

辽西早白垩世今鸟类一新属种¹⁾

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摘要:根据发现于辽宁西部建昌早白垩世九佛堂组一件保存较为完好的标本,描述了原始今鸟类一新属种,李氏叉尾鸟(*Schizooura lii* gen. et sp. nov.)。系统发育分析表明,它较建昌鸟和古喙鸟进步,但又较热河生物群中其他已知的今鸟类原始。这一新种叉骨呈V型,且具有一短的叉骨突,这是这一特征首次在早白垩世今鸟中发现。其胸骨加长,后缘无窗孔,且无很深的凹口。肱骨三角肌脊膨大,近乎达到肱骨长的一半。新鸟的头骨保存较好,显示其具喙的特征,前颌骨直接与额骨相关节。值得关注的是,这件标本首次展示了在中生代鸟类中,除扇形尾羽之外的第二种尾羽类型。新标本具叉形尾羽,中间分隔明显。对现生鸟类的研究表明,叉尾型的空气动力学效率比扇尾型要低,但在性选择方面具有优势。这一新的发现说明,在热河生物群生活的森林环境中,今鸟类的基干种类在尾羽性状上或许已经存在着不同的选择策略。

关键词:辽宁建昌,早白垩世,九佛堂组,今鸟类,喙,舵羽,叉尾型

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A NEW BASAL BEAKED ORNITHURINE BIRD FROM THE LOWER CRETACEOUS OF WESTERN LIAONING, CHINA

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Abstract We report a new species of basal ornithurine bird, *Schizooura lii* gen. et sp. nov., based on a well-preserved specimen from the Lower Cretaceous Jiufotang Formation in Jianchang, western Liaoning, China. Phylogenetic analysis indicates that it is more derived than *Jianchangornis* and *Archaeorhynchus*, but more basal than all other known Jehol ornithurines. The new specimen preserves a unique suite of characters that differentiate it from other known taxa, including several features previously unreported in Early Cretaceous ornithurines, including a V-shaped furcula with a short hypocleidium, a rostrocaudally elongate unperforated sternum with deep caudal notches absent, and a deltopectoral crest that extends for half the length of the humerus. The specimen preserves a nearly perfectly articulated skull that indicates the species was beaked and preserves details of the skull anatomy such as the premaxilla-frontal articulation. The most notable feature of this new specimen is the preservation of a feathered tail morphology previously unknown among Mesozoic birds. It is the second tail morphology known among early ornithurines, which have until now only preserved fan-shaped tails. The new specimen

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preserves a forked tail composed of elongate rectrices medially separated by a deep notch. This tail feather morphology in modern birds decreases aerodynamic efficiency relative to the fan-shaped tail, but increases chance of sexual reproduction. This discovery suggests that this tradeoff convergently evolved in basal members of Ornithurae, and is consistent with the wooded environment inferred for the Jehol.

Key words Jianchang, Liaoning, China; Early Cretaceous; Jiufotang Formation; ornithurine; beak; rectrices; forked tail

1 Introduction

Over 30 genera of Early Cretaceous birds have been reported in the last two decades from the Lower Cretaceous of northeastern China (Zhou et al., 2010); the Jehol avifauna is unique in that it preserves long-tailed birds, the oldest known birds with a pygostyle, the dominant enantiornithines and the earliest record of the clade that includes modern birds, the Ornithurae (= Ornithuromorpha), coexisting within a single ecosystem (Zhou and Zhang, 2006a). Not only does the Jehol Group record the earliest basal ornithurine fossils, but also the most complete Early Cretaceous fossils known to date; the global Cretaceous record of basal members of this group is largely limited to incomplete partial skeletons (e. g. *Ambiortus*, Kurochkin, 1982; *Patagopteryx*, Alvarenga and Bonaparte, 1992; *Vorona*, Forster et al., 1996; *Gansus*, Hou and Liu, 1984; You et al., 2006), none of which preserve information regarding the integument of these birds.

The first few specimens from the Jehol Group referred to Ornithurae were, like other specimens known at the time, fairly fragmentary, revealing limited anatomical information and did not preserve integument (e. g. *Chaoyangia*, Hou and Zhang, 1993; *Liaoningornis*, Hou, 1997a; *Songlingornis*, Hou, 1997b). Within the past decade, numerous complete and articulated specimens of ornithurine birds have been discovered: *Yanornis*, *Yixianornis* (Zhou and Zhang, 2001; Clarke et al., 2006), the hongshanornithids (Zhou and Zhang, 2005; O'Connor et al., 2010), *Archaeorhynchus* (Zhou and Zhang, 2006b), and *Jianchangornis* (Zhou et al., 2009). These specimens have revealed not only the skeletal anatomy of basal ornithurines, but also their biology, with preserved gut contents, gastroliths, and feather impressions (Zhou et al., 2004; Clarke et al., 2006). What the post-cranial anatomy reveals supports the hypothesis that the early ancestors to extant birds occupied a shore-bird or littoral ecology (Feduccia, 1995); nearly all known taxa show skeletal adaptations for near lakeshore terrestrial life such as a dorsal supracondylar process on the humerus (*Longicrusavis*; O'Connor et al., 2010), enlarged, proximally projecting cnemial crests (Zhou et al., 2009), and elongate hindlimbs (*Hongshanornis*; Zhou and Zhang, 2005).

Despite the wealth of information these new fossil finds have revealed, ornithurine integument remained poorly known relative to the diversity of feather patterns recognized among the sympatric enantiornithines, inferred to be the dominant clade at the time (O'Connor et al., 2009). Remiges of modern shape and arrangement are plesiomorphic for Aves (present in *Archaeopteryx* and even some non-avian dinosaurs), and the alula is present in both enantiornithines and ornithurines in the Jehol, suggesting this feature may be a synapomorphy of Ornithothoraces. Tail feather morphologies in non-ornithothoracine birds are limited to the frond-like tail morphology of *Archaeopteryx* (Gatesy and Dial, 1996) and other long-tailed birds, and the paired 'streamer' tail feathers of Confuciusornithiformes (Martin et al., 1998). The latter tail morphology is also known in enantiornithines (*Protopteryx*; Zhang and Zhou, 2000), with one taxon reportedly preserving two pairs of streamers (*Paraprotopteryx*; Zheng et al., 2007), however most commonly these birds lacked elongate rectrices completely (e. g. *Longipteryx*; Zhang et al., 2001). More recently, one enantiornithine has been reported with a fan-shaped tail

(*Shanweinia*o, O'Connor et al., 2009); preservation in this specimen is poor, however the feather impressions suggest a tail composed of more than four rectrices forming a continuous surface, which may have had aerodynamic function. Among ornithurines, tail impressions are rare—only a single morphology is recognized, that of a large, elongate, graded fan (e. g. *Yixianornis*, Clarke et al., 2006; *Hongshanornis*; O'Connor et al., 2010). In the holotype of *Yixianornis*, preservation is nearly complete and at least eight feathers are preserved; the feathers are pennaceous and symmetrical, and overlap medially, forming a single surface. The length of the feathers suggests the tail may have generated substantial lift. The absence of diversity among ornithurine rectricial patterns when compared to enantiornithines, together with the morphological disparity between ornithothoracine pygostyles, suggests several hypotheses: that the fan morphology evolved independently within each clade, supported by the derived phylogenetic position of *Shanweinia*o (O'Connor et al., 2009); and that the rectricial bulb may have co-evolved with the osteologically modern pygostyle within the ornithurine clade. With only a single known tail morphology reported in only two specimens, the discovery of additional fossils or a well-resolved phylogenetic analysis are required to elucidate the latter hypothesis.

Recently, a new ornithurine bird was collected from the Lower Cretaceous Jiufotang Formation in Liaoning Province, northeastern China. The new specimen is a nearly complete, articulated skeleton, preserving numerous characters that align it with the ornithurines. However, it also preserves features that suggest the new taxon is primitive within this clade. A previously unknown furcular morphology among ornithurines and several other autapomorphies indicate this bird represents a new taxon, adding to our understanding of the early diversification of ornithurines and revealing new information regarding the complex pattern of character evolution among early birds.

2 Systematic paleontology

Aves Linnaeus, 1758

Pygostylia Chiappe, 2002

Ornithurae Haeckel, 1866

Ord. and Fam. Indet.

***Schizooura lii* gen. et sp. nov.**

Holotype IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China) collection number V 16861; a nearly complete, articulated skeleton with feather impressions preserved around the wings, legs, and tail (Figs. 1, 2).

Etymology The genus name is derived from the greek word schizo and oura, which meaning split and tail, and the species name is dedicated to Mr. Li Yutong (IVPP), who prepared this delicate specimen and many other birds and feathered dinosaurs.

Location and horizon Jianchang, Liaoning Province; Jiufotang Formation. Early Cretaceous, Aptian; approximately 120 Ma (He et al., 2004).

Diagnosis A medium-sized basal ornithurine bird, with the unique combination of the following features: jaws edentulous; nasal process of the premaxilla elongated (contacting the frontals) completely separating the two nasals medially; slender jugals; robust V-shaped furcula with a short hypocleidium; robust humerus with large deltopectoral crest that extends for approximately 50% the length of the humerus; intermebral index (humerus + ulna + major metacarpal/femur + tibiotarsus + metatarsal III) is about 1.01 (Table 1); and tarsometatarsus elongate relative to the tibiotarsus (the length ratio of the tarsometatarsus to tibiotarsus is 0.58).



Fig. 1 Photo of the holotype of *Schizoura lii* gen. et sp. nov. (IVPP V 16861)

3 Description

Skull and mandibles Although the skull is largely complete (Fig. 3), the thin bones of both sides of the skull have been laterally compacted, so that they overlay each other making it difficult to recognize structures and interpret their details. The ratio of the skull length to height is 2.2; the rostrum forms approximately 50% of the skull length. Both the upper and lower jaws are toothless. The premaxillae are entirely unfused. The premaxillary corpus is relatively short, as in most other basal birds; the ventrolateral margin bears several small foramina, suggesting the presence of a horny sheath or beak. The maxillary and nasal processes of the premaxilla form an angle of approximately 21° , and demarcate a majority of the external nares'

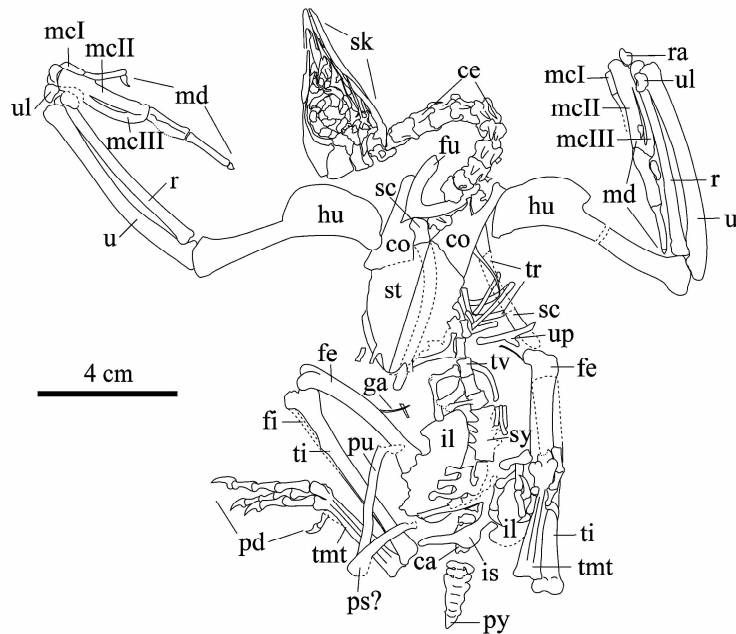


Fig. 2 Line drawing of the holotype of *Schizoura lii* gen. et sp. nov. (IVPP V 16861)
 Abbreviations; ca. caudal vertebra 尾椎; ce. cervical vertebrae 颈椎; co. coracoid 乌喙骨; fe. femur 股骨; fi. fibula 腓骨;
 fu. furcula 叉骨; ga. gastralia 腹膜肋; hu. humerus 肱骨; il. ilium 髌骨; is. ischium 坐骨; mcl-I-III. metacarpals I-III 第
 一至第三掌骨; md. manual digits 指骨; pd. pedal digits 趾骨; ps?. pubic symphysis 耻骨联合; pu. pubis 耻骨; py?.
 pygostyle 尾综骨; r. radius 桡骨; ra. radiale 桡腕骨; sc. scapula 肩胛骨; sk. skull 头骨; st. sternum 胸骨; sy. synsa-
 crum 愈合荐椎; ti. tibiotarsus 胫跗骨; tmt. tarsometatarsus 跗跖骨; tr. thoracic rib 胸肋; tv. thoracic vertebra 胸椎;
 u. ulna 尺骨; ul. ulnare 尺腕骨; up. uncinat process 钩状突

Table 1 Measurements of some skeletal elements of *Schizoura lii* gen. et sp. nov. (IVPP V 16861)
 (mm)

Elements	Measurements	Elements	Measurements
Skull L	52	Minor digit I L	5
Skull H	24	Pubis L	45 *
Skull L/H	2.2	Pygostyle L	20
Scapula L	50	Femur L	45 *
Coracoid L	29	Tibiotarsus L	62
Humerus L	60	Tarsometatarsus L	36
Ulna L	64	Pedal digit I -1 L	5
Radius L	57	Pedal digit I -2 L	4
Carpometacarpus L	30	Pedal digit II -1 L	10
Alular Metacarpal L	6	Pedal digit II -2 L	7
Alular Metacarpal W	2	Pedal digit II -3 L	5
Major Metacarpal L	22	Pedal digit III -1 L	10
Major Metacarpal W	3.5	Pedal digit III -2 L	7
Minor Metacarpal L	23	Pedal digit III -3 L	6
Minor Metacarpal W	2	Pedal digit III -4 L	6
Alular digit I L	12	Pedal digit IV -1 L	9 *
Alular digit II L	3.5	Pedal digit IV -2 L	6
major digit I L	14	Pedal digit IV -3 L	4
major digit II L	14	Pedal digit IV -4 L	4
major digit III L	3.5	Pedal digit IV -5 L	5
Femur/Tibiotarsus	0.37	Forelimb/Hindlimb	1.01

* estimated value; L. length; W. width; H. height.

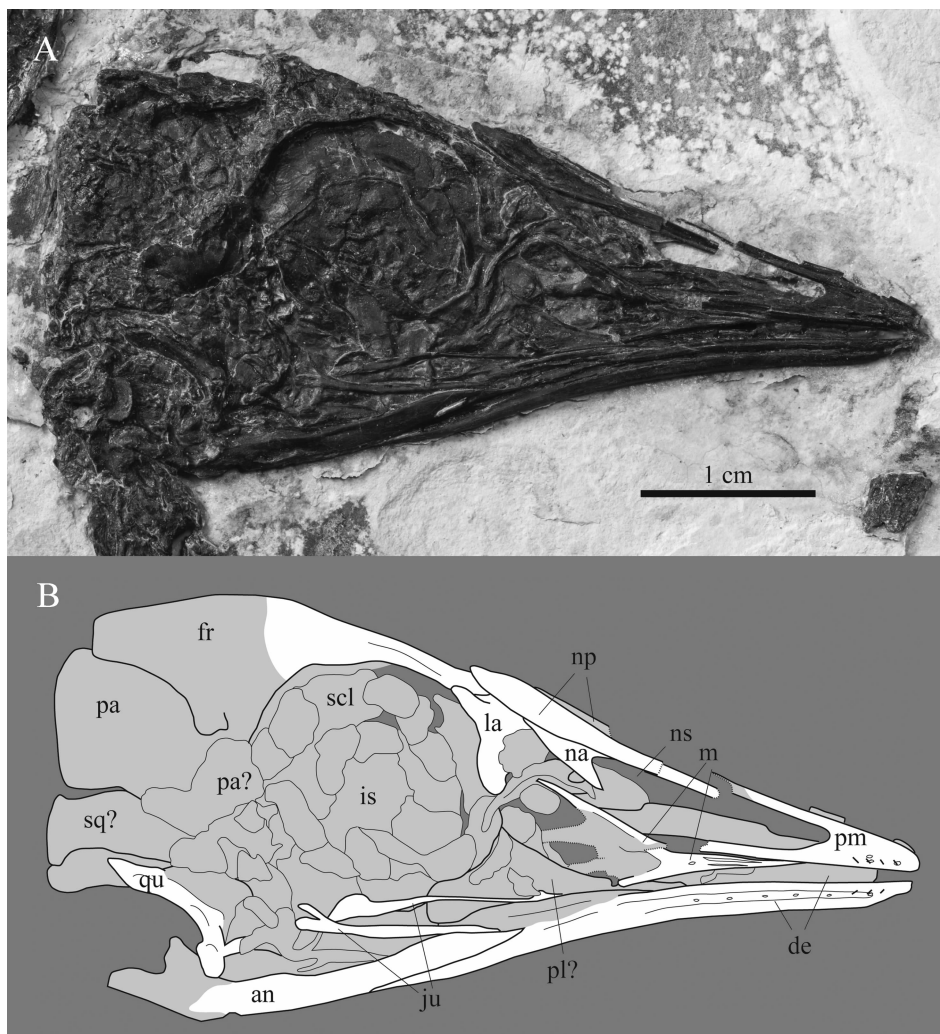


Fig. 3 Photo (A) and line drawing (B) of the skull of the holotype of *Schizoura lii* gen. et sp. nov. (IVPP V 16861)

Abbreviations: an. angular 隅骨; de. dentary 齿骨; fr. frontal 额骨; is. interorbital septum 眶间隔; ju. jugal 颧骨; la. lachrymal 泪骨; m. maxilla 颌骨; na. nasal 鼻骨; np. nasal process of the premaxilla 前上颌骨鼻突; ns. nostril 鼻孔; pa. parietal 顶骨; pl?. palatine 腭骨; pm. premaxilla 前颌骨; qu. quadrate 方骨; scl. sclerotic bones 巩膜骨; sq?. squamosals 鳞状骨

margins (dorsal, rostral, ventral). The caudal half of the nasal process (processus frontalis) is slightly expanded ventrally; the processes extend nearly to the level of the caudal margin of the lachrymal and articulate with the frontals. The nasals are short and separated medially by the elongate nasal processes of the premaxilla, as in modern birds. The maxillary process (descending ramus) of the nasal extends farther rostrally than the premaxillary process; both are sharply tapered rostrally. The nasal is triangular, tapering caudally; the cranial margin is deeply concave rostrally, defining the oval caudal margin of the external nares.

The premaxillary process of the maxilla is very delicate and sharply tapered rostrally; the dorsolateral surface bears a groove, presumably for articulation with the premaxilla. The nasal process is long and delicate and is interpreted as having contacted the nasal when in articula-

tion, forming the caudal half of the ventral margin of the external nares. The entire region between the nasal and jugal processes of the maxilla may have been medially lined by a recessed wall of thin bone, as in closely related non-avian maniraptorans (e. g. *Deinonychus*) and in some basal birds (*Archaeopteryx*, *Pengornis*; Zhou et al., 2008). In this specimen it appears that the recessed medial wall of the maxilla nearly entirely filled the antorbital fossa, so that the antorbital fenestra would have been very small in proportion. The medial wall also appears perforated by one or two very large maxillary fenestrae. Morphology in this region, however, is equivocal, given the large amount of overlap between these thin, black bones.

The lachrymal is T-shaped; although the dorsal rostral ramus appears considerably shorter than the caudal ramus. There are some bones overlaying this region preventing unequivocal assessment of the lachrymal morphology. The ventral ramus is straight and strap-like; the distal portion is not preserved so we cannot determine whether it contacted the jugal and fully closed the antorbital fenestra. The sclerotic ring is preserved inside the orbit. The interorbital septum also appears preserved; this is the earliest known occurrence of this feature in Aves. Two thin, straight elements ventral to the orbit are interpreted as the jugals; if this interpretation is correct, these bones are much more slender in this new taxon than reported in other known Mesozoic birds. Since we find no other plausible interpretation of these bones, we consider this character an autapomorphy of *Schizoura* until proven otherwise by new specimens. The distal end of one of these bones is forked, consistent with the jugal of *Archaeopteryx* (Elzanowski, 2001) and some enantiornithines (LP 4450; Sanz et al., 1997); the dorsally directed ramus is thinner than the caudal ramus, the opposite of the condition in *Archaeopteryx*. The caudal region of the skull, including the braincase, is very poorly preserved; no postorbital bone is preserved, consistent with other known ornithurines, suggesting supratemporal and infratemporal fenestrae were absent.

The slender dentary is more than half the total length of the lower jaw, unforked and tapering caudoventrally. There is a longitudinal groove perforated by small foramina on the dentary that may indicate the presence of a horny sheath in life. The degree of fusion between the mandibular bones cannot be determined, although they were certainly not unfused. The surangular is slender, rostrally deflected dorsally, tapering to a point. Although the quadrate is articulated with the lower jaw, details of the morphology of this bone and the articulation itself are unclear. The otic process is long, straight, and caudodorsally oriented. It appears single-headed, but this cannot be confirmed since it is in articulation. The lateral surface appears to have a projected longitudinal ridge. The mandibular process is short and quadrangular. The orbital process appears broad, but its rostral margin is unclear.

The frontals are petal shaped, very long and thin proximally, and rapidly expanding distally. The rostral end of the frontal articulates with the premaxilla, lachrymal, and nasal. The parietals are oval and appear unfused to the frontals. No postorbital is visible.

Vertebral column There are at least eleven cervical vertebrae preserved in articulation, exposed in ventral view. The proximal portion of the series is poorly preserved, preventing the identification of the axis and atlas, and the cervicothoracic transition is covered by the pectoral girdle; thus the total number of cervicals in this taxon is unknown. Because the series is in articulation and the cranial and caudal surfaces are not exposed, the type of articulation is unclear; however the vertebrae appear to be heterocoelous. The length of the cervicals is nearly equal to the width, although the anterior cervicals are more elongate than the posterior ones. The cervicals have well-developed costal processes that appear to become more blunt and slightly more robust distal in the series. Prominent carotid processes are visible on the intermediate cervicals. The proximal half of the thoracic vertebral series is covered by the sternum, however the posterior six can be observed semi-articulated with the synsacrum. Compared to the cervicals, the thoracic vertebrae are more slender, and they seem to be amphicoelous. The anterior

three dorsals are spool-like, while the caudal thoracic vertebrae are approximately equal in length and midpoint width. The vertebrae appear excavated laterally by a broad fossa, visible on the proximal most preserved thoracic which is preserved in ventrolateral view. The caudal articular surface of the last thoracic is concave, however a ball-like convex articular surface of the synsacrum is not observed.

The synsacrum is not well preserved. Judging from the number of transverse processes, at least eight sacrals are preserved and at least nine vertebrae are estimated to have formed the synsacrum. This is consistent with other ornithurines, which possess longer synsacra than the enantiornithines and other more basal birds. The ventral margin of the synsacrum possesses a shallow groove at least proximally. The transverse processes increase in length distally. The processes on the distal four vertebrae are caudolaterally directed, and appear tightly associated with the postacetabular ilium, although unfused.

At least three free caudal vertebrae are preserved proximally; a complete count and morphological description is hindered by the overlying ischium. Distally, eight more caudal vertebrae are preserved in tight articulation, separated by a small distance. Within this series, it is very difficult to differentiate individual vertebral bodies, but the number of elements can be distinguished by the transverse processes and a slight differentiation between centra. The first two caudals in this series have short, wide transverse processes and are easier to identify than the following vertebrae. The distal most caudal vertebra is small, wide and triangular, rapidly tapering distally. This last vertebra appears partially fused to the preceding two caudals, although they can still be differentiated from each other. The ‘pygostyle’ appears only partially ankylosed, and it is unclear how many vertebrae are already incorporated in this structure and how many of the discernable vertebrae might fuse with the pygostyle later in ontogeny. However, if this entire series of eight vertebrae were to fuse, the length of the pygostyle would be estimated to exceed that of the free caudals, a character previously unrecognized among ornithuromorphs which typically have proportionately very small pygostyles. The morphology of the caudal series in this specimen may suggest it is a subadult.

The proximal thoracic ribs are slender, while the last three dorsal vertebrae in the series are more robust. At least one uncinat process is observed; it is short and appears fused to its associated rib (Fig. 2). A single gastral rib fragment is also preserved.

Pectoral girdle Only part of the left scapula is visibly preserved; most of the bone is overlain by the coracoid and the distal half is missing, preserving only a void. The right scapula underlies the sternum although the proximal end is visible between the furcula, coracoids and sternum. The scapula is shorter than the humerus, and slightly curved; the caudal half of the scapula tapers to the end. The coracoids are exposed in ventral view (Fig. 2). The ratio of length to width is about 1.8. Proximally, the acroracoid does not appear hooked. The left coracoid preserves a long proximomedially projecting procoracoid process; the medial margin of the base of this process is incised by the supracoracoidal nerve foramen, not forming a fully enclosed foramen. The lateral margin is straight. The coracoid is in ventral view, but the pattern of crushing suggests a slight dorsal fossa was present, as in other Early Cretaceous ornithurines (e. g. *Yixianornis*). The straight sternal margin is strongly angled proximally so that the lateral margin of the coracoid is longer than the medial margin. A lateral process, like that present in most basal ornithurines (e. g. *Gansus*, *Yixianornis*, *Yanornis*), is absent. The furcula is robust, nearly V-shaped with a short hypocleidium. Among ornithurines which typically possess delicate U-shaped furculae with no hypocleidium (e. g. *Archaeorhynchus*, *Yixianornis*, *Gansus*), this morphology is reminiscent of the enantiornithine condition (Chiappe and Walker, 2002; O'Connor et al., 2009) (Fig. 4). There is a shallow groove along the entire length of the furcular rami; this is interpreted as an artifact of crushing, and suggests that the furcula may have been pneumatized. The interclavicular angle is approximately 60°.

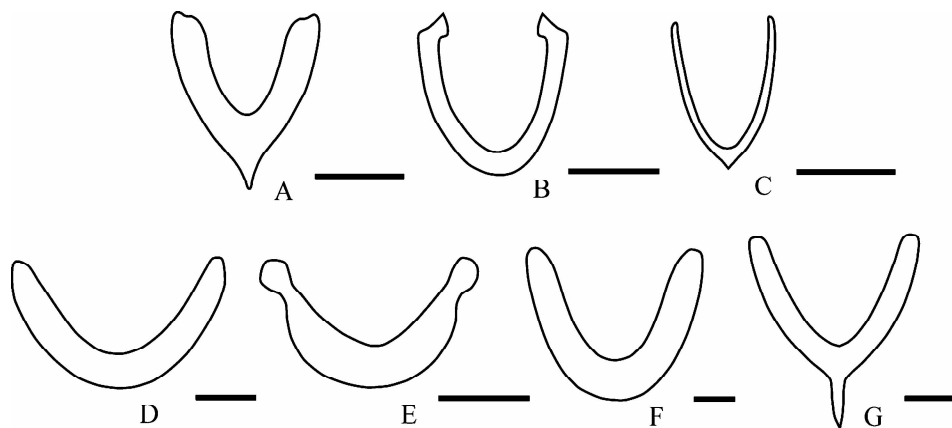


Fig. 4 Comparison of the furcula of *Schizooura lii* (A), *Archaeorhynchus spathula* (B), *Hongshanornis longicresta* (C), *Archaeopteryx lithographica* (D), *Confuciusornis sanctus* (E), *Jeholornis prima* (F), *Pengornis houï* (G); scale bars = 5 mm

Schizooura has a craniocaudally elongate, imperforate sternum (Figs. 1, 2); the ratio of the length to width is approximately 2.0. The coracoidal sulci, which define the rostral margin, are straight and meet medially to caudally define an obtuse angle of approximately 117° . The coracoids were either adjacent or slightly crossed medially. Sternolateral processes appear absent; the lateral margins also appear simple, lacking any processes (i. e. the zyphoid process present in *Yixianornis*; Clarke et al., 2006). The midline of the sternum bears a low ridge, which extends along most of its length ending just short of the rostral margin. We interpret this ridge as either the base of a keel that has been broken and lost, or, considering this specimen may represent a subadult, may have anchored a cartilaginous keel that had yet to ossify when this bird died. The caudal margin of the sternum is poorly preserved; only one pair of caudal trabeculae can be recognized. The caudal trabeculae form a small, deeply concave notch with the blunt, triangular caudal margin. Given the poor preservation of the caudal margin of the sternum, we cannot rule out that an additional pair of outer caudal trabeculae may also have been present.

Forelimb The forelimb is almost as long as the hindlimb with a ratio of 1.01 (Table 1), which is comparable to *Yixianornis*. Both humeri are preserved in cranial view (Figs. 1, 2). The deltopectoral crest of the humerus is well developed, equal to the shaft in width, and slightly over $1/2$ the length of the humerus. The dorsodistal corner of the deltopectoral crest is projected distally so that the distal margin of the crest is concave; this distinguishes the new specimen from previously known ornithurine birds, although a similar feature is present in the basal pygostylian *Zhongjianornis* (Zhou et al., 2009). The proximocranial surface is flat, lacking the convex, globe-shape that characterizes the humerus of more derived ornithurines. A well-developed bicipital crest is also absent; however, there exists an oval pit-shaped fossa for muscular attachment on the craniodistal surface of the bicipital region. Distally, the condyles are poorly preserved, whereas the dorsal condyle appears angled from the long axis of the humerus at an angle of approximately 45° . The ventral condyle appears more rounded. Although not entirely clear due to preservation, the dorsal margin, just proximal to the condyles, appears to have a small dorsal supracondylar process, as in *Longicrusavis* (O'Connor et al., 2010). The ulna is longer than the radius, and slightly longer than the humerus. The ulna and the radius are poorly preserved at their proximal and distal ends. The ulna is bowed slightly; the radius is straight and 60% the width of the ulna. The ulnare is larger than the radiale, and U-shaped,

although the metacarpal incisure is shallow. The radiale is interpreted in either medial or lateral view; although the morphology cannot be interpreted, several distinct facets are visible indicating the evolution of the derived modern radiale was well underway.

Both hands are interpreted in dorsal view. The carpometacarpus is either nearly or fully fused proximally; the semilunate carpal is entirely fused over the major metacarpal surface (Figs. 1, 2). The alular metacarpal is very slender, approximately $1/3$ the width of the major metacarpal; it is rectangular with a straight dorsal margin (extensor process absent). The major metacarpal is very robust and straight; an intermetacarpal process is absent. The minor metacarpal is shorter than the major metacarpal, with lesser proximal and distal extent, and slightly curved, but more than $1/2$ of the major metacarpal width. The major and minor metacarpals also appear fused distally closing a narrow intermetacarpal space. The alular digit is short, not distally surpassing the distal end of the major metacarpal. The first phalanx is about 50% longer than the alular metacarpal; the second phalanx is a small claw. The first phalanx of the major digit possesses a well developed cranial pila (Baumel and Witmer, 1993); it does not, however, appear dorsoventrally expanded, as in other ornithurines (e. g. hongshanornithids, *Yixianornis*), although preservation of the caudal margin is not clear. The second phalanx is slender, and nearly equal to the first phalanx in length. The major digit claw is very reduced, smaller than the claw on the alular digit. The minor digit retains only the first phalanx, which is small, short, and rectangular. The manus (semilunate carpal + major metacarpal and major digit) is slightly longer than the humerus.

Pelvic girdle The pelvic girdle is ventrally preserved (Figs. 1, 2). The proximal halves of the ilia are separated from the synsacrum, whereas the distal halves are in close contact although not fully fused to the synsacrum. The cranial margin of the ilium is broadly rounded; the lateral margin between the proximocranial corner and the acetabulum is concave. The postacetabular ilium is unclear. The pubis is slender. The exact length of the pubic symphysis is unknown, but it appears to be shorter than $1/3$ of the total length of the pubis; the distal ends of the pubes are expanded where they contact, and are unfused. The ischium is shorter than the pubis and unfused to the ilium. A dorsal process is developed at approximately the midpoint of the bone, formed by a gradual swelling of the dorsal margin. This morphology is consistent with ornithuromorphs (e. g. *Yixianornis*, *Yanornis*) as well as some more primitive birds (*Zhongjianornis*) and distinct from the proximally located tongue-like process present in enantiornithines and saepeornithiformes. The distal end of the ischium tapers bluntly.

Hindlimbs Only the right femur preserves some morphology; a fragment is interpreted as the distal half of the left femur, although the overlying bones of the hindlimb obscure interpretations. The femur is slightly bowed so that the caudal margin is concave (Figs. 1, 2). The femur is more than half the length of the tibiotarsus with a length ratio of 0.73. Proximally, the right femur preserves a small, ball-shaped head; distally, visible on the left femur, the cranial surface possesses a shallow patellar. Both tibiotarsi are nearly completely preserved; the right is preserved in medial view, the left in cranial view. Proximally, a prominent but proximally restricted cnemial crest is present; in profile, the crest has a rounded margin. The distal ends of both tibiotarsi are poorly preserved; the condyles are visible, albeit abraded, on the left. The medial and lateral condyles appear nearly equal in size. The distal end of the tibiotarsus is expanded relative to the shaft. The fibula is partly preserved on the right side, but broken into two main pieces. The fibula is slender and long. The proximal half is preserved caudolateral to the tibiotarsus; it is fat proximally and tapers quickly. The second half is preserved on the cranial margin and nearly extends to the distal end of the tibiotarsus (Figs. 1, 2).

Both feet are preserved. The left foot is poorly preserved, overlying the tibiotarsus and femur, with the caudal margin exposed. The right foot is well preserved in craniomedial view, and thus both sides of the tarsometatarsus are largely visible. The tarsometatarsus is more than

half the length of the tibiotarsus and well fused, as in other ornithurines, although fusion does not appear complete and individual metatarsals can easily be distinguished in caudal view. A fifth metatarsal is not preserved. Metatarsals II-IV are almost the same width. Metatarsal III is the longest, followed by IV and then II. Metatarsal IV extends to the proximal margin of the metatarsal III trochlea, and metatarsal II is only slightly shorter. A small, proximodistally elongate oval tubercle is located on the cranio-lateral surface of the proximal end of metatarsal II, interpreted as the attachment site of the *m. tibialis cranialis*. The proximal cranial surface of metatarsal III does not appear caudally displaced, as in other ornithurines, and the plantar surface of the tarsometatarsus is not excavated. The metatarsals are primarily in a single plane, except the distal end of metatarsal II appears slightly displaced plantarly. In plantar view, a hypotarsus is absent—the proximocaudal surface lacks any form of plantar projection, such as that present in *Yixianornis* and other basal ornithurines (Clarke, 2004; Clarke et al., 2006; You et al., 2006). Instead, the plantar surface of metatarsal III possesses two small tubercles, the proximal one located on the margin of metatarsal IV and the more distal one located on the margin of metatarsal II. Distally, the halves of the metatarsal II and IV trochlea that contact metatarsal III project further distally than the rest of the trochlea. The hallux is located high on the caudomedial margin of metatarsal II; the distal margin of its trochlea is located well above the proximal margin of the metatarsal II trochlea. Metatarsal I is short, 15% of the length of metatarsal II, and shaped similar to an inverted P; the proximal end is tapered, and the distal end is expanded, perpendicular to the long axis of the metatarsal, into the trochlea. Metatarsal I is crushed distally, making it difficult to say how the two articular planes related to each other, however, it appears they were nearly parallel.

The pedal phalanges are robust, and the claws are heterogeneous. The proximal phalanges are longer than the distal ones, and the unguals are short and not strongly curved. The hallux is formed by two phalanges; the first is short and slender, followed by the smallest claw in the foot. The second digit is composed of three phalanges; the first phalanx is the longest in the foot (same length as digit III-1), followed by a phalanx 50% shorter, and a claw. The third digit is the most robust in the foot, composed of four phalanges. The first phalanx is the biggest in the foot (same length as digit II-1 but more robust); the phalanges decrease in length by approximately 30% distally, ending in the largest claw of the foot. The fourth digit is covered proximally but we estimate the first phalanx is approximately the length of phalanx III-3. The following phalanx is approximately 30% shorter, followed by two subequal phalanges 30% shorter than it; the digit ends in a small claw, approximately equal to that of digit II (both of which are larger than that of digit I and smaller than that of digit III).

4 Comparison and discussion

This new specimen can be referred to Ornithurae based on the following features: a synsacrum composed of approximately nine vertebrae, a keel extending along almost the full length of the sternum, coracoid with procoracoid process, major and minor metacarpals equal in distal extent and well fused at the distal end, a large cnemial crest on the tibiotarsus, and a well fused tarsometatarsus.

The new specimen represents a new taxon distinguishable from other known ornithurines by the presence of the following features: edentulous jaws, nasal process of the premaxilla elongated (contacting the frontals) completely separating the two nasals medially, slender jugals, V-shaped furcula with short hypocleidium, robust humerus with an extremely enlarged deltopectoral crest with hooked dorsodistal margin, tarsometatarsus elongate compared to the tibiotarsus, the ratio of which is larger than in other basal ornithurines, and an intermebral index (ratio of the humerus + ulna + major metacarpal to the femur + tibiotarsus + metatarsal III) of about 1.01.

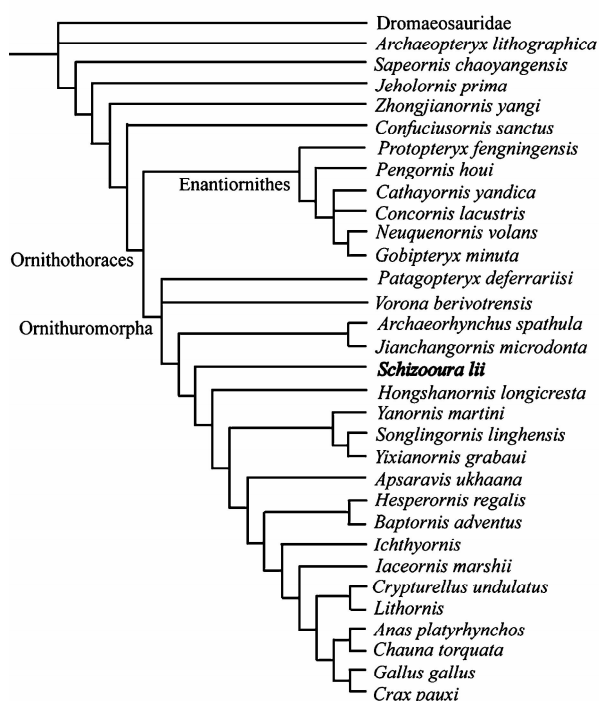


Fig.5 Strict consensus cladogram illustrating the hypothetical phylogenetic position of *Schizooura lii* gen. et sp. nov. Tree length: 538 steps, consistency = 0.50, retention index = 0.76

less derived than *Jeholornis* (O'Connor et al., 2009; Zhou et al., 2009). *Confuciusornis* is resolved as the ornithothoracine sister taxon, with *Zhongjianornis* falling basal to *Confuciusornis*. Ornithothoraces is formed by a dichotomy between Enantiornithes and Ornithurae, consistent with previous analyses, and is well resolved. Because this paper deals with relationships within Ornithurae, the lack of resolution basal in the clade was not further investigated. However, the trend in recent analyses towards a lack of resolution among non-ornithothoracine birds (O'Connor et al., 2009; Zhou et al., 2009) suggests the need for in depth research into the relationships of long-tailed birds and basal pygostylians.

The phylogenetic analysis confirms morphological inferences that *Schizooura* is a member of basal Ornithurae. Ichthyornithiformes is resolved as the sister clade to Neornithes, with Hesperornithiformes, *Apsaravis*, 'Songlingornithidae,' *Hongshanornis*, *Schizooura*, and a clade formed by *Jianchangornis* and *Archaeorhynchus* forming successive sistergroups. *Patagopteryx* and *Vorona* and the clade of all more advanced ornithurines form a basal polytomy. *Schizooura* is excluded from the clade formed by *Hongshanornis* and more derived ornithurines.

The distribution of characters within Ornithurae in this phylogenetic hypothesis suggests a high amount of evolutionary plasticity; for example, the relative placement of toothless taxa (not forming a distinct clade) suggests that tooth reduction occurred multiple times within Ornithurae. Teeth are absent in *Schizooura* and *Hongshanornis*, but present in the more derived 'songlingornithids' *Yixianornis* and *Yanornis*, as well as present in Ichthyornithiformes and Hesperornithiformes. Whether teeth were present or not in the basal *Patagopteryx* and *Vorona* is unknown, but in the clade formed by *Jianchangornis* and *Archaeorhynchus*, teeth are both present and absent, suggesting teeth may have been easily lost in ornithurines (Stock, 2001). This is not observed in enantiornithines, with only one Late Cretaceous taxon known to have evolved

A phylogenetic analysis was conducted using a modified version of the Zhou et al. (2008) data matrix. The clade Dromaeosauridae was scored as the out group. A total of 205 characters (195 parsimony-informative; 38 ordered, and all equally weighted) were evaluated for 32 taxon using Paup 4.1 with a heuristic search. The analysis produced six most parsimonious trees (MPTs) of equal length (length = 538 steps). The MPTs varied in the relative placement of *Patagopteryx deferrariisi* and *Vorona berivotrensis* at the base of the ornithurine clade, and *Cathayornis yandica* and *Concornis lacustris* within Enantiornithes. Here we present the strict consensus of these six trees (Fig. 5).

The basal part of the tree lacks resolution, placing *Archaeopteryx* in a polytomy with Dromaeosauridae, and the clade containing all other taxa, and thus not resolving a traditional clade Aves. Following trends in recent analyses, a pygostylian clade is also no longer resolved; *Sapeornis* is resolved as

edentulousness (*Gobipteryx*; Elzanowski, 1974). Early Cretaceous enantiornithines show a wide range of tooth sizes and morphologies, and vary in their distribution within the mouth. This may suggest trophic partitioning between early members of the two clades.

The fairly basal position of this new taxon is not surprising given some of the observed primitive features (e. g. the absence of sternolateral processes on the coracoid, a dorsoventrally expanded first phalanx on the manus, a delicate U-shaped furcula, and an incipient hypotarsus); however, *Schizooura* is still considered more derived than *Archaeorhynchus* and *Jianchangornis*.

Schizooura preserves several new features and morphological combinations, revealing new information on the morphology of basal ornithurines. The result of this current phylogenetic hypothesis sheds new light on the early character evolution of Ornithurae. Basal ornithurines (e. g. *Archaeorhynchus*, *Schizooura*) are already known to lack the globe shaped proximal humerus that characterizes most members of the clade (e. g. *Gansus*, *Ichthyornis*) (Fig. 6). This new taxon shares this feature, but, like *Confuciusornis* and other basal birds, *Schizooura* also has a well developed deltopectoral crest; the crest, however, lacks the fenestra present in *Confuciusornis*, as well as *Sapeornis* (Zhou and Zhang, 2003). The length of the deltopectoral crest is about 50% the length of the humerus, which is larger than that the crest preserved in the basal bird *Zhongjianornis* (Fig. 7). The crest in most ornithurines is less than 50% the humeral length and is rounded, tapering into the shaft distally. In *Schizooura*, the dorsodistal corner of the crest is projected, and the distal margin is concave, which is unique in ornithurine birds, although *Zhongjianornis* possesses a very similar feature. Until now, all known early birds that have a larger deltopectoral crest, including *Confuciusornis*, *Zhongjianornis*, *Jeholornis* and *Sapeornis*, lack an elongated sternum or a prominent sternal keel (Zhou et al., 2009). However, *Schizooura* has a well developed sternum, with a length to the width ratio of about 1.5. The keel spans almost the full length of the sternum, and only diminishes approximately 10% from the proximal end. This suggests that ornithurines enlarged their sternum early during their evolution, before the reduction of the robust humeral deltopectoral crest and the evolution of the globe shaped humeral head. However, *Archaeorhynchus*, a taxon resolved as more basal than *Schizooura*, possesses a small sternum with deep caudal notches that relative to other known ornithurines strongly resembles that of enantiornithines. This taxon, however, has the rounded and tapered deltopectoral crest typical of ornithurines. The pattern in which advanced characters were acquired among basal ornithurines is not clear from the current fossil record.

The furcula of the new taxon also appears to retain primitive features, and departs from other known ornithurines (Fig. 4). *Schizooura* possesses a V-shaped, flat furcula with a short hypocleidium; the latter feature is unknown among most basal ornithurines (possible exception being *Hongshanornis*; Zhou and Zhang, 2005; O'Connor et al., 2010). This furcular morphology is more similar to enantiornithines than that of other ornithurines; in enantiornithines the furcular rami always define a V-shape, as opposed to curved medially forming a U-shape as in ornithurines (Zhou and Zhang, 2001, 2005, 2006b; Clarke et al., 2006; Zhou et al., 2009; O'Connor et al., 2010). The interclavicular angle is about 60°, comparable to other ornithoth-

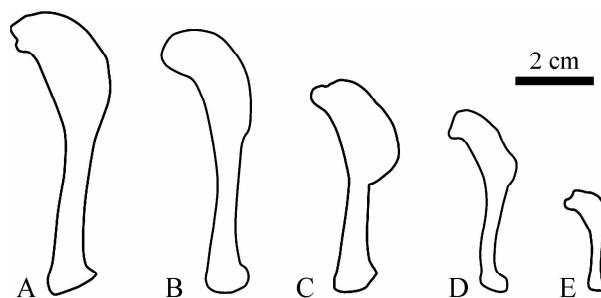


Fig. 6 Comparison of the left humerus of basal ornithurines: *Schizooura lii* gen. et sp. nov. (IVPP V 16861) (C); *Jianchangornis microdonta* (IVPP V 16708) (A); *Yanornis martini* (IVPP V 12558) (B); *Yixianornis grabau* (IVPP V 12631) (D); *Hongshanornis longicresta* (IVPP V 14533) (E)

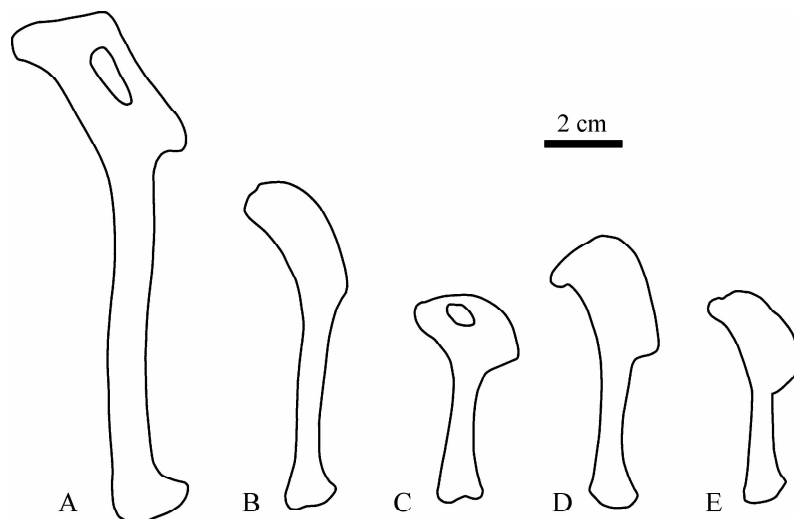


Fig. 7 Comparison of the left humerus of *Schizooura lü* gen. et sp. nov. (IVPP V 16861) (E) with that of more basal birds *Sapeornis chaoyangensis* (IVPP V 13275) (A), *Archaeopteryx lithographica* (the Solnhofen specimen) (B), *Confuciusornis sanctus* (IVPP V 11619) (C), *Zhongjianornis yangi* (IVPP V 15900) (D)

oracines and narrower than basal pygostylians *Confuciusornis*, and *Jeholornis* (Zhou and Zhang, 2002). Enantiornithines also typically possess a hypocleidium, however this feature is much longer in most members of this clade, nearly subequal to the length of the furcular rami (O'Connor, 2009); the morphology in *Schizooura* differentiates itself from enantiornithines in that the hypocleidium is short, the rami are robust, and although the lateral margins define a V, the medial margins define a more gentle U-shape.

Several features hint at the ecology of this new taxon. The morphology of the tarsometatarsus, with metatarsal III longest and in a single plane with II and IV, as well as the proportions of the pedal phalanges, with the proximal phalanges longer than the distal ones, and weakly curved unguis, suggests that *Schizooura* was cursorial (Hopson, 2001). *Schizooura*, like ornithurines appears adapted for the ground; we propose that *Schizooura* possibly lived a terrestrial or near lakeshore environment, like most other basal ornithurines. On the other hand, compared to its strong forelimb, the hindlimb seems relatively long and slender (Table 2).

Table 2 The length and proportion of selected elements of *Schizooura lü* gen. et sp. nov. compared with other birds (mm)

Taxon	Hu	Ul	Cmc	Fe	Ti	Tmt	Hu + Ul + Cmc/ Fe + Ti + Tmt
<i>Schizooura lü</i> (IVPP V 16861)	60	64	30	45 *	62	36	1.01
<i>Yixianornis grabaui</i> (IVPP V 12631)	49	50	21	42	54	26	0.98
<i>Yanornis martini</i> (IVPP V 12558)	79	81	35	52	78	38	1.12
<i>Archaeorhynchus spathula</i> (IVPP V 14287)	53	56	25	37	42	20	1.35
<i>Hongshanornis longicresta</i> (IVPP V 14533)	26	24	13	22	38	22	0.79
<i>Jianchangornis microdonta</i> (IVPP V 16708)	75	82	34	59	75	35 *	1.1

* estimated measurement; Hu. humerus; Ul. ulna; Cmc. carpopectacarpus; Fe. femur; Ti. tibiotarsus; Tmt. tarsometatarsus.

The incompletely formed pygostyle suggests that *Schizooura* died when its development was unfinished; this suggests features such as the ossification between the pelvic elements or distal margin of the sternum, may be subject to ontogenetic change. The formation of the pygostyle in ornithurines is poorly known, and the preservation of the caudal vertebrae in *Schizooura* is unclear, making it impossible to observe how many vertebrae are incorporated in the incipient pygostyle, and how many vertebrae have yet to fully fuse into it. Despite the possible subadult ontogenetic stage of IVPP V 16861 and incomplete fusion of the pygostyle, the specimen preserves a well-developed rectricial morphology previously unknown among Mesozoic birds. Among previously collected Early Cretaceous ornithurine specimens preserving caudal integument, the tail feathers form a fan-shaped arrangement (*Yixianornis*, Clarke et al., 2006; *Hongshanornis*, Zhou and Zhang, 2005, O'Connor et al., 2010). The new specimen preserves a forked tail composed of elongate rectrices medially separated by a deep notch. In modern birds, the forked tail is more susceptible to damage than other tail morphologies, and suffers a greater loss of performance following damage (Thomas, 1993). Forked tails also confer less inherent stability than any other type of tail (Thomas, 1993). Aerodynamic performance may not be an important optimization criterion for birds that fly in a cluttered environment, or do not fly very much. Observations suggest the long forked tail increases chance of sexual reproduction (Thomas, 1993). This discovery indicates that this tradeoff may have convergently evolved in basal members of Ornithurae and neornithines. The basal placement of *Schizooura* relative to taxa with a fan-shaped tail (present in *Yixianornis* and *Hongshanornis*, which are more derived in the current phylogenetic hypothesis (Fig. 5)) suggests that sexual selection may have been a stronger evolutionary force than selection for aerodynamic performance among birds from the Jehol Group.

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