated medially by the elongate nasal processes of the premaxillae, as in modern birds. The nasal tapers caudally, and has two robust elongate processes: the premaxillary process is more slender and longer than the maxillary process, the region in between forming the caudal margin of a large elliptical narial foramen. The lacrimal is not well preserved and it appears to be ‘L’-shaped; its ventral branch is angled slightly rostrally (IVPP V17091). The maxilla is long and slender with a very short and broad dorsal process, forming the rostral margin of the antorbital fenestra (Zhou and Zhang, 2006). The frontals are long, taper anteriorly, and become rapidly expanded posteriorly. The rostral end of the frontal contacts the premaxilla, lacrimal, and nasal. In IVPP V17091, the two parietals are not fused with each other; in IVPP V17075, they are in close contact but remain unfused. In the holotype, the quadrate possesses a well-developed orbital process and a long otic process, and lacks pneumatic foramina. IVPP V17075 preserves the jugal and pterygoid in articulation, with the quadrate in close association. The quadrate, apparently preserved in caudolateral view, is slightly bowed laterally, and either lacks a broad orbital process or it is not visible. The otic process appears to be double-headed with a medial concavity separating two small round capitulae. The pterygoid appears to be in dorsal view but is poorly preserved, leaving no anatomical details; the rostral and distal margins are expanded relative to the midpoint width.

In all specimens, all elements of the mandible (dentary, angular, splenial, surangular) are discrete. As the three known specimens are either juvenile or subadult individuals, the degree of fusion in an adult cannot be determined. The dentary is slender and its cranial half is spathulate, with elongated foramina or grooves on its medial surface. The slender dentary tapers caudoventrally, without obvious forking as seen in many basal birds, and its caudal half has a concave medial surface. The articular is well developed, with a distinctive pneumatic foramen, which can be seen in the holotype. The splenial is well exposed in IVPP V17091; it is dorsoventrally narrow and tapers

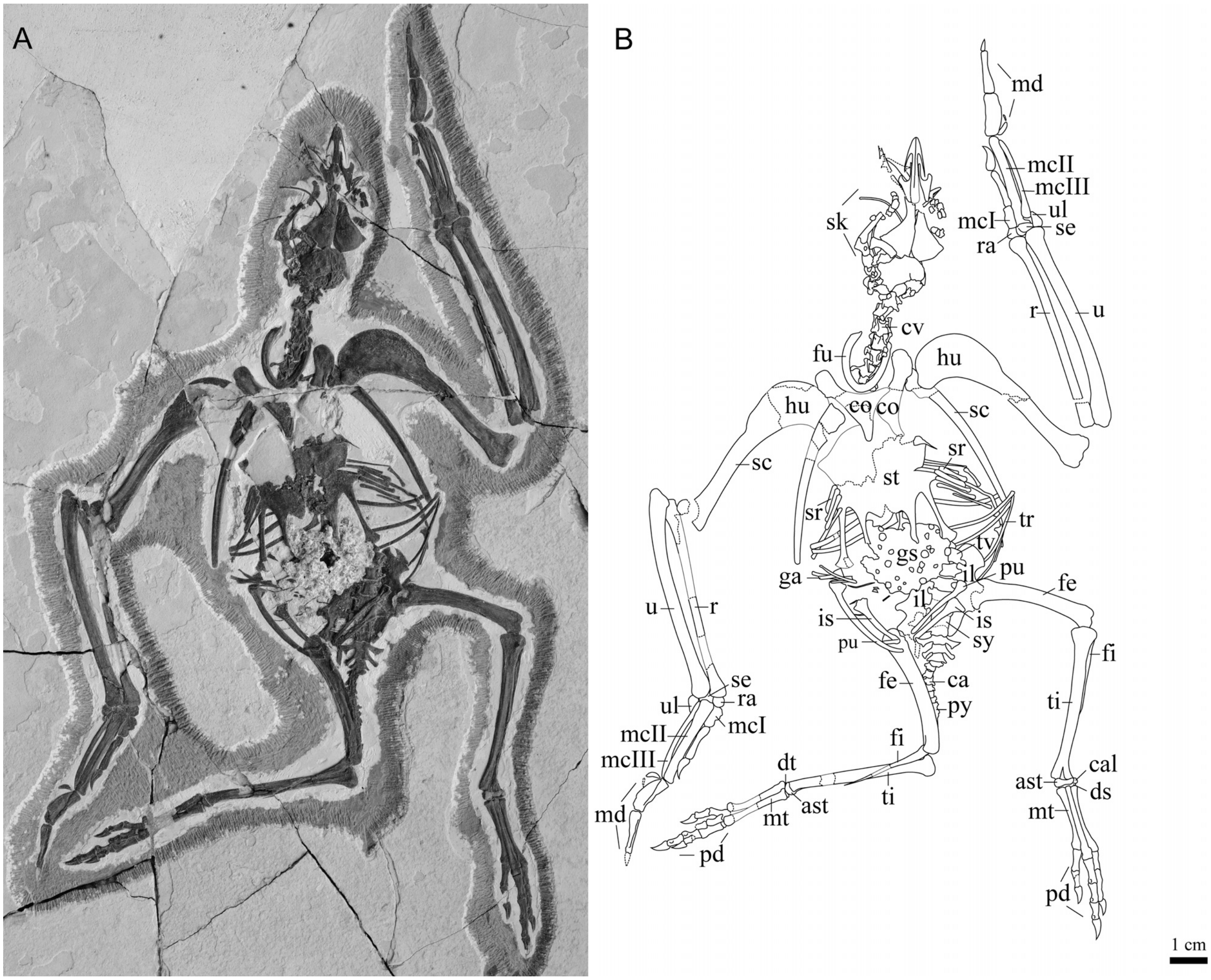

FIGURE 2. Photograph (**A**) and line drawing (**B**) of IVPP V17075. **Abbreviations**: **ast**, astragalus; **ca**, caudal vertebra; **cal**, calcaneum; **co**, coracoid; **cv**, cervical vertebra; **dt**, distal tarsal; **fe**, femur; **fi**, fibula; **fu**, furcula; **ga**, gastralia; **gs**, gastroliths; **hu**, humerus; **il**, ilium; **is**, ischium; **md**, manual digits; **mcI**; alular metacarpal; **mcII**, major metacarpal; **mcIII**, minor metacarpal; **mt**, metatarsus; **pd**, pedal digits; **pu**, pubis; **py**, pygostyle; **r**, radius; **ra**, radiale; **sc**, scapula; **se**, semilunate carpal; **sk**, skull; **sr**, sternal rib; **st**, sternum; **sy**, synsacrum; **ti**, tibia; **tr**, thoracic rib; **u**, ulna; **ul**, ulnare. Scale bar equals 1 cm.

towards both the cranial and caudal ends. The surangular is long and tapers rostrally. Two pairs of slender and rod-shaped bones preserved in both new specimens are interpreted as the hyoid bones.

The occipital bones are preserved in cranial view in IVPP V17091, revealing the interior surface of the occiput (Fig. 6). A large oval foramen magnum is bound by the supraoccipital, two exoccipitals, and the basioccipital; the broader transverse axis is about 4.5 mm in diameter, and the shorter sagittal axis about 2 mm in diameter. There is an obvious internal occipital protuberance, with two symmetrical pit-shaped fossae on each side. There is also an arcuate eminence (eminentia arcuata). Two bones, each shaped like a right-angled triangle, conjoin to form an isosceles triangle-shaped structure close to the occipital complex (Fig. 5). These are interpreted as the os parasphenoidale. The palatine, only preserved in the holotype, bears two small foramina and has a hook-shaped choanal process, similar to that of *Archaeopteryx*. It also appears to be triradiate, as in more derived birds (Zhou and Zhang, 2006).

Vertebral Column

All three specimens preserve the vertebral column; although it is not complete in any specimen (Figs. 2, 3), combining information from them all allows the entire vertebral column to be reconstructed, with the exception of the proximal thoracic vertebrae.

The estimated total number of cervical vertebrae is 9 or 10. In IVPP V17075, the atlas and axis are partly covered by the skull bones. However, the neural arch of the atlas and the odontoid processes of the axis can be recognized; the atlantal hemiarches appear unfused in this specimen. The cervicals possess well-developed costal processes. The cervical centra are fairly short with a width slightly greater than the length. One cervical in IVPP V17091 is preserved in caudal view, and appears to be heterocoelous. The rest of the series is preserved in ventral view revealing small carotid processes and long postzygapophyses.

The thoracic vertebrae are not well preserved in any of the known specimens, especially the anterior thoracics, which are either covered by the sternum or missing (Figs. 2, 3). In IVPP

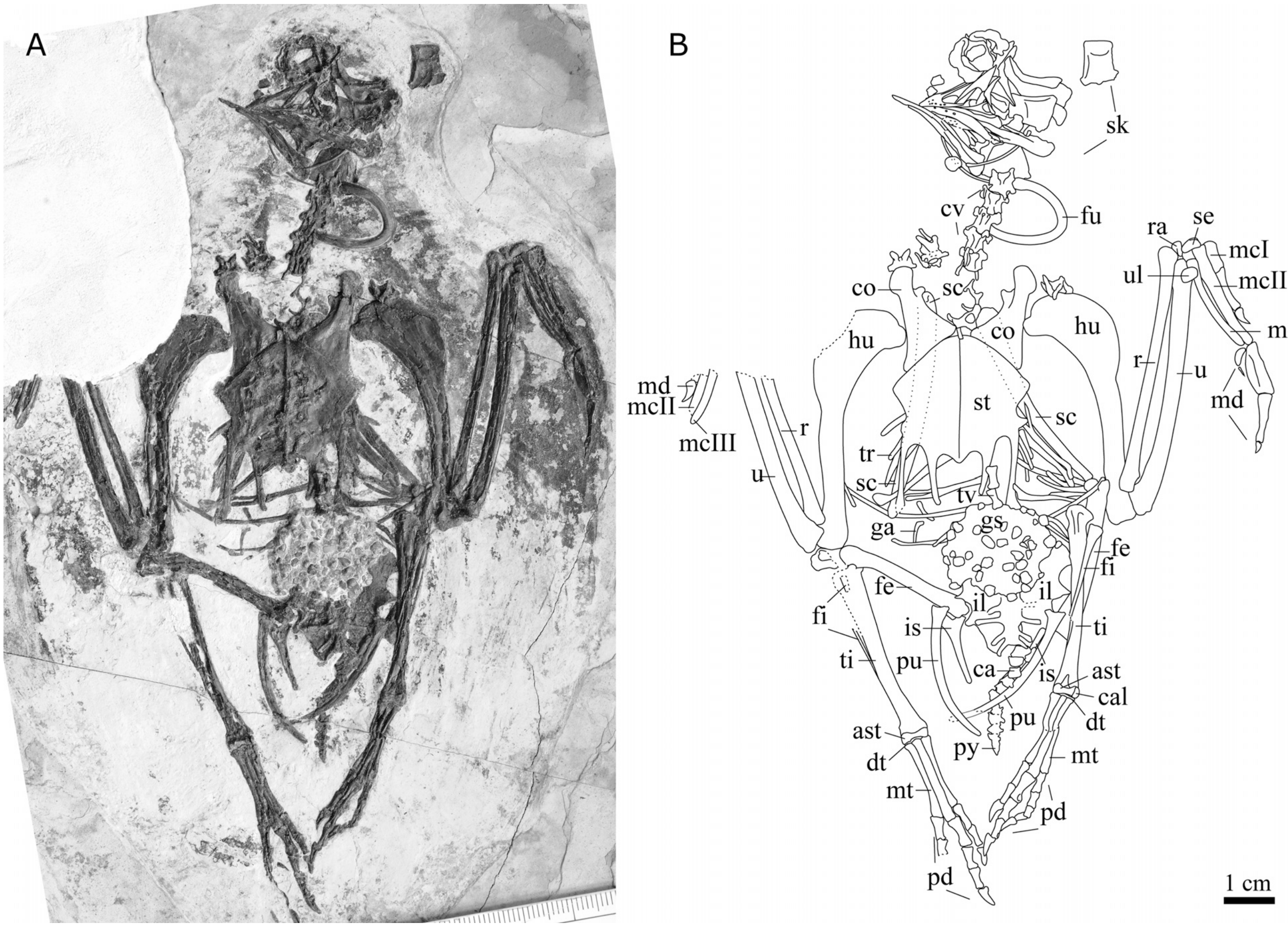

FIGURE 3. Photograph (**A**) and line drawing (**B**) of IVPP V17091. **Abbreviations**: **ast**, astragalus; **ca**, caudal vertebra; **cal**, calcaneum; **co**, coracoid; **cv**, cervical vertebra; **dt**, distal tarsal; **fe**, femur; **fi**, fibula; **fu**, furcula; **ga**, gastralia; **gs**; gastroliths; **hu**, humerus; **il**, ilium; **is**, ischium; **md**, manual digits; **mcI**; alular metacarpal; **mcII**, major metacarpal; **mcIII**, minor metacarpal; **mt**, metatarsus; **pd**, pedal digits; **pu**, pubis; **py**, pygostyle; **r**, radius; **ra**, radiale; **sc**, scapula; **se**, semilunate carpal; **sk**, skull; **sr**, sternal rib; **st**, sternum; **sy**, synsacrum; **ti**, tibia; **tr**, thoracic rib; **u**, ulna; **ul**, ulnare. Scale bar equals 1 cm.

V17091, two dorsals are preserved near the gastroliths and are spool-like in ventral view. The length of each centrum is nearly twice its width. All caudal thoracic vertebrae visible in both IVPP V14287 and IVPP V17075 have approximately equal lengths and midpoint widths.

The synsacrum is well preserved in both the holotype (IVPP V14287) and IVPP V17075. In the holotype, it comprises seven sacrals, as in *Confuciusornis* (Chiappe et al., 1999), the basalmost enantiornithine *Protopteryx* (Zhang and Zhou, 2000), and *Sapeornis* (Zhou and Zhang, 2003), but has fewer sacrals than in *Apsaravis ukhaana* (which has 10 ankylosed sacral vertebrae; see Norell and Clarke, 2001), *Yanornis* (which has 9 sacrals; Zhou and Zhang, 2001), or *Jianchangornis* (with 9–10 sacrals; Zhou et al., 2009). This number is low for ornithuromorphs, suggesting that in an adult specimen of *Archaeorhynchus*, additional vertebrae may have been incorporated into the synsacrum. The transverse processes of the sacrals become longer and more robust towards the caudal end of the pelvis. The distal ends of the transverse processes of the posterior sacrals are slightly expanded but are not in contact with each other. In the holotype, all the sacrals are nearly fused. In IVPP V17075, the fused part of the synsacrum comprises only four sacrals and three vertebrae are incompletely fused to the posterior end. In IVPP V17091, most of sacral vertebrae are obscured by gastroliths; only the three posterior sacrals are visible and they are partially fused. This ontogenetic variation indicates that IVPP V17075 is a more juvenile individual than IVPP V17091.

There are at least nine caudal vertebrae preserved in the holotype. However, almost all of the caudal vertebrae are preserved in the two new specimens (Fig. 7). In IVPP V17075, which based on the degree of sacral fusion is the most juvenile specimen of the three, there are seven free caudal vertebrae, followed by a pygostyle with a laterally oriented crest. The pygostyle appears formed by at least two vertebrae, although this is impossible to determine unequivocally because it is partially covered by the femur. In IVPP V17091, there are at least six free caudal vertebrae preserved, but several of the distal vertebrae are badly preserved, followed by a short pygostyle composed of four vertebrae, although this is difficult to determine conclusively because of the poor preservation in this region. The pygostyle in IVPP V17091 is more robust than in IVPP V17075. In ventral view, the bone is broad and triangular, tapering distally.

Ribs and Gastralia

The vertebral ribs are slender and slightly curved, whereas the proximal ones are more robust and shorter. Uncinate process can be recognized in the holotype, but neither of the two

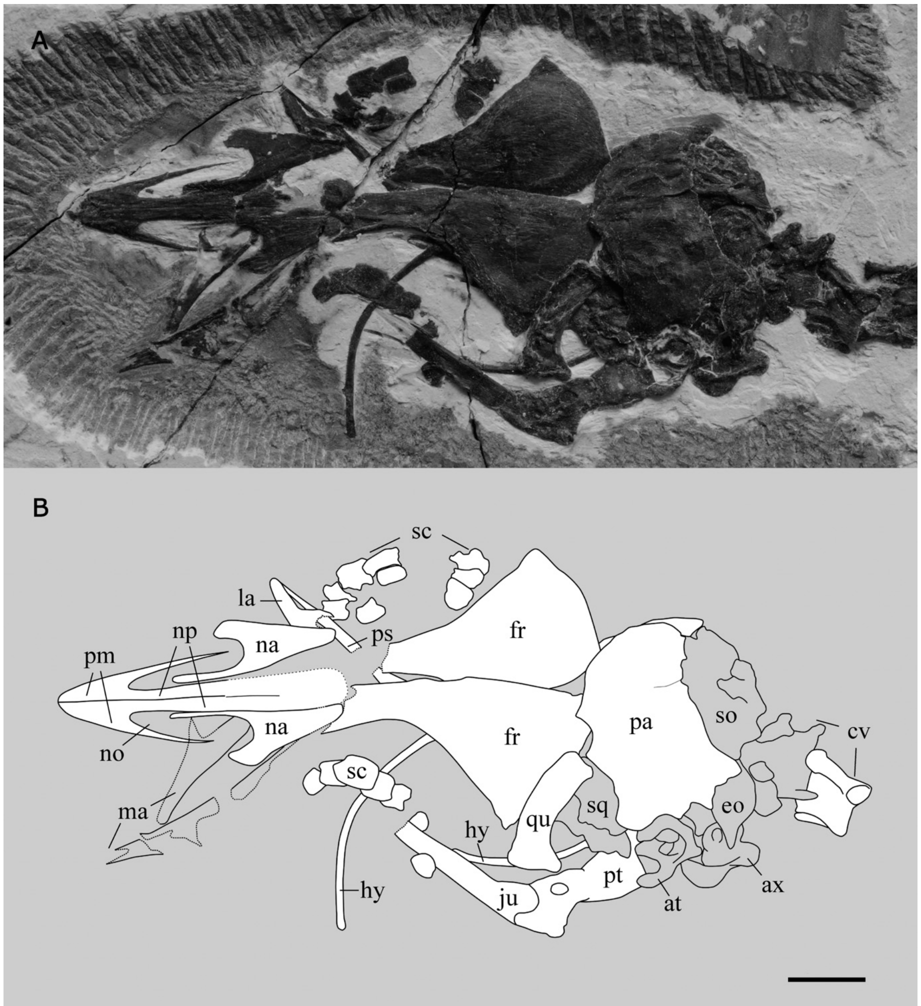

FIGURE 4. Photograph (**A**) and line drawing (**B**) of the skull of IVPP V17075. **Abbreviations**: **an**, angular; **at**, atlas; **ax**, axis; **cv**, cervical vertebra; **de**, dentary; **eo**, exoccipital; **fr**, frontal; **hy**, hyoid bone; **ju**, jugal; **la**, lachrymal; **ma**, maxilla; **na**, nasal; **np**, nasal process of the premaxilla; **no**, nostril; **pa**, parietal; **ps**, part of parasphenoid; **pm**, premaxilla; **pt**, pteygoid; **qu**, quadrate; **sc**, sclerotic ossicles; **so**, supraoccipital; **sq**, squamosal. Scale bar equals 5 mm.

referred specimens preserves uncinate processes, potentially due to their young ontogenetic age. The sternal ribs are most completely preserved in IVPP V17075; they are short and have nearly the same width as the anterior vertebral ribs. Gastralia are found in all three specimens; they are short and small, yet fairly robust.

Pectoral Girdle

The furcula, as seen in the holotype and IVPP V17075, is robust and ‘U’-shaped, with long and tapered acromion processes, and lacks both a hypocleidum and indicators of pneumatization, such as grooves or pits, on its cranial surface.

The scapula, visible in the holotype and IVPP V17075, is shorter than the humerus, has a short acromion, a dorsolaterally directed glenoid facet, is only slightly curved, and tapers towards the distal end.

The coracoid is best preserved in IVPP V17091 where it is visible in ventral view. It is short and robust, with a large sternal articular facet that is strongly angled caudolaterally so that the lateral margin of the coracoid is longer than the medial margin. Although the coracoid is more elongate than in *Archaeopteryx* and *Sapeornis*, the ratio of its width to length is much larger than in other ornithuromorphs (e.g., *Apsaravis ukhaana, Hongshanornis*, *Yanornis*, *Yixianornis*). It has a craniomedially oriented procoracoid process that is short and bluntly tapered. Neither a fully enclosed supracoracoidal nerve foramen nor a medial incision is observed.

The caudal part of the sternum is not complete in the holotype (IVPP V14287), and only one pair of long caudal trabeculae was recognized. Based on information from the two new specimens, the sternum can now be more accurately reconstructed (Fig. 8). The sternum is broad, with a keel extending along its entire length. It has short laterally directed zyphoid processes, which are also present in *Yixianornis* (Clarke et al., 2006) and *Longicrusavis* (O’Connor et al., 2010), in which they are much larger. Caudally, the sternum is deeply notched; the lateral trabeculae are long with their distal ends expanded into fan-like shapes. The intermediate trabeculae almost reach the same level at the distal ends as the lateral trabeculae (which are much shorter in *Hongshanornis*). The median trabecula is much shorter and ends proximal to the outer trabeculae. In most other ornithuromorphs, the xiphial region formed by the fused median trabeculae ends caudally at approximately the same level as the outer trabeculae (Fig. 9).

Forelimbs

The forelimbs are not completely preserved in the holotype: the ulna and radius are broken and the manual elements are disarticulated. However, the forelimbs are much better preserved in the two referred specimens; we combine information from all

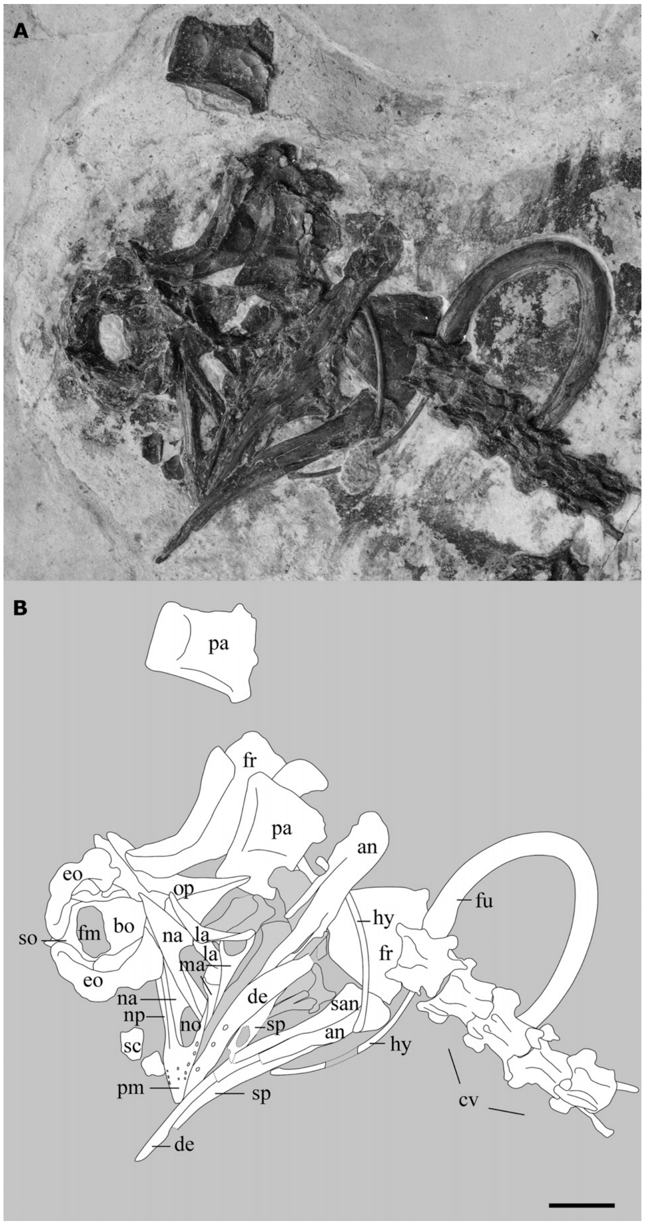

FIGURE 5. Photograph (**A**) and line drawing (**B**) of the skull of IVPP V17091. **Abbreviations**: **an**, angular; **bo**, basioccipital; **op**, os parasphenoidale; **cv**, cervical vertebra; **de**, dentary; **eo**, exoccipital; **fr**, frontal; **fm**, foramen magnum; **hy**, hyoid bone; **ju**, jugal; **la**, lachrymal; **ma**, maxilla; **na**, nasal; **np**, nasal process of the premaxilla; **no**, nostril; **pa**, parietal; **pm**, premaxilla; **san**, surangular; **sc**, sclerotic ossicles; **so**, supraoccipital; **sp**, splenial. Scale bar equals 5 mm.

three specimens to provide a better reconstruction of the forelimb anatomy of *Archaeorhynchus*.

The humerus has a large, rounded deltopectoral crest that extends for one-third of its total length and a well-developed ventral tubercle. Distally, the humerus is slightly expanded. A brachial impression appears to be present, although this is uncertain due to crushing. The dorsal and ventral condyles are not prominent, possibly due to the juvenile status of the specimens; the orientation of the dorsal condyle is ambiguous, whereas the ventral condyle appears to be more or less round. The distal margin of

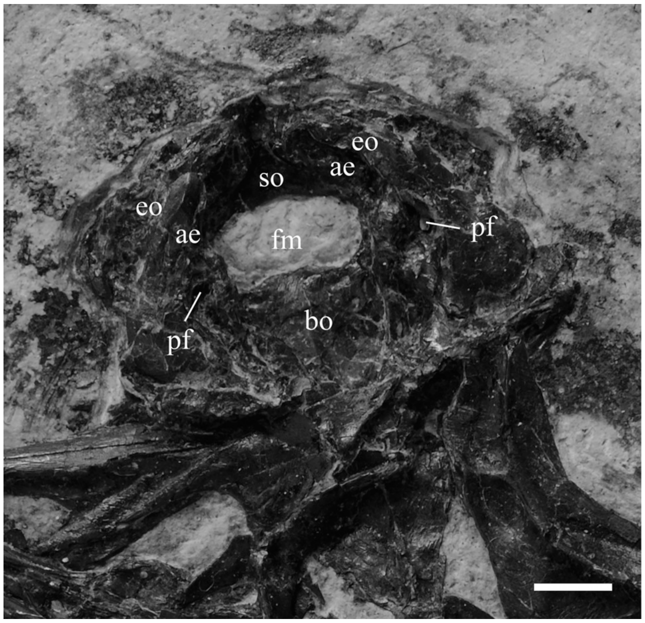

FIGURE 6. Photograph of the occiput of IVPP V17091. **Abbreviations**: **ae**, arcuate eminence; **bo**, basioccipital; **eo**, exoccipital; **so**, supraoccipital; **fm**, foramen magnum; **pf**, pit-shaped fossa. Scale bar equals 2 mm.

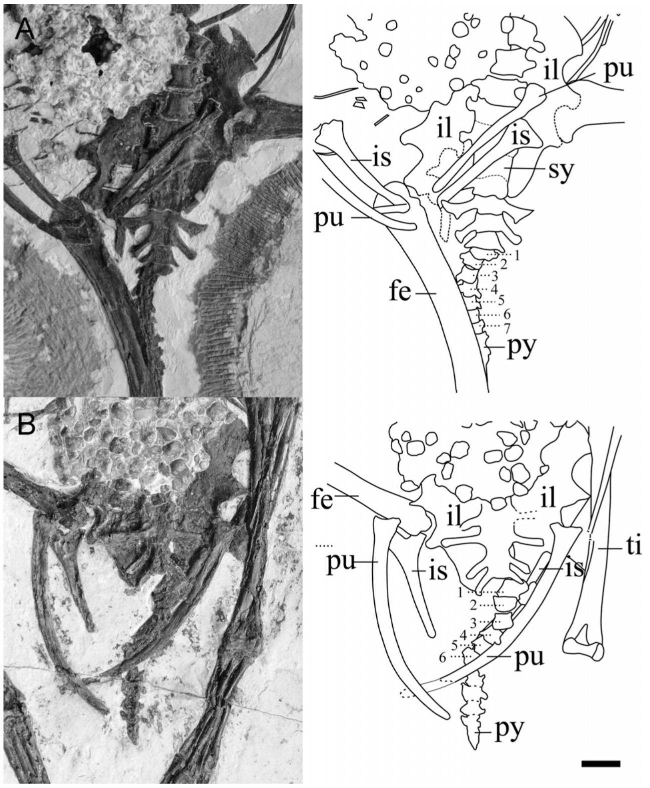

FIGURE 7. Photographs and line drawings of the caudal vertebrae of the specimens IVPP V17075 (**A**) and IVPP V17091 (**B**). **Abbreviations**: **ca**, caudal vertebra; **fe**, femur; **fi**, fibula; **il**, ilium; **is**, ischium; **pu**, pubis; **py**, pygostyle; **sy**, synsacrum; **ti**, tibiotarsus. Scale bar equals 5 mm.

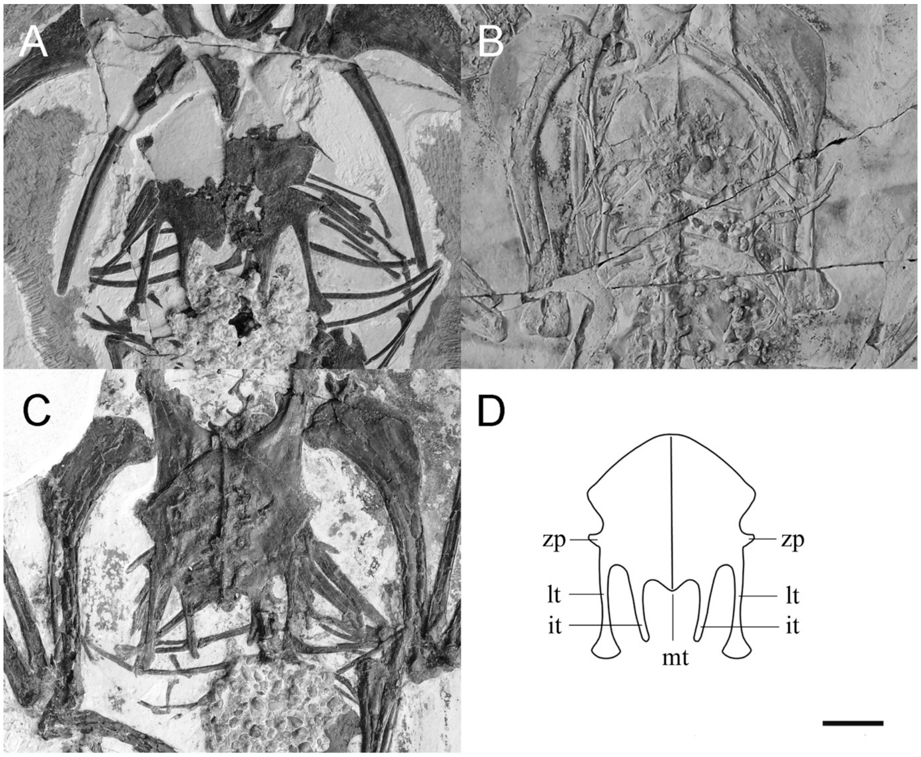

FIGURE 8. Photographs of the three specimens of the sternum of *Archaeorhynchus spathula*. **A**, IVPP V17075; **B**, IVPP V14287; **C**, IVPP V17091; **D**, reconstruction. **Abbreviations**: **it**, intermediate trabecula; **lt**, lateral trabecula; **mt**, median trabecula; **zp**, zyphoid process. Scale bar equals 1 cm.

the humerus is slightly angled distoventrally relative to the longitudinal axis of the shaft. The ulna is longer than the radius, and both the ulna and radius are slightly longer than the humerus. The ulna is only slightly bowed near the proximal end. Both ends of the ulna are slightly expanded relative to the middle part of the shaft. Proximally, the dorsal and ventral cotylae lack well-developed concave articular surfaces (IVPP V17091). The radius is relatively straighter than the ulna and its width at midlength is slightly greater than half that of the ulna. Proximally, a prominent bicipital tubercle is well developed; distally, the radius is rounded and slightly expanded.

The ulnare (Fig. 10) is not developed into distinct rami, and it is about the same size as the radiale. In the holotype, the semilunate carpal has a prominent carpal trochlea. In IVPP V17075, the ontogenetically youngest of the three specimens, the left manus is preserved in ventral view, and a small triangular carpal bone can be observed between the proximal end of the minor metacarpal and the semilunate carpal (Fig. 10). This carpal is in a comparable position to the 'carpal X' of *Archaeopteryx* and modern birds (Chiappe et al., 2007).

The manus is best preserved in IVPP V17075 (Fig. 10). The alular metacarpal appears to have a ginglymoid distal

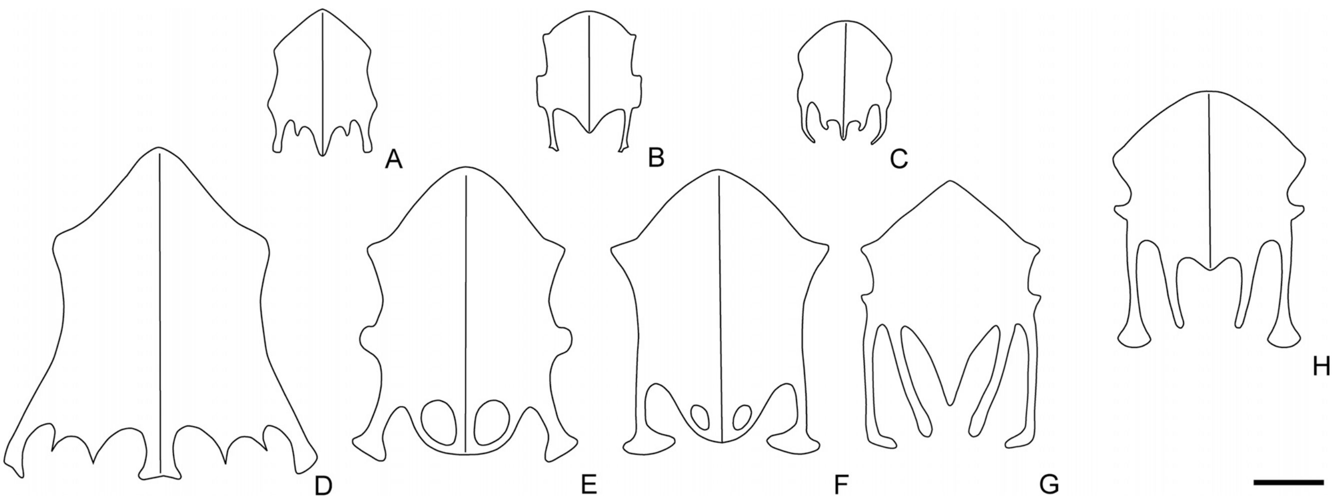

FIGURE 9. Comparison of the sternum of *Archaeorhynchus spathula* with other Early Cretaceous ornithuromorphs. **A**, *Parahongshanornis chaoyangensis*; **B**, *Longicrusavis houi*; **C**, *Hongshanornis longicresta*; **D**, *Jianchangornis microdonta*; **E**, *Yixianornis grabaui*; **F**, *Yanornis martini*; **G**, FRDC-05-CM-02; **H**, *Archaeorhynchus spathula*. Scale bar equals 1 cm.

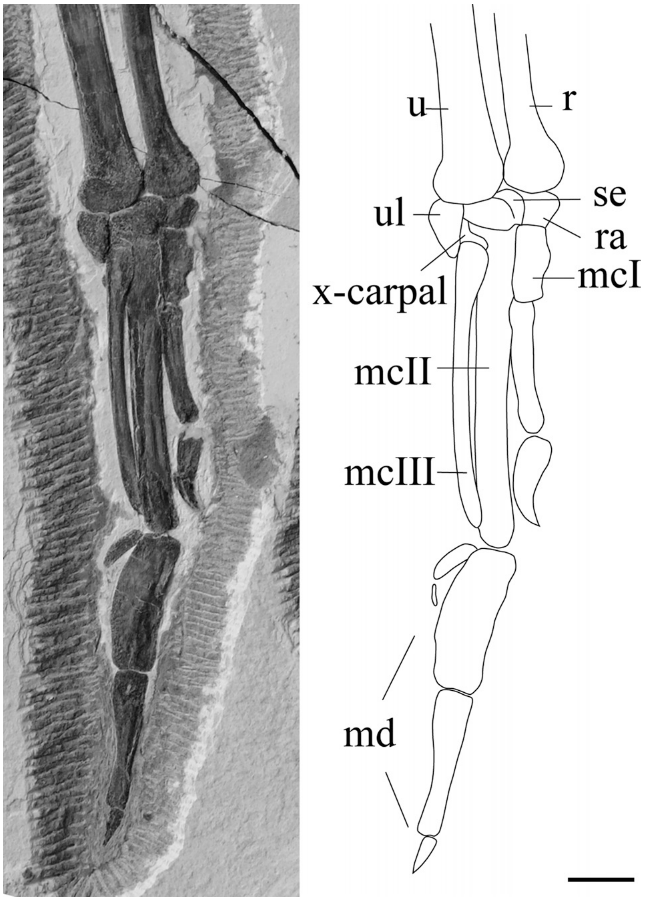

FIGURE 10. Photograph and line drawing of left manus of *Archaeorhynchus spathula* (IVPP V17075). **Abbreviations**: **md**, manual digits; **mcI**; alular metacarpal; **mcII**, major metacarpal; **mcIII**, minor metacarpal; **r**, radius; **ra**, radiale; **se**, semilunate carpal; **u**, ulna; **ul**, ulnare. Scale bar equals 5 mm.

articulation with the first phalanx of the alular digit. The major and minor metacarpals are not fused to each other, either proximally or distally, nor are they fused with the semilunate carpal. The major metacarpal is more robust than the minor metacarpal. The minor metacarpal ends proximal to the distal end of the major metacarpal, and it is slightly bowed caudally at midlength, creating a long and narrow intermetacarpal space. The alular digit is short, not distally surpassing the distal end of the major metacarpal. The first phalanx is approximately twice as long as the alular metacarpal itself; the second phalanx is a well-developed ungual, more than half of the length of the first phalanx, although weakly recurved. 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 and the ungual is much smaller and even less curved than that of the alular digit. The minor digit is short and comprises two small phalanges (IVPP V17075 and V17091): the first is less than half of the length of the penultimate phalanx of the major digit, wedge-shaped, with small undeveloped proximal and distal articular surfaces; the second phalanx is less than half of the length of the first and sharply tapered. The phalangeal formula of *Archaeorhynchus* can be reconstructed as 2-3-2, as in *Hongshanornis*.

Pelvic Girdle

In the two referred specimens, the bones of the pelvic girdles are largely covered by gastroliths, so little new anatomical information is provided. The preacetabular wing of the ilium is slightly longer and twice as high as the postacetabular wing; in ventral view, the rostrolateral corner of the preacetabular wing of the ilium projects ventrally so that the lateral margin is deeply concave and it is closed posteriorly by the pubic pedicel (IVPP V17091, V17075). The ilium appears to be unfused to the synsacrum (IVPP V17091). In the holotype, the retroverted pubis is slender and curved with a small pubic foot. Whereas the pubis is broken distally in both referred specimens, the ischium is strap-like and shorter than the pubis, lacking both the strut-like proximal dorsal process that is often seen in enantiornithines and more basal birds and the gradual distal dorsal expansion present in ornithuromorphs (e.g., *Yixianornis*). Clearly visible in both referred specimens, the ischium is proximally broad, forming short peduncles for the ilium and pubis; the corpus rapidly becomes strap-like and has a blunt untapered distal end.

Hind Limb

The hind limb is short compared with the forelimb, with a forelimb to hind limb length ratio (intermembral index) of about 1.36 (Table 1). The femur is robust and bowed with a ball-shaped head. In IVPP V17075, the distal left femur is in cranial view; no distinct patellar groove is developed. All specimens are juvenile and none possesses a fully fused tibiotarsus or tarsometatarsus. The tibia is only slightly longer than the femur. The ratio of femur to tibia length is approximately 0.86 (Table 1). The right tibia in IVPP V17075, seen in lateral view, has a poorly developed cnemial crest that projects cranially but not proximally, and so is similar to other ornithuromorphs (e.g., *Chaoyangia*, *Gansus*, *Yanornis*, *Yixianornis*). The fibula is slender and almost the same length as the tibia (IVPP V14287); the proximal end is broad and triangular, and the bone rapidly tapers distally so that the distal two-thirds are needle-shaped. In all three specimens, the tibia is not fused with the proximal tarsals—this is inferred to be due to the subadult ontogenetic status of all specimens. The proximal tarsals are not fused to each other; the calcaneum is nearly round and much smaller than the astragalus (approximately one-fifth its size on transverse width). The astragalus has a broad, triangular ascending process as in other basal birds (Chiappe et al., 2007) (Figs. 2, 3).

In the two referred specimens, the distal tarsals form a cap that covers, but are unfused with, the proximal ends of the metatarsals (Figs. 2, 3). Metatarsals II–IV appear completely unfused to each other along their entire lengths (IVPP V17075); metatarsal V is not present. The three metatarsi are in a single plane, with metatarsal III lacking the proximal plantar displacement present in other ornithuromorph taxa (e.g., *Yanornis*, *Yixianornis*). Metatarsal III is the longest and the widest; metatarsals II and IV are subequal in width. Metatarsal IV is slightly longer than metatarsal II and extends to the proximal margin of the metatarsal III trochlea. Unlike the holotype, in the referred specimens the feet are preserved in partial articulation, although metatarsal I is not preserved in either. However, a slightly wedge-shaped bone preserved near the proximal end of the left tarsometatarsus in the holotype is interpreted as metatarsal I. None of the three specimens preserves a hallux, whereas the other digits are nearly completely preserved in the referred specimens.

The pedal digits are slightly longer than metatarsal III, and more robust. The proximal phalanges are longer than the distal ones, and the unguals are short and not significantly curved, suggesting a terrestrial ecological niche. The flexor pits at the

TABLE 1. Length (mm) of some skeletal elements of *Archaeorhynchus spathula*.

	Specimen (IVPP)		
Skeletal element	V 14287	V 17075	V 17091
Scapula (l)	46	46	43*
Coracoid (l)	20	20	19
Humerus (l)	54	53	49
Ulna (l)	57	58	54
Radius (l)	56	55	52
Carpometacarpus (l)	27	28.5	25
Alular metacarpal (l)	6	6	5
Alular metacarpal (w)	3	2	2.5
Major metacarpal (l)	25	25	23
Major metacarpal (w)	2	3	2.5
Minor metacarpal (l)	24	23	21
Minor metacarpal (w)	2	1.5	1.5
Alular digit 1 (l)	10.5	10	9
Alular digit 2 (l)		6	4
Major digit 1 (l)		12	11
Major digit 2 (l)		12	10
Major digit 3 (l)		3.5	2.5
Minor digit 1 (l)		4	5
Ischium l	20*	17*	14*
Pubis (l)	37	28*	30*
Fibula (l)	33	21*	28
Femur (l)	37	36	34
Tibiotarsus (l)	43	42	39
Tarsometatarsus (l)	20	22	19
Pedal digit II-1 (l)		6	5.5
Pedal digit II-2 (l)		5	4
Pedal digit II-3 (l)		5	4
Pedal digit III-1 (l)		6.5	6
Pedal digit III-2 (l)		5	5
Pedal digit III-3 (l)		4	4
Pedal digit III-4 (l)		5	4
Pedal digit IV-1 (l)		5	4.5
Pedal digit IV-2 (l)		3	3.5
Pedal digit IV-3 (l)		2.5	2
Pedal digit IV-4 (l)		2	2
Pedal digit IV-5 (l)		4	3.5
Forelimb/hind limb	1.36	1.36	1.37
Femur/tibiotarsus	0.86	0.86	0.87

Abbreviations: **l**, length; **w**, width. * indicates an estimated measurement.

distal ends of the phalanges are distinct. Digit II has three phalanges; the first phalanx is the second longest in the foot (slightly shorter than phalanx III-1), followed by a phalanx that is 20% shorter, and the ungual. The third digit is the longest and most robust in the foot and has four phalanges. Phalanx III-1 is the longest and most robust in the foot, with more distal phalanges that are each approximately 20% shorter than its proximally adjacent one, ending in the largest ungual of the foot. The fourth digit is the most slender, with five phalanges. The phalanges also decrease in length distally, but the distal two have nearly the same length. The digit ends in a small ungual, approximately equal in size to that on digit II.

Gastroliths and Feathers

In the holotype and the two referred specimens, numerous gastroliths are present (Figs. 2, 3). In the holotype, gastroliths are spread between the sternum and the pelvis, whereas in the two new specimens, a large aggregate of gastroliths are preserved in the abdominal areas, overlying the pelvic girdle. The stones are not rounded and vary in morphology, although they are consistent in size, measuring approximately 2 mm in diameter.

Feathers are preserved in the holotype and IVPP V17091, associated with the skeleton, particularly in the skull, neck, wing, and tail regions. The primaries are very long and asymmetric. There is no evidence for the presence of long pennaceous feathers having been attached to the tibial part of the leg, unlike in *Archaeopteryx*, *Confuciusornis*, and some enantiornithines (Zhang and Zhou, 2004), probably indicating that the leg feathers, which first occurred in non-avian theropods, may have been lost in some lineages of early ornithuromorpha (Zhou and Zhang, 2006). The recently reported basal ornithuromorphs *Hongshanornis* and *Jianchangornis* also lack leg feathers. However, this feature was not lost entirely within ornithuromorphs and was retained by the neornithines, as evidenced by the presence of crural feathers in most living taxa, exemplified by the leg feathers of predatorial birds.

DISCUSSION

The two new specimens of *Archaeorhynchus* were found in the Jiufotang Formation (120 Ma), whereas the holotype is from the Yixian Formation (125 Ma); thus, these new discoveries extend the range of this taxon by at least 5 Ma (Swisher et al., 1999, 2002; He et al., 2004).

The new material provides much new information regarding the anatomy of this basal ornithuromorph. The new specimens confirm some of the unique features observed in the holotype, such as the dentary decorated with elongated foramina or grooves and a longitudinal ridge; a furcula with a long and pointed acromion processes; metatarsals II and IV that are nearly subequal in length; and hind limbs that are short compared with the forelimbs. Furthermore, the new material also elucidates many important characters that were either unknown or misinterpreted in the holotype, such as the shape of the sternum, hand, and foot.

In previous cladistic analyses, *Archaeorhynchus* is typically resolved as a basal ornithuromorph taxon more derived than enantiornithines and most closely related to known ornithuromorphs (Zhou and Zhang, 2006; Zhou et al., 2009; You et al., 2010). *Archaeorhynchus* displays a mosaic of characters, as in other basal ornithuromorphs. Like other more derived avians, *Archaeorhynchus* has a ‘U’-shaped furcula, a keel extending along the full length of the sternum, a globose humeral head, and a dorsoventrally compressed and caudally expanded first phalanx of the major manual digit. However, as one of the most basal ornithuromorphs, *Archaeorhynchus* also retains several primitive features, such the dentary not being strongly forked posteriorly (it is forked in *Apsaravis*), and deep caudal notches in the sternum, which are present in enantiornithines (Zhou and Zhang, 2006).

Among known early ornithuromorph birds, the sternum displays a wide range of morphologies, especially in its caudal half (Fig. 9). The sterna of *Songlingornis*, *Yanornis*, and *Yixianornis* all have one pair of free caudal trabeculae, lateral trabeculae that are robust with expanded distal ends, and a pair of caudal fenestrae laterally enclosed by a pair of medially curved strap-like bones inferred to be the intermediate trabeculae. Free intermediate trabeculae and no caudal fenestrae are present in the sterna of hongshanornithids and *Jianchangornis*. Despite their differences, the sterna of all these early ornithuromorphs share at least one common feature: the imperforate region is craniocaudally elongate. However, in *Archaeorhynchus,* the sternum is not markedly elongated, being slightly shorter than wide, and the imperforate region is very short, due to the deep caudal incisions closed by the caudal trabeculae. The sternum of *Archaeorhynchus* is similar to that of the second known ornithuromorph (FRDC-05-CM-02) from the Xiagou Formation, Gansu Province (You et al., 2010): both have long lateral and intermediate caudal trabeculae separated by deep incisures. However, the two differ in that the xiphial region in *Archaeorhynchus* is very short, forming a large angle of about 100°, greater than in other ornithuromorphs, and lacking an elongate xiphial process like that in FRDC-05-CM-02.

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). Unfortunately, no sternal characters have yet been determined to be indicative of ecology. We suggest that *Archaeorhynchus* may have had a different flight strategy from other ornithuromorphs, i.e., by increasing the length of the forelimb instead of the elongation of the sternum.

Archaeorhynchus has an extremely elongate wing compared with the hind limb, compared with other early ornithuromorphs. The length ratio of humerus + ulna + major metacarpal to femur + tibiotarsus + metatarsal III in the known specimens is 1.36 (IVPP V14287; the original measurement is 1.35 in Zhou and Zhang, 2006), 1.36 (IVPP V17075), and 1.37 (IVPP V17091), which is most similar to that of the long-winged enantiornithine *Longipteryx* (1.32; Zhang et al., 2001), and slightly smaller than that of the basal bird *Sapeornis* (about 1.53; Zhou and Zhang, 2003). The ratio is much smaller in all other Lower Cretaceous ornithuromorphs such as *Hongshanornis* (0.79), *Jianchangornis* (1.1), *Longicrusavis* (0.77), *Parahongshanornis* (0.83), *Yanornis* (1.14), and *Yixianornis* (0.98).

Ontogenetic studies provide important evidence for understanding organismal character evolution and phylogeny (Chiappe et al., 2007). Information regarding early developmental stages in fossil birds is of great value for studying early avian evolution. Non-adult specimens of Mesozoic ornithuromorphs are extremely rare (though well known amongst enantiornithines); these three non-adult specimens represent the entire non-adult ornithuromorph record from the Jehol Group, and thus provide a rare and unique glimpse into the ontogenetic development of *Archaeorhynchus* and basal ornithuromorphs. As shown by synsacral fusion, IVPP V17091 is ontogenetically older than IVPP V17075, because they are in different stages of development, thus partially revealing its formation during early development.

The carpals in the holotype and IVPP V17091 are either broken or missing; however, in IVPP V17075, the carpals are well preserved (Fig. 10). The carpal composition of *Archaeorhynchus* in IVPP V17075 resembles that of *Archaeopteryx*, consisting of four carpals: the proximal ulnare and radiale, the distal semilunate, and 'carpal X' (Chiappe et al., 2007). Embryological evidence from modern birds reveals that the semilunate carpal is centered on the major metacarpal (Zhou and Martin, 1999), as it is in IVPP V17075. In this specimen, it is clear that the proximal end of the minor metacarpal lies distal to that of the major metacarpal, whereas 'carpal X' is preserved between the proximal end of the minor metacarpal and the semilunate bone. This observation indicates that, in ornithuromorphs, the semilunate carpal and 'carpal X' become fused to the proximal ends of the metacarpals, as in enantiornithines (Chiappe et al., 2007). However, it remains difficult to determine whether ornithuromorphs have the same development trajectory as modern birds or enantiornithines, in which the semilunate carpal incorporates 'carpal X' prior to these bones becoming fused to the proximal ends of the metacarpals (Chiappe et al., 2007).

In all the three specimens of *Archaeorhynchus*, there has been no fusion of bones to create a tibiotarsus or tarsometatarsus (Figs. 2, 3). The astragalus and calcaneum are discrete elements that are separate from each other and the tibia. The ascending process of the astragalus is visible in all three specimens. Huxley (1870) considered the similarity between the ascending process in birds and non-avian theropods as homologous. However, this has been rejected by some who consider the 'pretibial bone' in birds and the ascending process in non-avian theropods to have different origins (Martin and Bonner, 1977). Previous studies have shown that although some neognaths have a free ascending process, ratites retain the primitive condition in which it is fused to the astragalus (McGowan, 1985). The presence of this primitive condition in *Archaeorhynchus*, one of the most basal ornithuromorphs known, confirms this is the primitive condition for modern birds.

Distal tarsals have been previously reported in several early birds; a tarsal cap was once one of the characters used to separate living birds and their extinct relatives from primitive lineages such as the Enantiornithines and *Archaeopteryx* (Martin, 1983). *Archaeopteryx* preserves 2–3 distal tarsals that are reportedly free in some specimens, and partially fused to the metatarsals in others (Elzanowski, 2002). In the holotype of *Sapeornis*, one free tarsal is associated with the proximal tarsometatarsus (Zhou and Zhang, 2002a). *Rahonavis* preserves a single distal tarsal over the fourth metatarsal (Forster et al., 1996, 1998). Among enantiornithines, *Iberomesornis* preserves a single small, free distal tarsal located between the proximal ends of metatarsals II and III (Sanz and Bonaparte, 1992; O'Connor et al., 2011b), *Shenqiornis* preserves a single distal tarsal element (Wang et al., 2011), and *Rapaxavis* preserves a distal cap separate from the unfused metatarsals (O'Connor et al., 2011b). Until now, no distal tarsals have been recognized within Ornithuromorpha, because nearly all the described specimens are adults and thus have greater degrees of tarsometatarsal fusion. Tarsometatarsal development in fossil ornithuromorphs is assumed to have progressed similarly to modern birds, with a distal tarsal cap forming prior to its fusion with the proximal ends of metatarsals II–IV (O'Connor et al., 2011b). The newly discovered specimens lend support to this argument because they clearly show that the distal tarsals are fused together to form a cap, rather than first fusing with the proximal end of the unfused metatarsals.

In most modern birds, the distal 4–7 embryonic caudal vertebrae become fused into a tapered, single bone, the pygostyle, from which the rectrices emanate (Feduccia, 1999). The long-tailed birds, *Archaeopteryx*, *Rahonavis*, and *Jeholornis*, all possess a large number of free caudal vertebrae without forming a pygostyle (Martin, 1983; Zhou and Zhang, 2002b; O'Connor et al., 2011a). In *Zhongornis haoae*, the tail is shorter than in other 'long-tailed' birds (Gao et al., 2008); it has a reduced number of caudal vertebrae and an incipient pygostyle, suggesting that in at least one lineage of birds, the length of the tail was reduced through the loss of vertebrae, rather than by the miniaturization of a large number of caudals. All the described early ornithuromorphs that have reduced numbers of free caudals either possess a fused pygostyle or did not preserve a complete caudal series, providing limited information on caudal vertebrae development. The two referred specimens of *Archaeorhynchus* preserve almost the complete series of caudal vertebrae (Fig. 7). Their different ontogenetic ages partially reveal how the pygostyle formed. Based on the three subadult specimens, we conclude that the pygostyle of *Archaeorhynchus* is formed by at least four caudal vertebrae and that pygostyle formation starts from the distal end.

All three specimens of *Archaeorhynchus* preserve a large number of gastroliths. Not all gastroliths have a mechanical function, because accidental intake is relatively common in species with particular feeding habits. A low percentage of gastrolith-bearing individuals within a species indicate that the gastroliths were accidentally ingested, or fulfill a function that is not critical for survival (Wings, 2004). As a large quantity of grit and a high percentage of same-species individuals with grit-containing gizzards correlate with an increased frequency of seeds or other hard materials in the diet (Gionfriddo and Best, 1996), a large number of stones preserved in the abdominal region, as observed in these two new specimens, is typically considered to be evidence of an herbivorous diet. On the other hand, gastroliths have been proposed to help regulate buoyancy and stability while swimming and diving in specialized aquatic tetrapods, including crocodilians and pinnipeds; but only very little is known from specialized diving birds such as penguins and some cormorants (Zhou et al., 2004). However, because of the large amount of grit preserved in the three specimens and their conspicuous lack of diving specializations, this explanation of the grit in *Archaeorhynchus* is not supported. The absence of teeth, the distinctive spathulate dentary, and the gizzard stones preserved in all the specimens, to some extent, support the previous interpretations of the diet of *Archaeorhynchus* that it mainly fed on plants. Among birds in the Jehol Group, gastroliths have been reported in *Yanornis* and *Sapeornis*. *Yanornis* has been interpreted as having a variable diet, because one specimen preserves gastroliths whereas another preserves fish remains (Zhou et al., 2004). *Sapeornis* was considered herbivorous, consistent with the robust morphology of its beak. The herbivorous diet of *Archaeorhynchus* is the same as *Sapeornis*, but different from other ornithuromorph birds that are interpreted as having seasonal or piscivorous diets. However, the foot structure of *Archaeorhynchus* indicates a terrestrial habit, which is opposite that of *Sapeornis* but similar to that of *Yanornis*. Differing in size and proportions, *Archaeorhynchus* likely had an ecological niche that differed from other known ornithuromorph birds, being part of the early diversification of birds during the Lower Cretaceous.

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