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New Information on Hongshanornithidae (Aves: Ornithuromorpha) from a new subadult specimen

ZHENG Xiao-Ting[1,2] Jingmai K. O'CONNOR[3] WANG Xiao-Li[1,2]
ZHANG Xiao-Mei[1,2] WANG Yan[1,4]

(1 *Institute of Geology and Paleontology*, *Linyi University* Linyi, Shandong 276005)
(2 *Shandong Tianyu Museum of Nature* Pingyi, Shandong 273300 pyxm2006@163.com)
(3 *Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences*, *Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044)
(4 *State Key Laboratory of Palaeobiology and Stratigraphy*, *Nanjing Institute of Geology and Palaeontology*, *Chinese Academy of Sciences* Nanjing 210008)

Abstract We report on a new species of basal ornithuromorph bird, *Tianyuornis cheni* gen. et sp. nov., based on a nearly complete and articulated subadult individual from the Lower Cretaceous Yixian Formation in the eastern region of Nei Mongol, China. The new specimen shows features characteristic of the Hongshanornithidae (*Hongshanornis longicresta*, *Longicrusavis houi*, and *Parahongshanornis chaoyangensis*), such as small body size and elongate hindlimbs relative to their forelimbs, but it also possesses some unique features that support the erection of a new genus and species, including a straight dentary (a sigmoidal dentary was previously considered an autapomorphy of hongshanornithids), teeth preserved on both the upper and lower jaws, sternal caudolateral trabecula has a distinct fan-shaped expanded distal end. With the addition of this new taxon, Hongshanornithidae represents the most diverse recognized clade of Early Cretaceous ornithuromorphs. The new specimen reveals new important morphological information regarding the Hongshanornithidae and confirms the controversial presence of teeth in this clade.

Key words Ningcheng, Nei Mongol, China; Lower Cretaceous; Yixian Formation; Ornithuromorpha, Hongshanornithidae

1 Introduction

Ornithuromorpha represents the most derived group of Early Cretaceous birds; their earliest record is in the Yixian Formation of the Jehol Group in northeastern China. Over the past two decades, well-preserved specimens from the Jehol Group have greatly increased our understanding of species-level diversity among the earliest ornithuromorphs (e.g. *Yanornis martini*, Zhou and Zhang, 2001; *Yixianornis grabaui*, Zhou and Zhang, 2001; Clarke et al., 2006; *Hongshanornis longicresta*, Zhou and Zhang, 2005; *Archaeorhynchus spathula*, Zhou and Zhang, 2006; *Jianchangornis microdonta*, Zhou et al., 2009; and *Schizooura lii*, Zhou

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et al., 2012). However, most taxa are known only from a single specimen and most genera are monospecific and are not resolved into family level clades, yielding little information about Early Cretaceous avian paleogeographic and temporal ranges or higher-level diversity. However, three taxa, *Hongshanornis longicresta* (Zhou and Zhang, 2005), *Longicrusavis houi* (O'Connor et al., 2010), and *Parahongshanornis chaoyangensis* (Li et al., 2011) have been inferred to form a phylogenetically supported monophyletic clade of specialized waders, the Hongshanornithidae; all three taxa have distinct elongate hindlimbs relative to their forelimbs.

Here we describe a new ornithuromorph from the Lower Cretaceous Yixian Formation in Nei Mongol, northeastern China based on a nearly complete and articulated specimen (STM7-53). The new specimen preserves numerous characters that align it with the Hongshanornithidae as well as unique features that suggest it is a new species of this clade. This new discovery provides important new information regarding the anatomy of hongshanornithids and highlights the existence of a diverse clade of specialized early Cretaceous ornithuromorph birds..

2 Systematic paleontology

Aves Linnaeus, 1758

Ornithuromorpha Chiappe, 2002

Hongshanornithidae O'Connor et al., 2010

***Tianyuornis cheni* gen. et sp. nov.**

(Figs. 1-6)

Holotype STM7-53, housed in Shandong Tianyu Museum of Nature (STM), a nearly complete, largely articulated subadult individual preserved in a light-grey tuffaceous shale, split into a slab (slab A; Fig. 1A) and counterslab (slab B; Fig. 2A), with well-preserved feather impressions.

Etymology The genus name refers to Shandong Tianyu Museum of Nature where the specimen is housed, and the specific name is in honor of Professor Chen Piji for his great contribution to Chinese geology and generous support of the development of STM.

Locality and horizon Xisanjia locality, Ningcheng, Nei Mongol, China. Lower Cretaceous Yixian Formation (approximately 125 Ma) (Zhou et al., 2003; Chang et al., 2009).

Diagnosis Hongshanornithid with the unique combination of the following features: teeth preserved on both the upper and lower jaws; premaxillary and maxillary teeth much larger than dentary teeth; rostral half of the dentary is very straight, rather than sigmoidal; ratio of the craniocaudal (omal-sternal) length of the coracoid relative to the distal width is approximately 1.6; U-shaped furcula without hypocleidium; sternum with angular rostral margin (~96°); sternal lateral trabecula distally expanded; uncinate processes elongate, crossing two adjacent ribs.

Measurements See Table 1.

Table 1 Selected measurements of *Tianyuornis cheni* gen. et sp. nov. (STM7-53) (mm)

Skull length	30	Femur length (L)	23.5
Dentary (mandible) length	21.5*	Tibiotarsus length (R)	33*
Coracoid length (R)	11.5	Tibiotarsus length (L)	34*
Coracoid maximum width (R)	7*	Tarsometatarsus I length (L)	3.5
Coracoid length (L)	11	Tarsometatarsus II length (L)	17.8
Coracoid maximum width (L)	6.7*	Tarsometatarsus III length (L)	20
Sternum length	19	Tarsometatarsus IV length (L)	18.5
Sternum width (cranial)	13	Pedal digit I-1 length (L)	4.1
Humerus length (L)	24.3*	Pedal digit I-2 length (L)	2.5
Ulna length (L)	24.5*	Pedal digit II-1 length (L)	6
Radius length (L)	23.8	Pedal digit II-2 length (R)	5.1
Carpometacarpus length (L)	13	Pedal digit II-3 length (L)	3.2
Metacarpal I length (L)	2.7	Pedal digit III-1 length (L)	7.5*
Metacarpal II length (L)	13	Pedal digit III-2 length (R)	5.3*
Metacarpal III length (L)	10.7	Pedal digit III-3 length (R)	4.5
Manual digit I-1 length (L)	6.6	Pedal digit III-4 length (R)	4
Manual digit I-2 length (L)	3.7*	Pedal digit IV-1 length (L)	3.8*
Manual digit II-1 length (L)	6.2	Pedal digit IV-2 length (R)	3.5
Manual digit II-2 length (L)	4.9	Pedal digit IV-3 length (R)	3.3
Manual digit II-3 length (L)	2.6*	Pedal digit IV-4 length (R)	3
Manual digit III-1 length (L)	3	Pedal digit IV-5 length (R)	2.6
Manual digit III-2 length (L)	Just a dot	Pygostyle length	3.3

The asterisk denotes estimated lengths; L. left; R. right.

3 Comparative description

The holotype of *Tianyuornis cheni* gen. et sp. nov. (STM7-53) is preserved in two slabs; the bones are torn between the two slabs so that a majority of the skeleton is exposed in ventral view in the slab (slab A) and dorsal view in the counterslab (slab B). Most of the anatomical information is preserved in slab A. The bone is poorly preserved and permineralized by an iron rich (inferred by its reddish color) mineral that obscures some morphologies (particularly in the skull). The new specimen is similar in size to *Hongshanornis longicresta* and *Longicrusavis houi* (Zhou and Zhang, 2005; O'Connor et al., 2010), but probably represents a subadult individual because several compound bones are poorly fused (e.g. carpometacarpus and tibiotarsus).

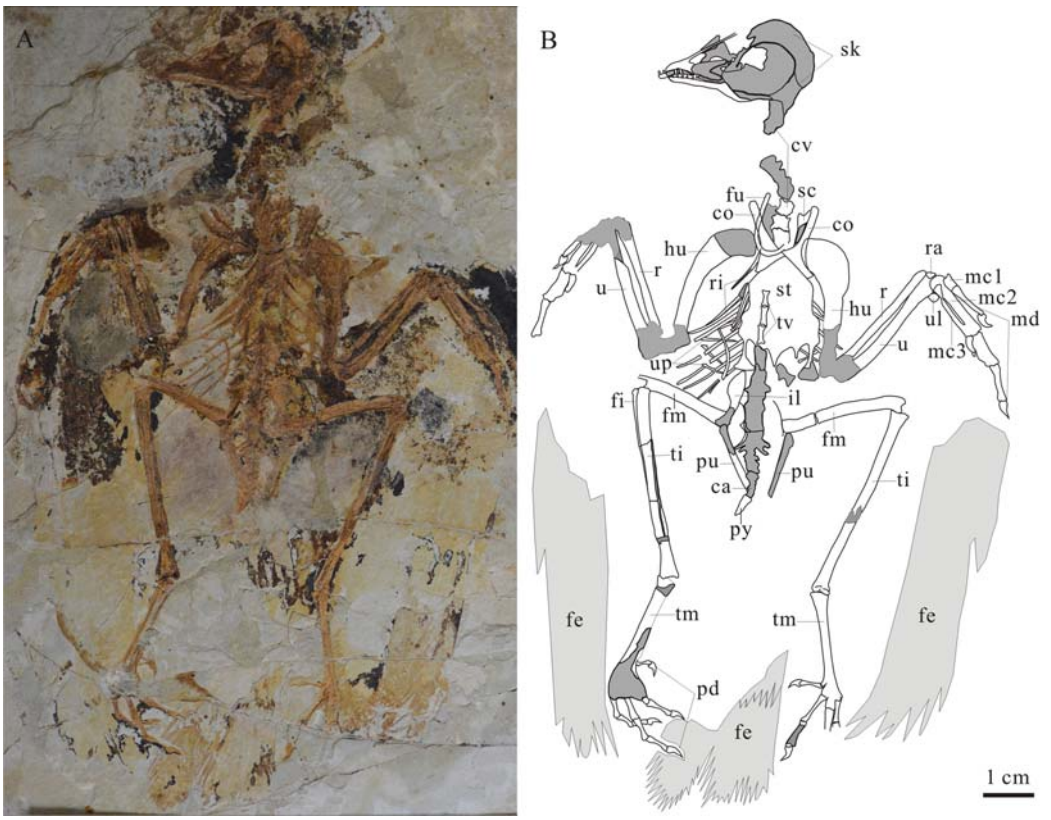

Fig. 1 Photograph (A) and line drawing (B) of *Tianyuornis cheni* gen. et sp. nov. (STM7-53A)
Dashed regions in the line drawing indicate the obscure margin of bones, and the gray part indicates the broken or crushed areas and feather impressions
Abbreviations: ca. caudal vertebrae 尾椎; co. coracoid 乌喙骨; cv. cervical vertebrae 颈椎; fe. feather 羽毛; fi. fibula 腓骨; fm. femur 股骨; fu. furcula 叉骨; hu. humerus 肱骨; il. ilium 髂骨; mc1. alular metacarpal 翼掌骨; mc2. major metacarpal 大掌骨; mc3. minor metacarpal 小掌骨; md. manual digit 指骨; pd. pedal digit 趾骨; pu. pubis 耻骨; py. pygostyle 尾综骨; r. radius 桡骨; ra. radiale 桡腕骨; ri. ribs 肋骨; sc. scapula 肩胛骨; sk. skull 头骨； st. sternum 胸骨; ti. tibiotarsus 胫跗骨; tm. tarsometatarsus 跗跖骨; tv. thoracic vertebrae 胸椎; u. ulna 尺骨; ul. ulnare 尺腕骨; up. uncinate process 钩状突

Skull Although the skull is largely complete, the thin skull bones have been laterally compacted, making it difficult to recognize structures and interpret their details. In slab A, the skull is exposed in left lateral view, showing an expanded braincase, large orbit, and tapered rostrum, giving the skull an overall triangular shape (Figs. 2, 3). The base of the rostrum is poorly preserved but it is not marked by a strong constriction of the skull, as in *H. longicresta* (Zhou and Zhang, 2005), so that the dorsal margin of the skull is only slightly concave, as in *L. houi* (O'Connor et al., 2010).

The premaxilla appears fused rostrally but unfused along the length of the slender frontal (nasal) processes (Fig. 3). These processes appear to be elongate, ending level with the distal margin of the nasal (slab B), suggesting they articulated with the frontals, as in Neornithes. The

rostrum of *Tianyuornis* is more robust than *H. longicresta* (Zhou and Zhang, 2005) based on the angle formed by the nasal and maxillary processes of the premaxilla, but similar to *L. houi* (O'Connor et al., 2010). The maxilla and premaxilla are unfused; the corpus of the premaxilla appears short and is dotted by numerous nutrient foramina, as in *H. longicresta*. The maxilla is poorly preserved. The nasal process of the maxilla is delicate, longer than that preserved in *L. houi* (O'Connor et al., 2010) and articulates with the nasal, forming the ventral margin of the external nares. The naris is large and elliptical (Fig. 3). The right nasal is disarticulated and in dorsal view, completely preserved in slab B (Fig. 2). The rostral third is sharply tapered. The short maxillary process defines a rostral concavity that forms the caudal margin of the external nares. The caudal end of the left nasal is poorly preserved; it appears to have a tapered caudal margin and articulate with the frontal.

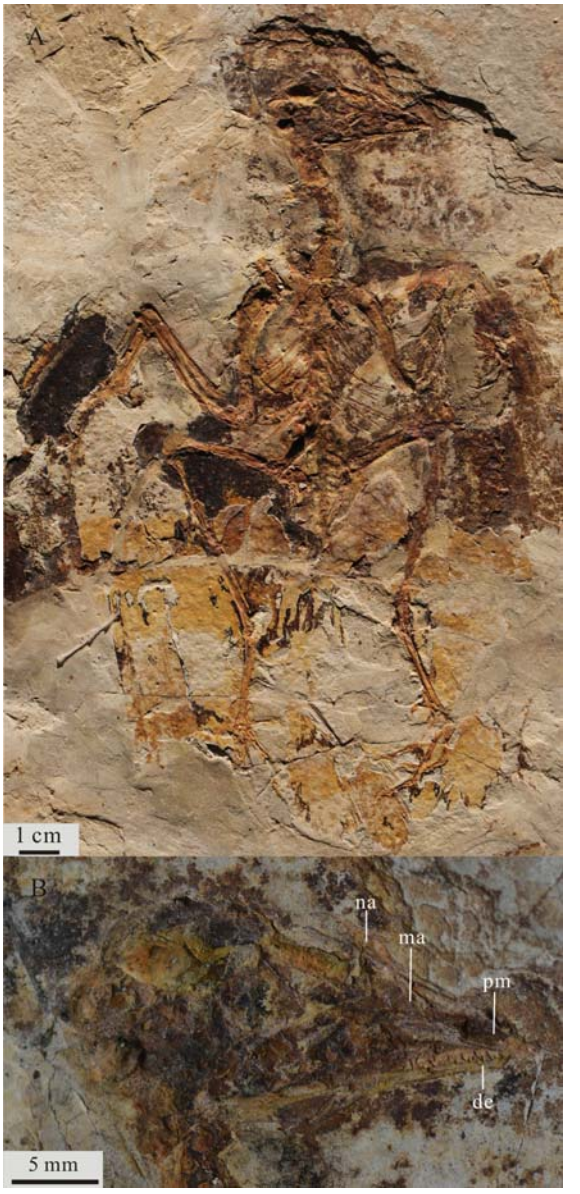

Fig. 2 Photograph (A) and close-up of the skull (B) of *Tianyuornis cheni* gen. et sp. nov. (STM7-53B)
Abbreviations: de. dentary 齿骨; ma. maxilla 上颌骨; na. nasal 鼻骨; pm. premaxilla 前上颌骨

The mandibular symphysis appears to be unfused although the rostral portion is broken so this is unclear; the dentaries are preserved separatedly with the right dentary displaced from the left one (Fig. 3). No predentary is preserved. The dentary forms more than half the length of the lower jaw. The rostral half of the dentary is very straight; while those of both *H. longicresta* and *L. houi* have a distinctly sigmoidal shape (Zhou and Zhang, 2005; O'Connor et al., 2010). The dentary expands ventrally along the distal quarter, and tapers caudally lacking a dorsal process (Fig. 3). As in *H. longicresta* and *L. houi*, no mandibular fenestrae is present (Zhou and Zhang, 2005; O'Connor et al., 2010). The holotype of *Parahongshanornis chaoyangensis* (Li et al., 2011) lacks a skull, so it cannot be compared to the new specimen.

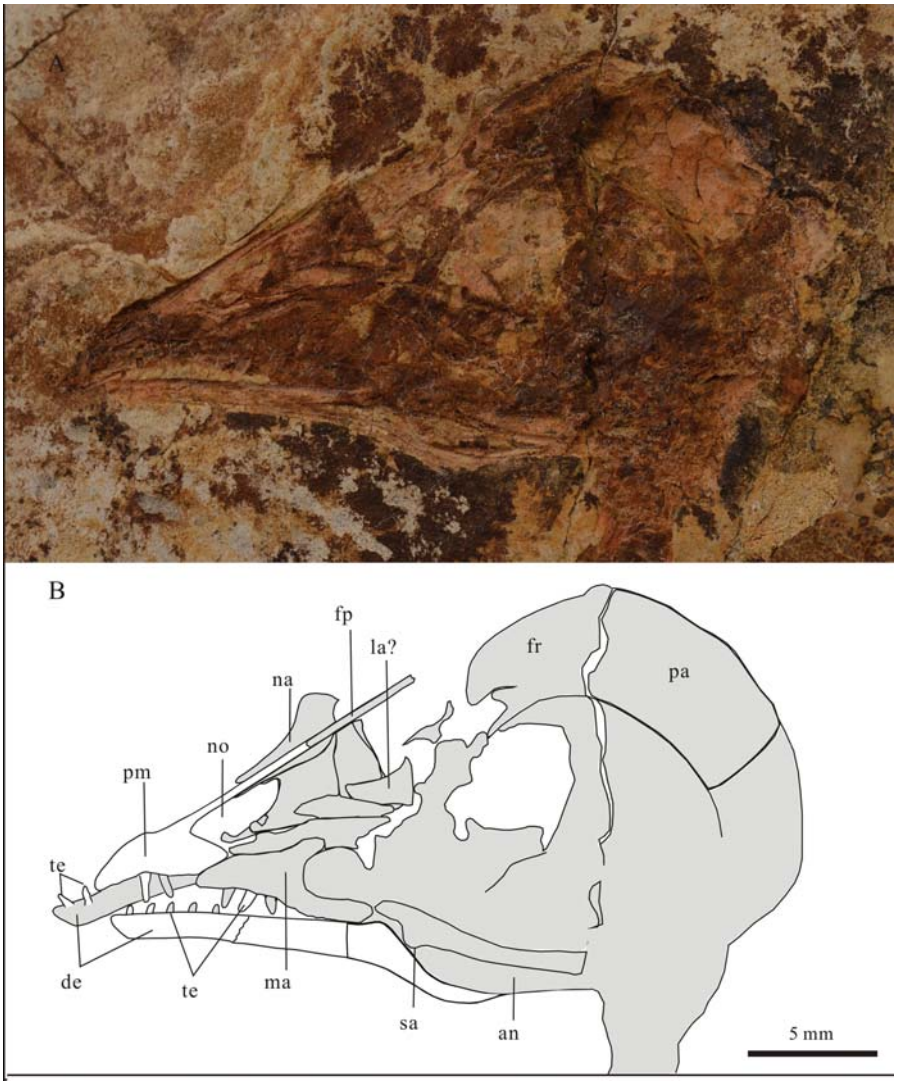

Fig. 3 Photograph (A) and line drawing (B) of the skull of *Tianyuornis cheni* gen. et sp. nov. (STM7-53A) Abbreviations: an. angular 隅骨; de. dentary 齿骨; fp. frontal processes of premaxilla 前颌骨额突; fr. frontal 额骨; la?. lacrimal? 泪骨?; ma. maxilla 上颌骨; na. nasal 鼻骨; no. naris 鼻孔; pa. parietal 顶骨; pm. premaxilla 前颌骨; sa. surangular 上隅骨; te. teeth 牙齿

Teeth are preserved on both the upper and lower jaws (Figs. 2, 3). *Hongshanornis* (Zhou and Zhang, 2005) is described as toothless, but O'Connor et al. (2010) noted the presence of alveoli in both the premaxilla and maxilla of the holotype of *L. houi* and *H. longicresta*. *Tianyuornis* preserves two teeth in the right premaxillary corpus (Fig. 3). The root and crown are both exposed; the teeth are not strongly constricted at the base of the crown. There are three large, conical teeth preserved in the right maxillary (Fig. 3). Five small teeth are clearly preserved in the left dentary. The teeth are sparsely arranged; the space between two adjacent

teeth is more than twice the width of a single tooth (Fig. 3). The teeth are subconical with slightly caudally recurved tips (as in other early birds, e.g. *Eoenantiornis buhleri*, Zhou et al., 2005; *Yanornis martini*, Zhou and Zhang, 2001). The premaxillary and maxillary teeth are more closely arranged and considerably larger than the dentary teeth.

Vertebral column The vertebral column is poorly preserved. Several distal cervical vertebrae are missing, so the exact number of cervicals can not be determined. The first two cervical vertebrae are preserved in articulation with the skull, but no morphological details can be discerned. Visible in slab A, three distal cervicals reveal distinctly keeled ventral margins (Fig. 4). Cervical ribs are delicate.

The thoracic vertebrae are articulated but largely covered by elements of the thoracic girdle. In slab A, two or three thoracic vertebrae are visible as impressions underlying the sternum (Fig. 4). These vertebrae are longer and narrower than the cervical vertebrae, with spool-shaped centra. At least ten pairs of long thoracic ribs are present, with long, unfused uncinate processes (visible in slab A) that cross two ribs (Figs. 1, 4). The uncinate processes are expanded at their base, as in *Chaoyangia* (O'Connor and Zhou, 2013). The holotype of *H. longicresta* (Zhou and Zhang, 2005) only preserves free uncinate processes, which are much shorter. Uncinate processes are not preserved in *L. houi* (O'Connor et al., 2010) or *P. chaoyangensis* (Li et al., 2011). Sternal ribs are preserved in articulation with the sternum; they are more than half the length of the thoracic ribs. A few gastralia are preserved overlapped by the pelvic girdle.

The synsacrum is poorly preserved in both slabs, yielding limited anatomical details (Fig. 1). The caudal-most sacral transverse processes are caudally deflected. A short, plough shaped pygostyle is preserved in articulation with the free caudal vertebrae. The caudal vertebrae are poorly preserved, the last free caudal appears to have elongate transverse processes that exceeded the width of the centrum. The pygostyle does not appear to fuse completely, suggesting STM7-53 is a subadult.

Thoracic girdle Only the proximal end of the left scapula is visible in slab A (Fig. 4). The distal half is overlain by the coracoid and sternum, although a very faint impression of the tapered and curved scapular blade is visible through the sternum. Although very poorly preserved, the acromion appears short and delicate, as in other hongshanornithids.

Both strut-like coracoids are exposed in ventral view in slab A (Figs. 1, 4). The ratio of the craniocaudal (omal-sternal) length of the coracoids to their width is approximately 1.6, which is less than the other hongshanornithids. In *H. longicresta* and *L. houi* (Zhou and Zhang, 2005; O'Connor et al., 2010), the length is approximately twice the width, while the same ratio in *P. chaoyangensis* (Li et al., 2011) is even larger (approximately 2.3). A procoracoidal process appears preserved on the right coracoid; it has a long base, is laterally oriented and the medial margin is blunt. A lateral process is present and lacks a cranially deflected projection, like other Jehol ornithuromorphs.

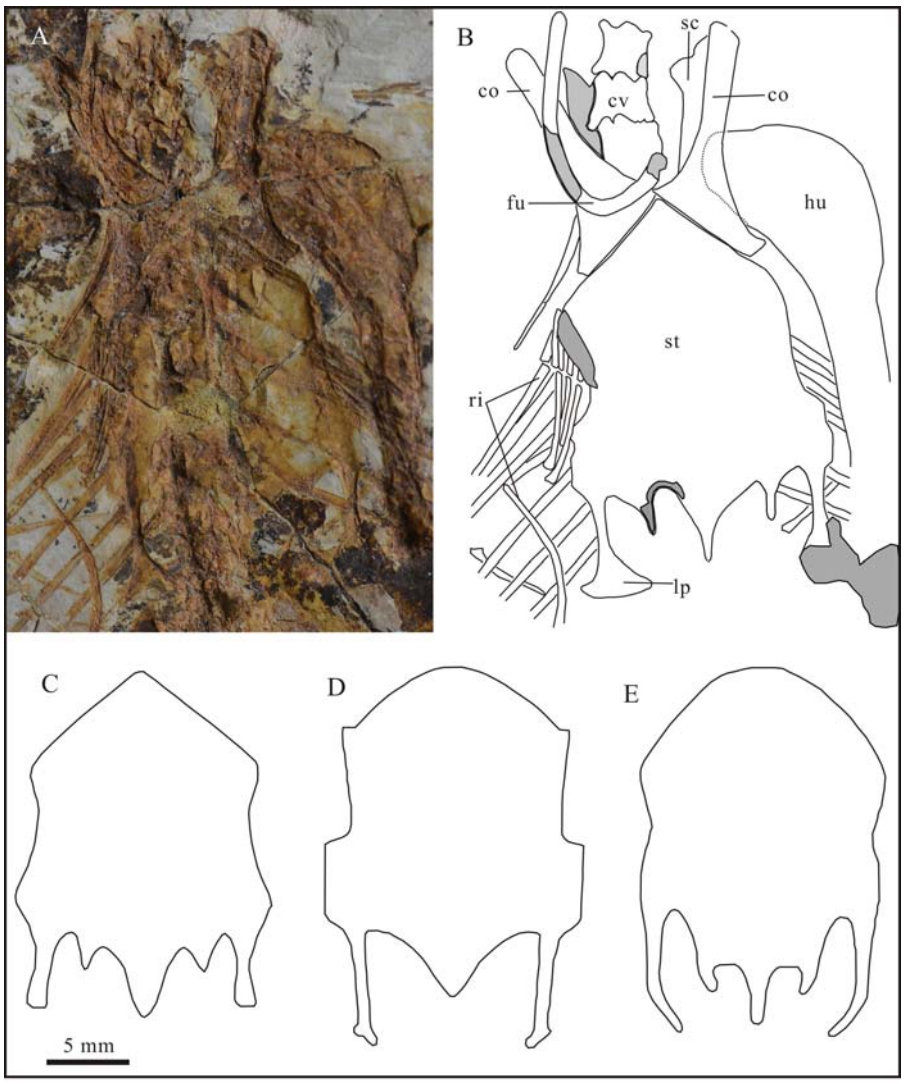

Fig. 4 Pectoral girdle and sternum of *Tianyuornis cheni* gen. et sp. nov. (STM7-53) and a comparison of sternum within Hongshanornithidae

A-B. Photograph (A) and line drawing (B) of *Tianyuornis cheni*, dashed line indicate the obscure margin of left humeral head, and the gray part indicates the broken or crushed areas (STM7-53); C. *Parahongshanornis chaoyangensis*; D. *Longicrusavis houi*; E. *Hongshanornis longicresta*; C, D and E modified from O'Connor et al. (2010) and Li et al. (2011)

Abbreviations: co. coracoid 乌喙骨; cv. cervical vertebrae 颈椎; fu. furcula 叉骨; hu. humerus 肱骨; lp. lateral process of sternum 胸骨后外侧突; ri. ribs 肋骨; sc. scapula 肩胛骨; st. sternum 胸骨

The furcula is broken, missing the omal two-thirds of the left ramus (Figs. 1, 4). As in other hongshanornithids, the bone is U-shaped and delicate. The clavicular symphysis lacks a prominent hypocleideum, possessing only a very small tubercle, similar to *L. houi* and *P. chaoyangensis* (O'Connor et al., 2010; Li et al., 2011), but different from *H. longicresta*

(Zhou and Zhang, 2005) in which the furcula possesses a short tapered hypocleidium (considered absent by O'Connor et al., 2010).

The sternum is nearly completely preserved in ventral view (Figs. 1, 4). It is craniocaudally elongate (length/width≈1.4). The rostral margin forms an obtuse angle (96°) defined by the coracoidal sulci, similar to *P. chaoyangensis* whose rostral margin angle is about 110° (Li et al., 2011), but different from that of *H. longicresta* and *L. houi* (Zhou and Zhang, 2005; O'Connor et al., 2010), in which the sternal cranial margin is more broadly parabolic. The craniolateral margins are rounded, not forming distinct processes. An ossified carina appears to have been present, extending nearly the entire length of the sternum, as in other ornithuromorphs (caudally restricted in enantiornithines, Zhou, 2002). The carina does not appear to reach the rostral margin, similar to *Yixianornis* (Zhou and Zhang, 2001; Clarke et al., 2006). Proximal to the lateral trabecula, the lateral margin bears a rostrodistally elongate rectangular lateral process (zyphoid process, Clarke et al., 2006) similar to that of *L. houi* (O'Connor et al., 2010). Caudally, the sternum has two pairs of incisions, unlike *L. houi* (O'Connor et al., 2010), which lacks intermediate trabeculae and thus has only a single pair of caudal incisions. In *Tianyuornis*, the lateral trabeculae are strap-like and parallel to each other (caudally directed), as in *L. houi* and *P. chaoyangensis* (O'Connor et al., 2010; Li et al., 2011) (curved in *H. longicresta* (Zhou and Zhang, 2005)), with distinct fan-shaped distal expansions. The distal ends are not distinctly expanded in other hongshanornithids, but distally expanded trabeculae are present in many other ornithuromorphs (e.g. *Yanornis*, *Yixianornis*, *Songlingornis*) (Zhou and Zhang, 2001; Clarke et al., 2006; Hou, 1997). The distal ends of the lateral trabeculae extend caudally slightly beyond the distal end of the xiphoid process. The intermediate trabeculae appear short but they are poorly preserved and their morphology remains unclear (Fig. 4). The xiphial region defines a wide V before constricting into a short xiphoid process.

Thoracic limb The forelimbs are preserved in articulation, clearer in slab A (humerus in cranial view) (Fig. 5). The humerus is fairly robust and twisted so that the distal end is in a different plane with the proximal end. The proximal head appears flat, but this may be due to artifact of poor preservation. The large, rounded deltopectoral crest extends approximately two-fifths the total length of the humerus, similar to *L. houi* (O'Connor et al., 2010). Distally, the cranial surface is excavated in the region of the brachial impression proximal to the bulbous condyles; no other morphological details can be recognized. The ulna is subequal to the humerus in length, as in other hongshanornithids. The ulna is slightly bowed proximally, while the radius is straight, and its midshaft thickness is about 2/3 that of the ulna. Quill knobs (remige papillae) are absent, as in other Early Cretaceous ornithuromorphs. The ulnare is larger than the radiale, and appears to be heart-shaped, but not V-shaped with well developed rami; the radiale is subtriangular. The ulnare and radiale are sub-equal in size in *L. houi* (O'Connor et al., 2010).

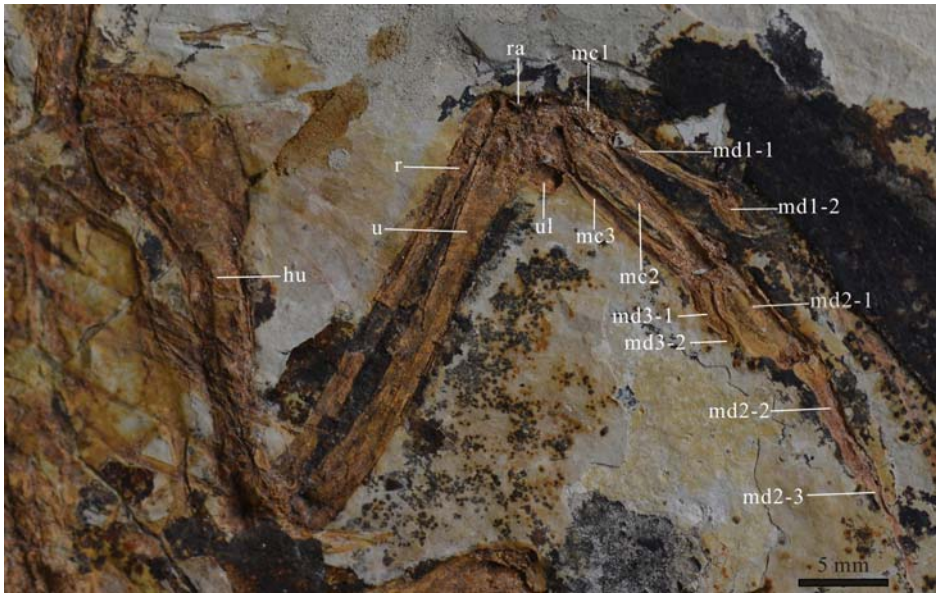

Fig. 5 The left wing of *Tianyuornis cheni* gen. et sp. nov. (STM7-53A)

Note that the minor metacarpal is not fused proximally with the semilunate carpal and major metacarpal completely while the distal end of the carpometacarpus appear fused

Abbreviations: hu. humerus 肱骨; mc1. alular metacarpal 翼掌骨; mc2. major metacarpal 大掌骨; mc3. minor metacarpal 小掌骨; md1-1 or 2. first or second phalanx of first digit 第一指第1或2指节; md2-1, 2 or 3. the first, second or third phalanx of the main digit 主指的第1, 2或3指节; md3-1 or 2. first or second phalanx of the minor digit 小指的第1或2指节; r. radius 桡骨; ra. radiale 桡腕骨; u. ulna 尺骨; ul. ulnare 尺腕骨

The manus is longer than the humerus and ulna as in other hongshanornithids and most basal birds. Proximally, the semilunate carpal covers the proximal end of the major metacarpal and the two are partially fused; the minor metacarpal appears unfused to the major metacarpal and the semilunate carpal indicating the specimen is a subadult (Fig. 5). Distally, the major and minor metacarpals appear fused; the major metacarpal extends slightly farther than the minor metacarpal, in contrast to the enantiornithines condition (Chiappe and Walker, 2002). The major metacarpal is straight, and the minor metacarpal is slightly bowed, creating a long and narrow intermetacarpal space. The proximal end of the minor metacarpal is expanded and extends onto the ventral surface of the major metacarpal forming a pisiform process. The minor metacarpal is pinched level with the distal margin of the alular metacarpal and is approximately half the width of the major metacarpal (Fig. 5). The alular metacarpal is rectangular and remains unfused to the major metacarpal; the craniolateral margin forms a slight proximal projection.

The manual phalangeal formula is 2-3-2-x-x, as in the other hongshanornithids (Fig. 5). The alular digit is slender, slightly distally surpassing the distal end of the major metacarpal. The first phalanx of the alular digit is long and tapers distally; the alular ungual is nearly the same size as the major ungual. The first phalanx of the major digit is dorsoventrally expanded

as in other ornithuromorphs. The second phalanx of the major digit is approximately the same length as the first phalanx but is much more slender and slightly sigmoidal. The minor digit is very short, comprised of two small phalanges, the distal of which is extremely reduced; this digit tightly abuts the first phalanx of the major digit (Fig. 5).

Pelvic girdle The pelvic girdle is in articulation, but the bones are badly crushed and overlapping; it is unclear whether the bones are fused. The ilia do not approach each other on the midline; the craniolateral margins are rounded and convex. The lateral margin appears concave. The ischia are not visible. The pubis is slender; the distal ends are not preserved but the two pubes approach each other distally as if to form a symphysis.

Pelvic limb As in other hongshanornithids, the hindlimb is much longer than the wing with an intermembral index (humerus+ulna+metacarpal II/femur+tibiotarsus+metatarsal III) of 0.78 (0.79 in *H. longicresta*; 0.78 in *L. houi*; 0.80 in *P. chaoyangensis*) (Zhou and Zhang, 2005; O'Connor et al., 2010; Li et al., 2011). The femur is slightly curved, as in other hongshanornithids. The length ratio of the femur to tibiotarsus is approximately 0.70, which is relatively larger than in other hongshanornithids (the same ratio is 0.58 in *H. longicresta*; 0.63 in *P. chaoyangensis*; and 0.65 in *L. houi*) (Zhou and Zhang, 2005; Li et al., 2011; O'Connor et al., 2010). The tibiotarsus is relatively shorter than other hongshanornithids, resulting in a larger femur to tibiotarsus ratio.

The tibia and the proximal tarsals appear incompletely fused, although well ankylosed, further supporting interpretations that this specimen is a subadult (Fig. 6). Proximally, the cranial surface of the tibiotarsus bears a cnemial crest. Poor preservation prevents determining if it projected proximally, as in some other ornithuromorph birds—the crest does not project proximally in *L. houi* (O'Connor et al., 2010). The distal end of the crest is medial to the proximal portion. A short laterally directed fibular crest is present, extending for less than one fifth of the tibiotarsus. Distally the condyles appear subequal and tapered

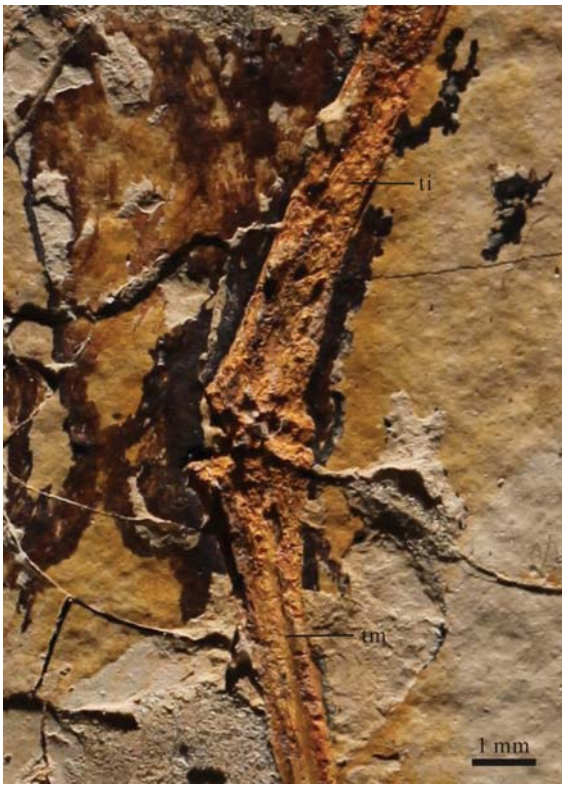

Fig. 6 The distal end of the left tibiotarsus of *Tianyuornis cheni* gen. et sp. nov. (STM7-53A), showing the tibia and the proximal tarsus seems not fused completely
Abbreviations: ti. tibiotarsus 胫跗骨; tm. tarsometatarsus 跗蹠骨

towards each other medially. The thin fibula extends more than halfway down the tibiotarsus.

The tarsometatarsus is completely fused proximally as in other ornithuromorphs; it is slightly more than half the length of the tibiotarsus (Fig. 1). Proximally, metatarsal III appears plantarly displaced relative to metatarsals II and IV, as in other ornithuromorphs (O'Connor et al., 2010). Metatarsal IV is subequal in width to metatarsal II, not reduced as in Enantiornithes (Chiappe, 1993). Metatarsal III is the longest; the proximal end of the metatarsal III trochlea is distal to the trochlea of metatarsals II and IV. Metatarsal IV projects distally slightly farther than metatarsal II, as in *L. houi* and *Archaeorhynchus spathula* (O'Connor et al., 2010; Zhou and Zhang, 2006). The distal trochlea of metatarsal III is slightly wider than that of metatarsals II and IV, which are subequal in width, as in *P. chaoyangensis* (Li et al., 2011). Metatarsal I articulates with the medial surface of metatarsal II at a relatively high position, not overlapping the proximal margin of the metatarsal II trochlea, and the distal end is curved medially.

Both feet are nearly complete, preserved in articulation with a phalangeal formula of 2-3-4-5-x. The proximal phalanges are longer than distal phalanges. The phalanges of the hallux are delicate. The claws are relatively uncurved, as in other hongshanornithids and terrestrial birds in general, and similar in size, although the third digit ungual is the largest and the hallucal claw is the smallest.

Feathers Feathers of the wing and tail are partially preserved as impressions. Although only the distal ends of two rectrices are clearly preserved, it appears a long, graded, fan-shaped feathered tail was present, as in *H. longicresta* (Zhou and Zhang, 2005). The rectrices have symmetrical vanes with broad and rounded caudal margins (Fig. 1).

4 Discussion

Although the holotype of *Tianyuornis cheni* is based on a subadult individual, it can still be distinguished from other known Mesozoic birds. Several ornithuromorph synapomorphies are preserved, such as a U-shaped furcula, craniocaudally elongate sternum, derived manus with a robust, craniocaudally expanded first phalanx in the major digit, metacarpals II and III subequal in distal extent, and a completely fused tarsometatarsus (Fig. 1). The new taxon is morphologically very similar to members of the clade Hongshanornithidae, which so far consists of three taxa, *Hongshanornis longicresta*, *Longicrusavis houi*, and *Parahongshanornis chaoyangensis* (Zhou and Zhang, 2005; O'Connor et al., 2010; Li et al., 2011). These taxa are all small (Table 1), comparable in size to a modern phoebe (*Sayornis*) and possess elongate hindlimbs relative to the forelimbs. With four taxa, Hongshanornithidae is currently the most diverse recognized clade of Early Cretaceous ornithuromor

The holotype of *Tianyuornis cheni* is found from Ningcheng, Nei Mongol, the same locality that yielded the holotype of *H. longicresta* (Zhou and Zhang, 2005), but it appears more similar to *L. houi* (O'Connor et al., 2010) from Lingyuan, Liaoning Province, in having a relatively more robust rostrum. Moreover, the new bird is also very similar to *P. chaoyangensis*

(Li et al., 2011) from Chaoyang, Liaoning Province, in that the rostral margin forms an obtuse angle (96°), the distal trochlea of metatarsal III is slightly wider than that of metatarsals II and IV, while the latter two are subequal in width. Nevertheless, the new specimen possesses a unique suite of morphologies that support the erection of a new taxon: teeth are preserved on both upper and lower jaws; sternal caudolateral trabecula with large distal expansion; straight dentary; uncinate processes elongate, crossing two adjacent ribs; proportionately shorter tibiotarsus and humerus (femur to tibiotarsus length ratio is 0.70, humerus is subequal to the ulna in length); and a proportionately shorter and wider coracoid.

Compared to previously described hongshanornithids, *Tianyuornis cheni* has a proportionately shorter tibiotarsus and humerus (Table 2), while the other long bones are nearly the same in length (e.g. ulna, carpometacarpus, femur, and tarsometatarsus); at the same time all hongshanornithids have a similar forelimb to hindlimb ratio. The holotype of *Tianyuornis cheni* is considered a subadult and thus potentially the relatively shorter tibiotarsus and humerus are the result of allometric growth and subadult ontogenetic stage of the new specimen, that is to say, the tibiotarsus and humerus are inferred to have still been growing when the individual died, so that the limb proportions would have been comparable to other hongshanornithid birds in the adult of *Tianyuornis cheni*. If this is the case, then suggest that, at least in hongshanornithids, the humerus is the last forelimb element to complete growth, while the tibiotarsus is the last element of the hindlimb to complete ossification. Alternatively, *Tianyuornis cheni* characteristically possesses a relatively shorter humerus and tibiotarsus compared to other hongshanornithid birds. But until new specimens are available to elucidate this issue, these two characters (relatively shorter humerus and tibiotarsus) can be regarded as diagnostic features of the new taxon. However, recent studies on enantiornithine histology show that during subadult growth, the humerus grows faster than the femur (O'Connor et al., 2014), supporting the former hypothesis.

Table 2 Measurements and proportions of *Tianyuornis cheni* gen. et sp. nov. (STM7-53), compared with the other three known Hongshanornithidae birds (mm)

	Hongshanornis longicresta (IVPP V 14533)	*Longicrusavis houi* (PKUP V 1069)	*Parahongshanornis chaoyangensis* (PMOL-AB00161)	*Tianyuornis cheni* (STM7-53)
Humerus length	26	26	29	24.3*
Ulna length	24	25	27	24.5*
Carpometacarpal II length	13	13.1	12.3	13
Femur length	22	24.3	24	23.5
Tibiotarsus length	38	37.6	38	34
Metatarsal III length	22	21.5	22	20
Femur/tibiotarsus	0.58	0.65	0.63	0.7
Hu+U+McII/Fe+Ti+TmIII	0.79	0.78	0.8	0.78

The asterisk denotes estimated lengths; Hu. humerus 肱骨; U. ulna 尺骨; McⅡ. major metacarpal 大掌骨; Fe. femur 股骨; Ti. tibiotarsus 胫跗骨; TmⅢ. tarsometatarsus Ⅲ 第三跗跖骨.

The carpometacarpus is only fused distally in the new specimen (Fig. 5), a condition that has only been previously reported in *Jianchangornis microdonta* (Zhou et al., 2009). This observation led authors to infer that fusion of the carpometacarpus in Ornithuromorpha proceeds from the distal end, the opposite of the condition observed in Enantiornithes. This interpretation is supported here and indicates that, although the new specimen is a subadult, it was most likely near somatic maturity.

One of the most important preserved features of the new specimen is the definitive presence of teeth. Teeth were reported absence in *H. longicresta*, which compared to other hongshanornithids has a more delicate rostrum. *L. houi* (O'Connor et al., 2010) does not preserve teeth but aveoli can be observed in the premaxilla and maxilla, which lead authors to suggest that teeth were in fact present in hongshanornithids; aveoli were also described as present in the upper jaw of *H. longicresta* (O'Connor et al., 2010). The new specimen preserves teeth in both the upper and lower jaws, confirming the presence of teeth in the clade and increasing their known distribution—dentary teeth were not previously recognized. Furthermore, the teeth of the upper jaw are considerably larger than the teeth of the lower jaw; this is the first report of heterodont dentition in an Early Cretaceous ornithuromorph. This indicates that, although there is a trend towards tooth reduction in the clade, dental adaptations were also far more diverse in this clade than previously inferred (O'Connor et al., 2013). Teeth are energetically costly structures, and thus are not without function. This suggests that in some ornithuromorph lineages, teeth remained important for manipulating food (Louchart and Viriot, 2011). Morphological differences in dentition between hongshanornithids and other ornithuromorphs can be attributed to ecological specialization in different lineages. The large, numerous, and recurved teeth of *Yanornis* are clearly suitable for a carnivorous diet, supported the associated fish remains in at least one specimen (Zhou et al., 2002). Direct evidence suggests hongshanornithids fed on seeds preserved in the crop and stomach of some specimens; gizzard stones are also preserved (Zheng et al., 2011). The robust, heterodont morphology of the teeth in hongshanornithids may suggest the group had a more omnivorous diet; this is supported by their inferred ecological niche, as shallow wading birds. Although one specimen preserves seeds, hongshanornithids may have been more opportunistic feeders.

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红山鸟科(今鸟类)一新属种

郑晓廷[1,2] 邹晶梅[3] 王孝理[1,2] 张晓梅[1,2] 王 岩[1,4]

(1 临沂大学地质与古生物研究所 山东临沂 276005)

(2 山东省天宇自然博物馆 山东平邑 273300)

(3 中国科学院脊椎动物演化与人类起源重点实验室，中国科学院古脊椎动物与古人类研究所 北京 100044)

(4 现代古生物学和地层学国家重点实验室，中国科学院南京地质古生物研究所 南京 210008)

摘要：根据发现于内蒙古宁城早白垩世义县组地层中一件保存近乎完整的亚成年鸟类标本，报道了早期今鸟型类一新属、新种——陈氏天宇鸟(*Tianyuornis cheni* gen. et sp. nov.)。新属种与红山鸟科(高冠红山鸟*Hongshanornis longicresta*, 侯氏长腿鸟*Longicrusavis houi*及朝阳副红山鸟*Parahongshanornis chaoyangensis*)的特征最为相近，如体型大小相似，后肢明显长于前肢等；但也具有一系列与其他红山鸟科成员不同的特征，包括上下颌都保存有牙齿，齿骨直(特殊的“S”形齿骨曾被认为是红山鸟科鸟类的近裔特征)，胸骨后外侧突远端呈扇形扩展等。这些特征表明新标本为红山鸟科一新属种。该新属种的发现使红山鸟科成为已知种属分化最丰富的早白垩世今鸟类群。另外，新标本也丰富了红山鸟科鸟类许多新的重要形态学信息，证实这一支系鸟类仍保留有牙齿结构。

关键词：内蒙古宁城，早白垩世，义县组，今鸟型类，红山鸟科

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