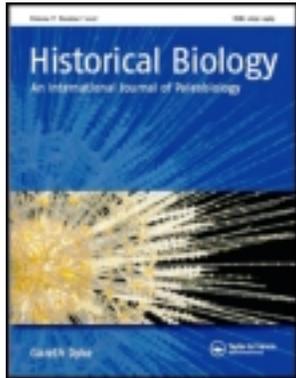


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A new species of *Jeholornis* with complete caudal integument

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The Early Cretaceous long bony-tailed bird *Jeholornis prima* displays characters both more basal than *Archaeopteryx* and more derived, exemplifying the mosaic distribution of advanced avian features that characterises early avian evolution and obfuscates attempts to understand early bird relationships. The current diversity of Jeholornithiformes is controversial, since multiple possibly synonymous genera were named simultaneously. Here, we provide the first definitive evidence of a second species belonging to this clade, and erect the new taxon *J. palmapenis* sp. nov. This new specimen reveals the tail integument of Jeholornithiformes, the morphology of which appears to have no aerodynamic benefit suggesting this clade evolved plumage patterns that were primarily for display.

Keywords: *Jeholornis*; feathers; rectrix; long-tailed birds; Jehol Group

Introduction

The Jehol Group of northeastern China preserves every major lineage of Mesozoic bird currently known (long-tailed birds, Confuciusornithiformes, Sapeornithiformes, Enantiornithes, Ornithurae, etc.) within a single ecosystem. Many lineages of birds are known entirely from this group (e.g. Confuciusornithiformes, Sapeornithiformes). The Jehol Group consists of three formations, namely the Dabeigou, Yixian and Jiufotang (Zhou 2006), which record primarily lake and volcanic deposits that are approximately 131 to 120 Ma old (He et al. 2004, 2006; Yang et al. 2007; Zhu et al. 2007). The youngest formation of the Jehol Group, the Jiufotang Formation, preserves the most diverse Mesozoic avifauna known in the world, with long-tailed birds most closely related to *Archaeopteryx* living alongside the earliest ornithurines (Zhou 2006). A long bony-tailed bird has also been reported from the Late Cretaceous Maevarano Formation of Madagascar (Forster et al. 1996; O'Connor et al. 2011); however, the avian status of *Rahonavis ostromi* has recently been called into question, and it has been suggested that this species is in fact a dromaeosaur (Makovicky et al. 2005; Norell et al. 2006; Turner et al. 2007). While the taxonomic affinity of *R. ostromi* is still being debated, the Jehol is the only geologic group that currently preserves definitive evidence of long-tailed birds outside the Solnhofen limestones that produce *Archaeopteryx*.

The non-Linnaean group 'long-tailed birds' refers to birds with an elongate bony tail (as opposed to a tail formed by elongate feathers) comprising typically more than

20 vertebrae (however, we suggest a minimum of 15 vertebrae must be present, thus excluding the abbreviated tail of *Zhongornis*; Gao et al. 2008) that does not end in a pygostyle (e.g. *Archaeopteryx*, *Jeholornis*, *Rahonavis*; O'Connor et al. 2011). Birds with an elongate bony tail have never been resolved as a true clade; an early analysis including three taxa resolved *Rahonavis* and *Jeholornis* in a polytomy with Pygostylia (all birds whose abbreviated bony tail ends in a pygostyle; Chiappe 2002), with *Archaeopteryx* as the out-group (Zhou and Zhang 2002a). A more recent, expanded analysis that included five taxa (additionally *Dalianraptor*, but since the specimen is tampered it is not considered here) resolved the same result, with all taxa in a polytomy with a 'pygostylian' clade and *Archaeopteryx* resolved as the out-group (O'Connor et al. 2011). Other analyses do not include more than *Archaeopteryx* and one other taxon, which typically form consecutive out-groups to Pygostylia, with *Archaeopteryx* always resolved in the basal most position (Ji et al. 2005; Gao et al. 2008; Zhou et al. 2008). More recently, the large Jehol pygostylian *Sapeornis* has been resolved basal to *Jeholornis* (Zhou et al. 2010), suggesting that the pygostylian clade may be paraphyletic. The phylogenetic relationships of Mesozoic birds are still rapidly changing as new discoveries are unearthed; currently, long-tailed birds is a colloquial term simply referring to birds with a long bony tail formed of 15 or more caudal vertebrae.

The discovery of the first long bony-tailed bird from China, *Jeholornis prima* (Zhou and Zhang 2002a), presented an interesting evolutionary puzzle because of

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the mosaic pattern of morphologies it displays, with some very advanced features relative to *Archaeopteryx* and even basal pygostylians (e.g. curved scapula), and others more basal (e.g. tail composed of 27 free caudals; Zhou and Zhang 2002a, 2003a). At nearly the same time, two other long-tailed birds were named: *Shenzhouraptor sinensis* (Ji, Ji, You, et al. 2002) and *Jixiangornis orientalis* (Ji, Ji, Zhang, et al. 2002). Both birds appear similar to *J. prima*, and it has been suggested that they may be junior synonyms of the latter taxon by some (O'Connor et al. 2011) and synonymised by others (Ji et al. 2003; Zhou et al. 2008a; Li et al. 2010); however, no detailed study or justification has ever been published in support of this taxonomic revision. While it is likely that these specimens are very closely related, it remains unclear as to what degree they are related. The publications report differences (e.g. teeth absent in *Shenzhouraptor*, smaller sternum in *Jixiangornis*); however, these are either unverifiable from the published photos or represent features that are ontogenetically variable (e.g. the sternum) and thus may or may not represent true differences.

Additional long-tailed birds have been reported; however, these discoveries have been even more controversial. Some specimens, such as *Dalianraptor cuhe* (Gao and Liu 2005), appear to be tampered with, require further inspection, and may prove not to represent an avian taxon, as was the case with *Jinfengopteryx elegans* (Ji et al. 2005), which has been re-identified (by some) as a troodontid (Turner et al. 2007). A single Late Cretaceous long-tailed bird has been reported from China, *Yandangornis longicaudus* (Cai and Zhao 1999); however, this taxon, even without in-depth study, likely represents a non-avian dinosaur given the absence of any definitively avian characters (Zhou and Zhang 2007). Currently, the taxonomy of Early Cretaceous long-tailed birds is largely in need of revision and clarification and the amount of diversity presently uncovered is unknown, with only a single taxon widely accepted as valid – *J. prima* (Zhou and Zhang 2007).

Here, we report on a new specimen (SDM 20090109.1/2) of long-tailed bird from the Jiufotang Formation at the Jianchang locality, northwestern Liaoning Province, China. This specimen strongly resembles *J. prima*, but after close inspection with other published specimens, despite preservational limitations, reveals autapomorphies that separate it from this taxon. The new fossil also reveals previously unknown information regarding the integument of Jeholornithiformes, for which we discuss the implications.

Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; SDM, Shandong Museum, Jinan, China; TNP, Tianjin Museum of Natural History, China.

Systematic paleontology

Aves Linnaeus 1758

Jeholornithiformes Zhou and Zhang 2007

Jeholornithidae Zhou and Zhang 2007

Distribution

Chaoyang, Liaoning, China; Jiufotang Formation (125–120 Ma; He et al. 2004; Yang et al. 2007; Zhu et al. 2007).

Characteristics

Large long-tailed bird with the following combination of features: premaxilla edentulous; teeth small, blunt and conical; robust mandibles with well-ossified symphysis; dorsal vertebrae laterally perforated by a pair of fenestrae that distally merge into a single fenestra; 27 total caudal vertebrae with 20–22 elongated caudals following the transition; pubis only slightly retroverted from the vertical position; hallux caudomedially oriented (modified from Zhou and Zhang 2007).

Type species

Jeholornis prima (Zhou and Zhang 2002a); holotype specimen, IVPP V13274.

Characteristics

A large bird with the following derived characters: lachrymal with two vertical and elongated pneumatic fossae; upper jaw edentulous; mandibles robust with well-ossified symphysis and rostrally restricted dentition; first phalanx of the third manual digit twice as long as the second phalanx; 27 total caudal vertebrae with the transition point occurring after the fifth vertebra; lateral trabecula of the sternum with a rounded fenestra at the distal end; ratio of forelimb (humerus plus ulna plus carpometacarpus) to hindlimb (femur plus tibiotarsus plus tarso metatarsus) of about 1.2; dorsal margin of the ilium nearly straight and craniodorsal-caudoventrally oriented (modified from Zhou and Zhang 2002b).

Jeholornis palmapenis sp. nov.

(Figures 1, 2).

Etymology

The Latin species name, *palma* meaning palm and *penis* meaning tail, refers to the palm tree like appearance of the preserved rectrices.

Material

A slab (SDM 20090109.1; Figures 1(A) and 2(A)) and counter slab (SDM 20090109.2; Figures 1(B) and 2(B)) preserving a nearly fully articulated but incomplete

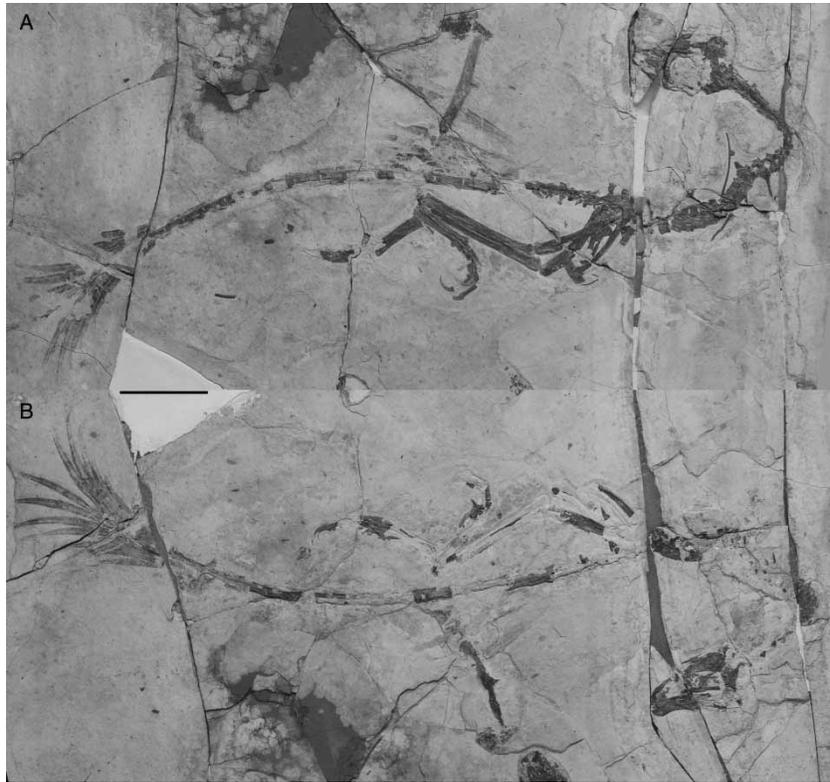


Figure 1. Photographs of the holotype of *J. palmapenis*: (A) slab SDM 20090109.1 and (B) counter slab SDM 20090109.2. Scale bar equals 10 cm.

skeleton missing the thoracic girdle and limb, with caudal integument.

Locality and horizon

Jiufotang Formation, Jianchang locality, northwestern Liaoning Province, China.

Characteristics

A large bird with a long bony tail and the unique combination of the following characteristics: maxilla toothed; thoracic vertebrae laterally excavated proximally by two fenestrae that converge centrally, forming a single lateral opening in the caudalmost thoracics; dorsal margin of ilium strongly convex; post-acetabular wing of ilium strongly concave ventrally; ischium curved dorsally; tail composed of 27 vertebrae, the proximal 6 which elongate towards the transition point, followed by 21 elongated vertebrae; elongated caudals possess chevrons with hooked articulations.

Description

Anatomical nomenclature mainly follows Baumel and Witmer (1993); certain structures not cited therein follow

Howard (1929). The new specimen is represented by a nearly fully articulated skeleton missing the pectoral girdle, forelimbs, gastralia and most dorsal ribs, preserved in a slab and counter slab (Figures 1–3). The specimen also preserves some integument, partially preserving a few remiges and completely preserving the caudal rectrices. Fully articulated specimens missing the pectoral girdle and forelimbs are not uncommon in the Jiufotang Formation of western Liaoning, and comparable specimens are known for a number of species representing different Mesozoic avian groups (e.g. Sapeornithiformes, Confuciusornithiformes) including other known specimens of *Jeholornis* (e.g. IVPP V13350) as well as non-avian theropods. The absence of preserved forelimbs is taphonomic, and the forelimbs commonly detach early during the disarticulation of a specimen (Davis and Briggs 1998).

Skull

The skull is fairly short and relatively high in proportion to its length; this skull shape is typical of basal birds *J. prima* and *Sapeornis*, and similar to the condition observed in basal oviraptorosaurs (e.g. *Incisivosaurus*; Xu et al. 2002) and apparently scansoriopterygids (e.g. *Epidexipteryx*; Zhang et al. 2008). The skull is nearly complete, but the

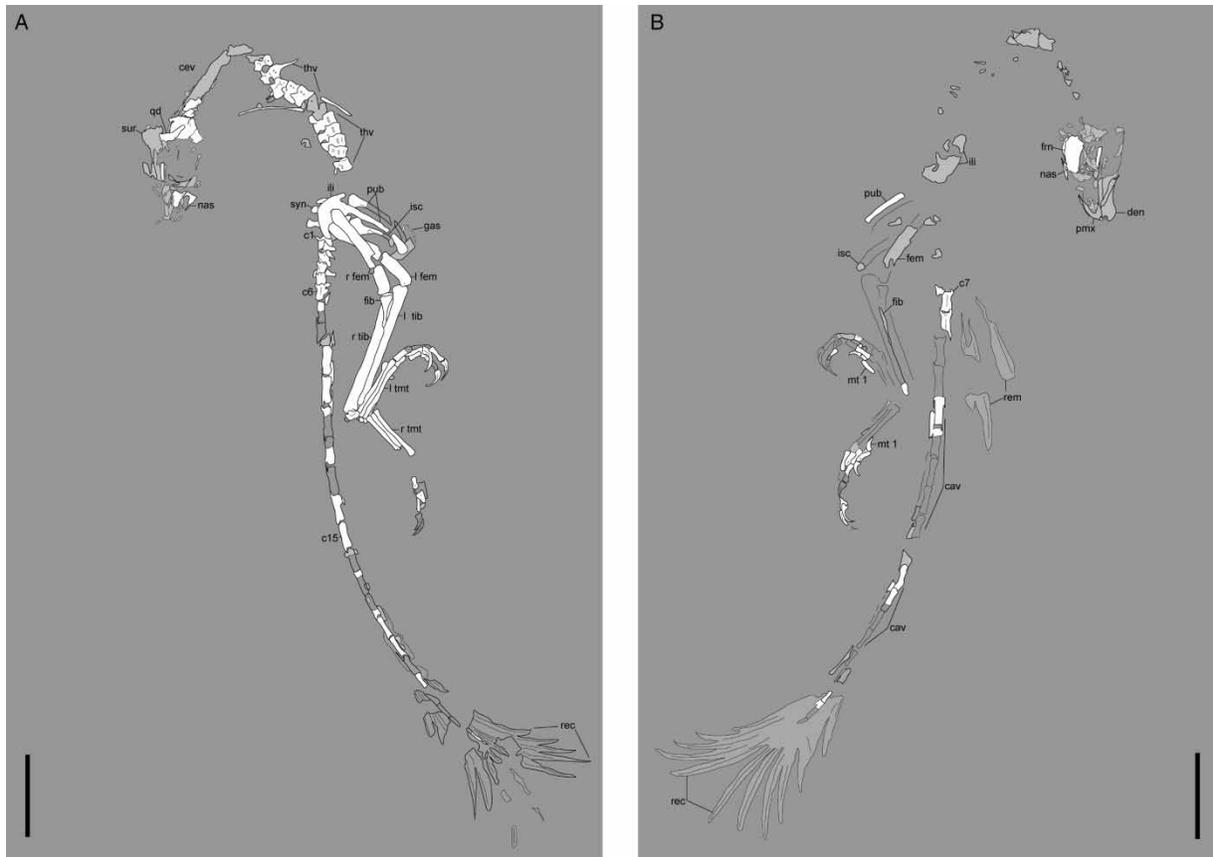


Figure 2. Camera lucida drawing of the (A) main slab SDM 20090109.1 and (B) counterslab SDM 20090109.2. Scale bars equal 10 cm. Anatomical abbreviations: c/cav, caudal vertebrae; cev, cervical vertebrae; den, dentary; fem, femur; fib, fibula; frn, frontal; gas, gastralia; ili, ilium; isc, ischium; l, left; nas, nasal; pmx, premaxilla; pub, pubis; qd, quadrate; r, right; rec, rectrices; rem, remiges; sur, surangular; syn, synsacrum; thv, thoracic vertebrae; tib, tibia; and tmt, metatarsals.

bones are split between the two slabs and thus some regions are very poorly preserved; most of the bones are preserved in the counter slab (Figure 3). The premaxilla has a very short and tall corpus; the nasal processes appear short, probably only reaching the caudal margin of the external nares, tapered and unfused. The maxilla is partially preserved in the main slab; little anatomical information is available; however, it is clear that a nasal process was present and the rostral process of the maxilla was robust and contributed to the ventral margin of the external nares. Although teeth are reportedly absent from the upper jaws in other known specimens of *J. prima* (Zhou and Zhang 2002a, 2003a), the maxilla of this specimen preserves a single tooth, caudal to which appears to be a second, empty alveolus (Figure 3). The tooth is procumbent; however, because of the ventrolateral preservation of the maxilla, we cannot rule out that the tooth was displaced from its original position. The very simple and peg-like tooth is similar in morphology to the dentary teeth of *J. prima*; serrations are absent, as in all other birds, and the occlusal tip is very blunt. The base of the tooth does not bear a marked constriction, and given

the slight disarticulation of the tooth, we cannot determine the exact height of the crown. The teeth of *Jeholornis* differ strongly from those of *Archaeopteryx*, which are more conical (occlusal tip sharp) and slightly recurved (Elzanowski 2002). In basal pygostylian *Sapeornis*, the teeth are conical (occlusal surface tapers to form a tip, absent in *Jeholornis*), but short and fat (Zhou and Zhang 2003b).

The rostral portion of the left nasal is preserved in the main slab; the rostrally projecting, sharply tapered premaxillary and maxillary processes are widely separated by a deep concavity that demarcates the caudal margin of the external nare. A pair of caudally tapered bone fragments just caudodorsal to the frontal in the counter slab may be the caudal halves of the nasal bones. Combining the preservation from both slabs, the external nares are oval, and high relative to their length, a feature characteristic of *J. prima* as well as oviraptorosaurs. The lachrymal is poorly preserved, split between both slabs; as in other basal birds, the bone is t-shaped, with a descending ramus (ventral process) that contacted the jugal, forming the rostral margin of the orbit. The rostral

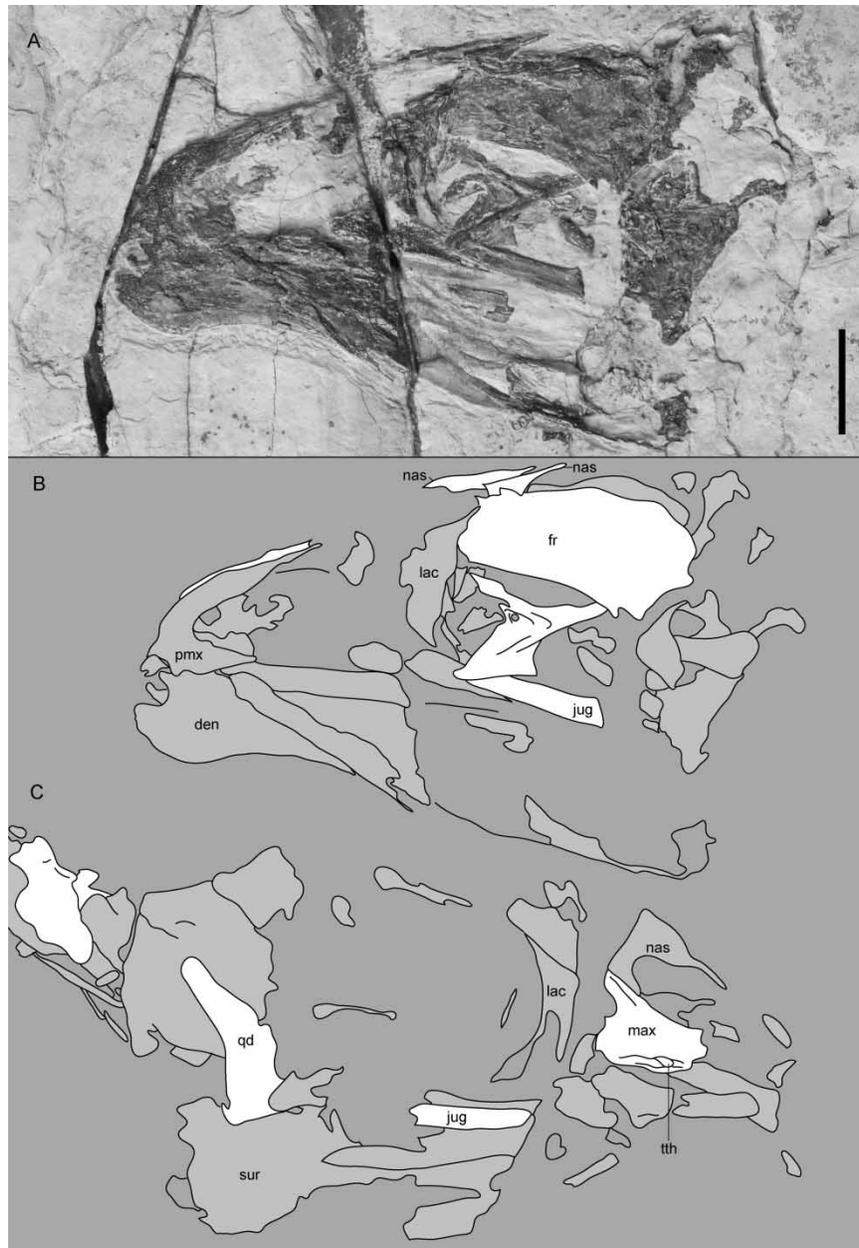


Figure 3. Skull of *J. palmapenis*: (A) close-up photograph of counter slab; (B) camera lucida drawing of counter slab; (C) camera lucida drawing of slab. Scale bars equal 1 cm. Anatomical abbreviations (not already listed in Figure 2): jug, jugal; lac, lacrimal; max, maxilla; tth, tooth.

and caudal dorsal processes appear to be oriented rostroventrally and caudodorsally, respectively. We cannot say if two vertically distributed fenestrae, like those in *J. prima*, were also present (Zhou and Zhang 2002a, 2003a). The jugal is strap-like, but both the proximal and distal ends are missing. Preserved in the orbit of the counter slab lies a bone with unusual morphology, which may represent a fragment of the palatine. The bone is long, thin and rod-like, with three large, sheet-like triangular

processes of bone projecting medially and laterally, and may be perforated by a small foramen (Figure 3).

The dentaries are very robust, which is characteristic of jeholornithiforms; they appear unfused rostrally (fused in *J. prima*), however, this region is very poorly preserved. The rostroventral margin is convex; distally the ventral margin of the dentary is concave, as in other basal avialans (e.g. *J. prima*, *Sapeornis*), oviraptorosaurs and to a lesser degree therizinosaur. In contrast, deinonychosaurs and

Archaeopteryx have much more slender mandibles with straight dorsal margins, and straight to gently concave ventral margins. This morphology in *Jeholornis* has been interpreted as a seed-eating adaptation (Zhou and Zhang 2002a, 2003a). No teeth are preserved; however, the dentary is poorly preserved and the small teeth that characterise Jeholornithiformes may have been lost in this specimen. Three small teeth are reported in the dentary of known specimens of *J. prima* (Zhou and Zhang 2002a, 2003a), which is a smaller number than that typical of toothed ornithothoracine birds. Tooth reduction in the dentary is not unique to Jeholornithiformes but common among basal birds (e.g. *Sapeornis*, *Confuciusornis*), as well as characteristic of oviraptorosaurs. The dentary is overlain by a straight, tapering rostradorsal caudoventrally oriented bone. It is unclear what this bone may be, given that it is preserved overlying the dentary and thus unlikely to be a hyoid; it is possible that it represents the ventrally displaced maxillary process of the premaxilla, but it appears too long. Alternatively, it may be a splenial bone but if the dentary is exposed in medial view, no Meckel's groove is apparent. Post-dentary bones are unclear.

The frontals are petal shaped, expanded caudally, forming the dorsal margin of the orbit. The contact with the parietals is unfused; the parietals are oval. The quadrate is partially preserved in the main slab; the otic process appears single headed and straight, but no other morphologies can be discerned.

Axial skeleton

The vertebral column is preserved nearly in its entirety (Figure 1). The cervical vertebrae, however, are poorly preserved and individual elements are either difficult to distinguish and/or crushed and abraded. The anterior cervical series is in articulation with the skull; the vertebrae are very poorly preserved, so that even their margins are difficult to discern. *Jeholornis prima* is reported to have a maximum of 10 cervical vertebrae (Zhou and Zhang 2002a, 2003a). Based on our observations, we estimate that the cervical series of the new specimen would have been comparable, composed of 9 or 10 vertebrae.

Twelve dorsal vertebrae are preserved, although the caudal end of the series may not be preserved. The proximal thoracics are not as long or robust as the middle and caudal vertebrae; the caudal thoracics show a slight decrease in length, but not robustness. A rib articulates with one of the most anterior thoracics; it is thick proximally and robust. The vertebrae are amphiplatan; exposed articular surfaces are flat to slightly concave. The anterior dorsal vertebrae have narrow pedicels and tall neural arches (together about almost twice the height of the centrum). On the anterior vertebrae, the pedicel is excavated laterally by a central fossa that shallows ventrally (Figure 4(A)). A ventral sagittal keel is absent from cranial and mid-series thoracic vertebrae.

The lateral surfaces of the anterior and middle thoracic vertebrae are not excavated by a groove or fossa as in some dromaeosaurs or more derived birds (e.g. enantiornithines); instead, there is a pair of centrally located pneumatic fenestrae (Figure 4(A)). The fenestrae are circular, equal in size, separated by a distance slightly less than their diameter, and located slightly dorsal to the equator of the centrum. The fenestrae become increasingly more oval, causing the bony bar between the fenestrae to become smaller until the two fenestrae form one anteroposteriorly elongate oval fenestra in the two posterior most preserved thoracic vertebrae. This condition resembles the oval pleurocoel that excavates the caudal thoracics of dromaeosaurs (Ostrom 1969) and is also present in *J. prima*. The cranially located parapophyses appear slightly stalked in the second to last thoracic. The pre-zygopophyses are long, projecting cranially past the proximal articular surface of the centrum. The post-zygopophyses project beyond the caudal articular surface although they are shorter than the pre-zygopophyses.

The synsacrum is entirely covered by the pelvis in lateral view although a few processes inferred to belong to the synsacrum can be observed projecting dorsally from between the ilia (Figure 4(D)). These processes strongly resemble the distal ends of the transverse processes of the sacral vertebrae in *J. prima*.

The new specimen preserves 27 caudal vertebrae, which is the same as the previously estimated total number preserved in *J. prima* (Zhou and Zhang 2003a). The most anterior caudal vertebrae are shortened relative to both the posterior dorsal and middle caudal vertebrae, a feature also seen in other basal paravians that retain an elongate bony tail (e.g. *Rahonavis*, *Shenzhouraptor*); where in the caudal series the morphology changes is referred to as the transition point. These proximal caudals have a distinct morphology: the pre-zygopophyses are elongate, extending cranially past the articular surface to clasp the short post-zygopophyses of the preceding vertebra (Figure 4(C)). The dorsal surface bears a short neural spine, restricted to the caudal half of the vertebrae. There are six preserved vertebrae with this morphology; all are shorter than the following middle and distal caudals, however, they elongate distally so that the sixth preserved vertebra is almost three times the length of the first; we use the absence of transverse processes to determine the transition point (Gauthier 1986). In *J. prima*, there are five short proximal vertebrae (IVPP V13550). As the caudals become more elongate, the pre-zygopophyses become shorter (Figure 4(B)). The chevrons on these proximal caudal vertebrae (visible on preserved caudal vertebrae 2–4) are longer dorsoventrally than axially, forming broad, rectangular elements.

The middle and distal caudal vertebrae are extremely elongated, characteristic of the morphology present in dromaeosaurs. The first elongated vertebra is nearly half the combined length of the entire series of proximal caudal

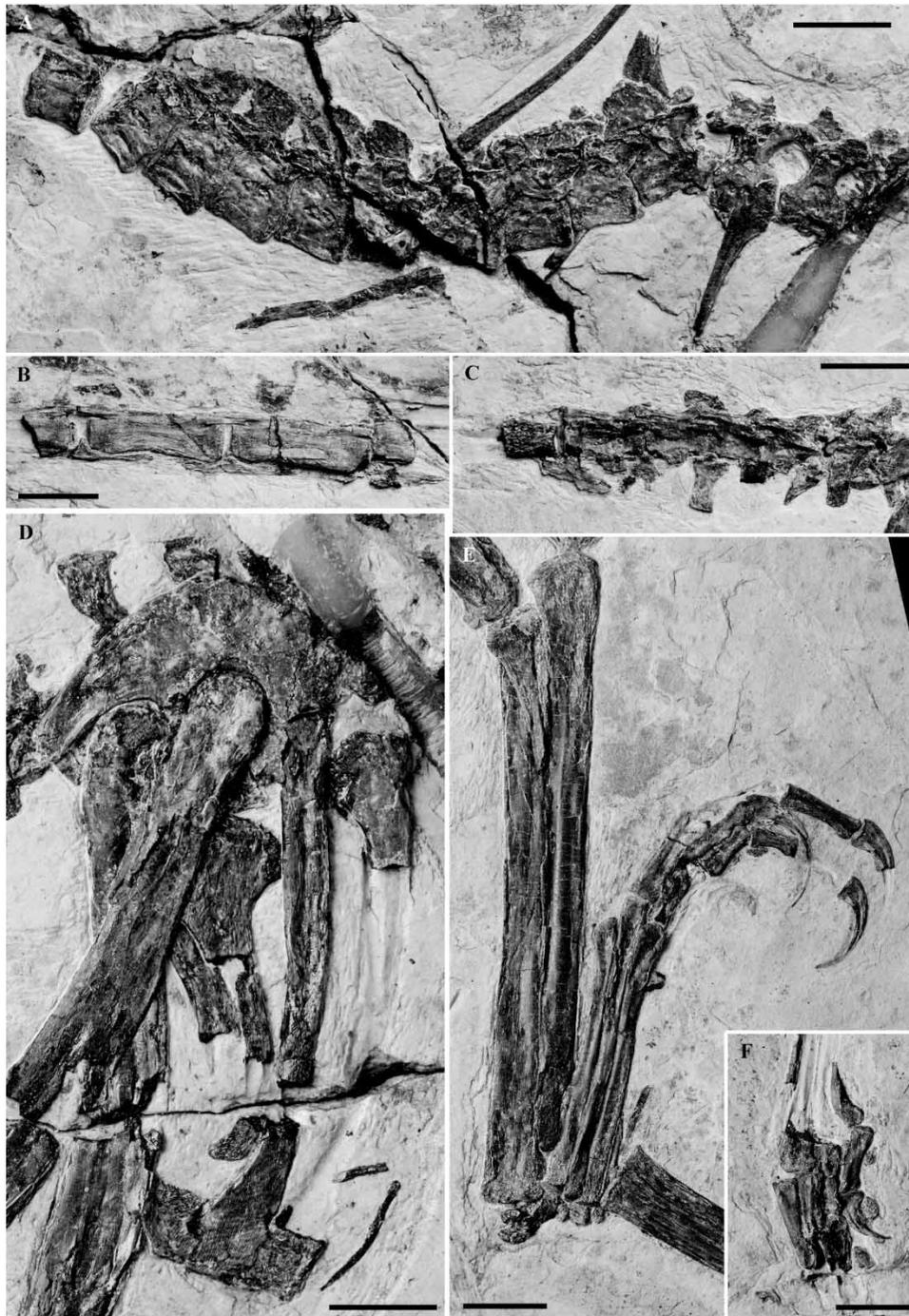


Figure 4. Detailed photographs of SDM 20090109.1/2: (A) thoracic vertebrae (B) mid-caudals (C) proximal caudals (D) pelvic girdle (E) right hindlimb and (F) distal left tarsometatarsus. Scale bars equal 1 cm.

vertebrae (150% the length of the sixth preserved caudal). The elongated vertebrae are more than three times as long as they are dorsoventrally tall. They decrease in height and length caudally, although they become more delicate but not significantly shorter; the 24th vertebra is approximately 75% the length of the seventh, but slightly less than half its height. The pre- and post-zygopophyses are thin,

tapering rostrally and overlapping the adjacent vertebrae (Figure 4(B)). Since these processes are so delicate, their precise lengths cannot be determined; however, it appears that the zygopophyses are longer distally in the series (visible caudals 13–15) than they are proximally (visible caudals 8–11). The chevrons on the middle and distal caudal vertebrae, like in closely related non-avian dinosaurs,

are thin and elongate. Preservation makes it impossible to determine the maximum length of the chevrons: the anterior process of the chevron extends to about the midpoint of the host vertebra (visible caudals 8–11), but caudal extension is unclear. The chevrons become increasingly robust, peaking around the 13–15th vertebrae before beginning to diminish in size. The proximal and distal margins of the chevrons are forked and interlocked, presumably to further reinforce the tail; the same morphology is observed in *J. prima* (Zhou and Zhang 2003a). The distalmost caudal vertebra is strongly reduced relative to preceding caudals; it has less than one-fifth of the lateral surface area present in the 24th caudal. In lateral profile, the distalmost caudal is subtriangular, tapering to a sharp point.

A single gastral rib and some associated fragments are preserved ventral to the pelvis (Figure 2(A)). The rib is very thin and weakly curved.

Pelvic girdle

The pelvic girdle is nearly completely preserved and articulated (Figure 4(D)). The proximal left ilium is preserved in the counter slab, while the rest of the pelvis is largely preserved in the main slab; the two alae are approximately equal in length, as opposed to more advanced birds (e.g. *Ichthyornis*, *Hesperornis*) in which the pre-acetabular wing is nearly twice as long as the post-acetabular one (Clarke 2004). The dorsal margin of the ilium is broadly convex so that the projection of the post-acetabular wing has a strong ventral component (Figure 4(D)). This separates this taxon from *J. prima* in which the dorsal margin of the ilium in lateral view is only weakly convex, and nearly straight over the acetabulum. The pre-acetabular wing of the ilium is dorsally convex and fairly broad, as opposed to sharply tapered as in *J. prima* (IVPP V13274). The post-acetabular wing is triangular, caudoventrally oriented (as in basal deinonychosaurs and some basal avialans), with a blunt distal margin (although this region is abraded). The ventral margin of the post-acetabular wing is concave, where it is nearly straight in the holotype of *J. prima* (IVPP V13274). The ilium demarcates the cranial, dorsal and caudal margins of what appears to be a very large acetabulum (Figure 4(D)). The pubic pedicel of the ilium is much wider than the pedicel for the ischium, as is reported in *Shenzhouraptor*; the former also extends ventrally beyond the ventral margin of the latter. The pubis is only slightly retroverted, directed caudoventrally. The pubic shaft is nearly straight. Distally, the pubis is slightly curved caudally and expands to form a large boot. The left pubis is exposed in medial view (Figure 4(D)); the symphyseal region of the pubis is textured, covered with delicate striations. The striations diminish into pits and then fade all together, indicating that the symphysis extended approximately for the distal 35–40% of the pubic shaft. The proximal end of the ischium is partially covered, but

what can be observed suggests a very wide pubic peduncle; the bone appears to continue under the femur suggesting a proximal dorsal process, like that preserved in *J. prima*, and similar to *Sapeornis* and enantiornithines, may have been present. As in scansoriopterygids, the ischium curves slightly caudodorsally, so that the caudal margin is slightly concave (unclear in all specimens of *J. prima*). However, a distinct increase in thickness, a feature that also characterises the distal ischium of scansoriopterygids, is absent in this specimen.

Pelvic limb

Both hindlimbs are complete; details concerning the proximal end of the femur are obscured by the articulation of this bone in the acetabulum. The femora are straight and robust, approximately 75% the length of the tibiotarsus. The right femur is exposed in lateral view; the cranio-lateral margin is expanded just distal to the proximal end, forming a proximodistally elongate oval tubercle interpreted as the posterior trochanter (Figure 4(D)). In some basal birds, this feature is observed as a shelf-like lateral excavation (e.g. *Enantiornithes*). In this specimen, the posterior trochanter demarcates the cranial margin of a shallow, lateral excavation, although this may be preservational. Distally, the ectocondylar tubercle is separated from the lateral condyle by a deep notch.

A true tibiotarsus is absent in SDM 20090109 (Figure 4(E)) as in some other basal birds (e.g. *Rahonavis*, *Shenqiornis*); the tibiotarsus in the holotype of *J. prima* is preserved in articulation, however, the calcaneum and astragalus also remain unfused (Zhou and Zhang 2002a). Proximally, the tibia is simple, with no obvious cnemial crests, indeed, even a fibular crest cannot be observed. The fibula is fat proximally, rapidly tapering distally giving a triangular appearance. The fibula, preserved broken between the two slabs, extends at least two-thirds of the length of the tibia (Figure 2). The tubercle for the attachment of the m. tibiofibularis appears to be laterally oriented. Distally, the right tibia is in caudal view; it has been slightly disarticulated from the proximal tarsals, revealing the caudal surface of what we interpret to be the astragalus (Figure 4(E)). Individual tarsals are difficult to identify because of the overlap between the proximal and distal bones. Two are preserved associated with the tibia, and two associated with the tarsometatarsus; since both ankles are overlapping, we cannot say unequivocally that the single small tarsal associated with the tibia is the calcaneum and not one of the distal tarsals. The small tarsal associated with the tibia lies on top (proximal surface, over the medial condyle) of the larger tarsal (the astragalus or astragalus plus calcaneum), which would indicate that, if this bone was the calcaneum, it is displaced. The large tarsal forms a cap for the tibia. The caudal margin of this tarsal is concave; the two halves of



Figure 5. Detailed photograph of the rectrices preserved in the counter slab of SDM 20090109.2. Scale bar equals 1 cm.

the bone taper towards each other in the middle so that the bone resembles a bow-tie (Figure 4(E)). The proximal margin appears to have a cranial extension; however, the overlying tibia obscures any information about the ascending process.

The distal segments of the hind limbs are not significantly elongated as in the typical cursorial theropod. The ‘tarsometatarsus’ is approximately half the length of the tibiotarsus (Figure 4(E)). Two distal tarsals are preserved capping the proximal end of the right metatarsals, preserved in dorsal view. The medial tarsal is partially overlain by the large proximal tarsal; it caps metatarsals II and III. The middle tarsal is quadrangular and lies over metatarsals III and IV. The metatarsals are unfused. The proximal end of the fifth metatarsal is displaced proximally, ending level with the proximal margins of the distal tarsals

(Figure 4(E)). Metatarsal V is less than half the length of metatarsal II. Metatarsal III is the longest; metatarsals II and IV are subequal and end at the proximal margin of the metatarsal III trochlea, considered a cursorial morphology (Zhang 2006). The same morphology is preserved in the assigned specimen of *J. prima* IVPP V13353. Proximally, metatarsal II is the widest; approximately a fifth from the proximal end, the dorsolateral surface of metatarsal II and dorsomedial surface of metatarsal III form a slight swelling. This may represent the attachment site of the *m. tibialis cranialis*. No proximal or distal vascular foramina are present.

Metatarsal I and the hallux are clearly preserved in the counter slab (Figure 4(F)); the lateral surface of metatarsal I is exposed revealing the small, flat, proximodistally oriented oval surface for articulation with the medial

surface of metatarsal II. This surface is oriented less than 90° from the articular surface for the first phalanx indicating the hallux was not fully reversed, but caudomedially oriented. The pedal phalangeal formula is 2-3-4-5-x; all phalanges are relatively robust with deep flexor pits. As in *J. prima*, the hallux is fairly short, with the claw, smaller and more strongly curved than those of the other digits, ending proximal to the distal end of the first phalanx of the second digit (Figure 4(F)). On the right side, the first phalanx of digit 2 is unclear; the second phalanx is long (subequal to the other longest phalanges in the foot). The claw of this digit is much larger and more robust than that of the hallux (Figure 4(E)). Digit 3 pedal phalanges are very robust. The proximal phalanx is the longest and most robust in the foot; the following two digits are subequal to each other, and slightly shorter and less robust than the preceding phalanx. The claw is slightly more robust and longer than that of digit 2. The first two phalanges of digit 4 are robust, and approximately two-third the length of phalanx III-1. The following phalanx is two-third the length of the preceding phalanx; the penultimate phalanx is approximately the same length as the first phalanx of the same digit, but 30% more slender. The claw is longer but more delicate and less recurved than the halluxal claw.

The claw of the second digit is commonly enlarged in some basal avians (e.g. *R. ostromi*, enantiornithines *Boluochia zhengi* and *Longipteryx chaoyangensis*) and the troodontid *Anchiornis*, but not to the degree in most other deinonychosaurs. This is entirely absent from this specimen, in which the third digit claw is the largest (although not enlarged to the degree observed in digit II of deinonychosaurs).

Integument

The specimen clearly preserves what appears to be the most complete jeholornithid tail plumage known from any specimen (Figure 5). A total of 11 feathers are preserved; 6 rectrices are attached to the dorsal side of the tail; and 5 to the ventral side. The proximalmost feathers appear to attach to the 20th free caudal. Individual barbs can be observed in several of the feathers, which appear to be closed vaned throughout their lengths. The individual rectrices range from approximately 60 to 90 mm in length; the proximalmost pair and single caudally directed rectrix are the shortest, and the penultimate pair are the longest, almost double the length of the femur. A few of the proximal rectrices have asymmetrical vanes (especially on the ventral side of the tail), however, most of the feathers appear symmetrical or nearly so. This may suggest that the asymmetry in the proximal tail feathers may be the result of preservation. The feathers on either side of the bony tail are curved so that the cranial surface is concave, and the caudal surface is convex (Figure 5). The rectrices all taper to a point.

An estimated four or five large, asymmetrical, pennaceous feathers are preserved extending from the caudal region of the pelvis, and probably represent remiges from the unpreserved forelimb. These remiges appear to radiate out from a single region (the dorsalmost remige creates an angle of 12° with the next feather; the other feathers are only separated by a few degrees), which is unpreserved (proximal end of the feathers not preserved). Their preserved lengths range from 70 to 90 mm.

Discussion

Comparative anatomy of *Jeholornis*

The new specimen is assigned to the Jeholornithiformes based on the presence of a relatively short and high skull with robust dentaries, edentulous premaxilla, small and blunt teeth, dorsal vertebrae with paired pneumatopores that form a single opening distal in the series, long bony tail composed of 27 free vertebrae, pubis only slightly retroverted from the vertical position and a caudomedially oriented hallux.

The ability to identify clear morphological characters that distinguish the new specimen from *J. prima* is complicated by our poor understanding of the latter taxon itself and the limited preservation of the new specimen. A comprehensive study of all named long-tailed birds (e.g. *Jixiangornis*, *Shenzhouraptor*) from the Jehol and newly collected material is greatly needed to fully understand the diversity of the jeholornithiforms, complete morphology of included taxa and the amount of intraspecific variation that characterizes individual species (e.g. variation in the location of the transition point in the caudal vertebrae). Such a review may invalidate the conclusions drawn here, based on comparisons with only currently available published material.

There are three specimens definitively assigned to *J. prima* (Zhou and Zhang 2002a, 2003a). Published specimens of *J. prima* occupy a large size range (Table 1; Zhou and Zhang 2003a), but with limited preserved overlap between specimens it is difficult to determine if this size difference is related to taxonomic diversity or ontogeny. For example, the holotype of *J. prima* (IVPP V13274) poorly preserves the skull, thoracic vertebrae and tarsometatarsus that are all well preserved in the assigned specimen IVPP V13350 (Zhou and Zhang 2003a). Although comparisons are limited, no major morphological differences have been identified that suggest known specimens of different sizes are not the same taxon (Zhang and Zhou 2003a). Although suggested to belong to this taxon (Zhou and Zhang 2007; Li et al. 2010), the taxonomic status of *Shenzhouraptor* and *Jixiangornis* is here considered controversial and pending further investigation and stronger citable evidence; these taxa are not considered junior synonyms of *Jeholornis* (O'Connor et al. 2011).

Table 1. Comparative measurements (in mm) of published specimens of *Jeholornis*.

| | <i>J. prima</i> (IVPP V13274) | <i>J. prima</i> (IVPP V13350) | <i>J. prima</i> (IVPP V13353) | <i>J. palmapenis</i> (SDM 20090109.1) |
|----------------|-------------------------------|-------------------------------|-------------------------------|---------------------------------------|
| Pubis | 73.6 | – | 51.8 | 49 |
| Femur | 78.3 | 55.6 | 64 | 57.9 |
| Tibia | 93 | 67 | 76 | 76.2 |
| Metatarsal III | – | 36.5 | 37 | 40.1 |

The new specimen is comparable in size to a smaller specimen assigned to *J. prima*, IVPP V13350, yet is morphologically distinct from all previously described specimens. These differences are osteological, as opposed to temporal or geographical, therefore we feel these differences justify erecting a new species. The skull of *J. prima* possesses only rostrally restricted dentary teeth, which are not preserved in SDM 20090109.1/2; however, a single maxillary tooth is preserved, the morphology of which is consistent with other jeholornithiforms and distinct from other basal birds. The very small teeth of Jeholornithiformes are often not preserved, and thus without further evidence, dentary teeth cannot be definitively considered absent in *J. palmapenis*; however, the presence of maxillary teeth differentiates this specimen from closely related taxa. The pelvic girdle is distinct in *J. prima*; the ilium is angled dorsocranial-ventrocaudally, with fairly straight dorsal and ventral margins, tapering at both ends. The ilium in the new specimen has a distinctly convex dorsal margin, whereas the ventral margin of the post-acetabular ilium is concave.

The new taxon also shows slight differences in tail morphology from *J. prima*. In the proximal caudal vertebrae of the new specimen, the caudals show a greater degree of elongation among themselves so that the transition point is considerably less distinct when compared to *J. prima* (IVPP V13350). The tail is disarticulated at the transition point in the holotype of *J. prima* (IVPP V13274) preventing unequivocal comparison; however, several short vertebrae are preserved together, separated from the first elongated vertebra by a vertebra approximately 50% longer than the proximal short caudals. In the complete and fully articulated tail of *J. prima* IVPP V13350, the transition point occurs after the fifth vertebra, whereas in the new specimen, the transition occurs after the sixth vertebra. The degree of intraspecific and interspecific variations in the transition point of the theropod tail is poorly understood; although located more distal within the tail in SDM 20090109.1/2, the transition point in this new specimen is still within that recognised for birds (occurs at C10–12 in dromaeosaurs, C9 in the controversial *Rahonavis*, and C5 in *Archaeopteryx* and *Jeholornis*; Turner et al. 2007).

The new specimen thus preserves morphologies – maxillary teeth, ilium dorsal margin convex – that differentiate it from *J. prima* justifying the naming of a

new species, for which we erect the taxon *J. palmapenis* sp. nov. This new species is the first taxon assigned to Jeholornithiformes for which there is clear morphological justification. We do not provide a phylogenetic analysis to support these morphological findings for the simple reason that current matrices are unable to differentiate *Jeholornis* from *Rahonavis*, two clearly distinct taxa, suggesting that the current phylogenetic matrices need to be updated and expanded to reflect the currently recognised morphological diversity (O'Connor et al. 2011).

Jeholornithiform integuments

Due to the limited preservation, the new specimen does not provide a great deal of morphological information; what is most unique about this specimen is the preserved integument. Feathers are preserved in one previously described assigned specimen of *J. prima* (IVPP V13350; Zhou and Zhang 2003a); however, the feathers are incomplete, preserving only the proximal halves of the most proximally located feathers. What could be discerned from IVPP V13350 suggested a tail morphology similar to closely related non-avian dinosaurs (e.g. *Caudipteryx zoui* and *Microraptor gui*; Ji et al. 1998; Xu et al. 2003; Zhou and Zhang 2003a), with elongate pennaceous feathers attached only to the caudal portion of the tail forming a distal rectricial fan (although presumably the rest of the tail was covered in unspecialised integument). The tail morphologies of *C. zoui* and *M. gui* both differ from *Archaeopteryx* that has rectrices attached along the entire length of the tail, gradually elongating giving the feathered tail a frond-like morphology (Figure 6; Gatesy and Dial 1996). A more recently discovered oviraptorosaur, *Similicaudipteryx*, preserves a tail similar to that of *Archaeopteryx*, with 12 pairs of rectrices attached along most of the length of the tail, although, like in *Caudipteryx*, these feathers are proportionately much longer than in *Archaeopteryx* (Xu et al. 2010). The holotype of *J. palmapenis* preserves what we interpret to be the complete feathered tail morphology, including the distal ends of the feathers (Figure 5). The feathers on both sides of the bony tail are tapered and preserved curved, with the concave surface directed towards the bony tail, and the tips of the feathers curving away from the vertebrae. This morphology is distinct from that observed in non-avian maniraptorans, in which the tail feathers are typically longer and straight

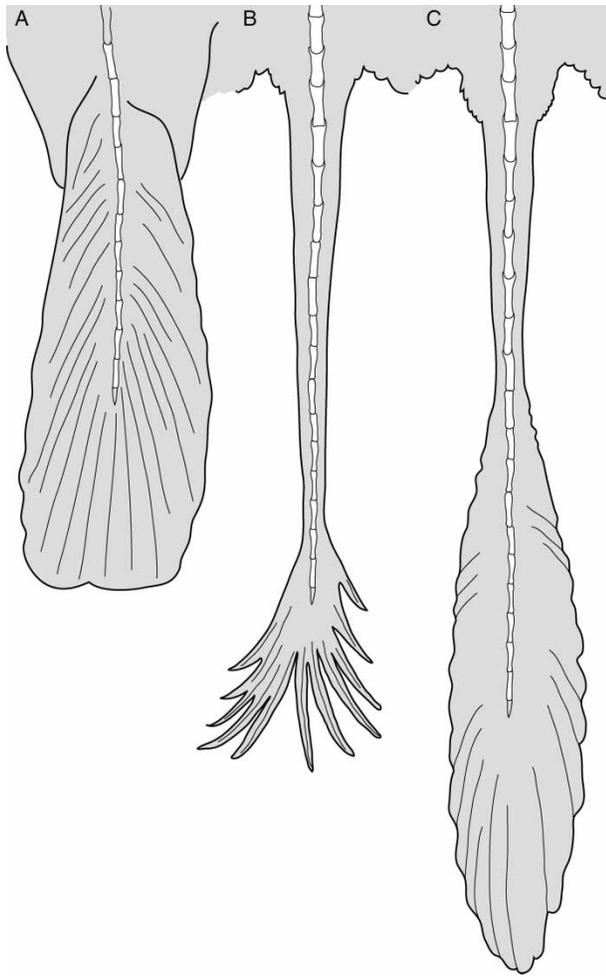


Figure 6. Reconstructions of long-tail bird tail morphology: (A) *A. lithographica* (B) *J. palmapenis* and (C) *M. gui*.

(Ji et al. 1998; Xu et al. 2010). In some taxa, the tail feathers also have a greater proximal extent in the tail (visible in *Microraptor* sp. TNP 00996, feathers begin at the 15–18th vertebrae and continue to the end; Xu et al. 2003; *Similicaudipteryx*). The feathers in *Archaeopteryx* are pennaceous, with rounded distal margins (where preservation allows), and appear to have some degree of overlap so that they form a cohesive surface with the potential to generate lift, albeit limited (Gatesy and Dial 1996).

The similar rectricial pattern observed in some non-avian maniraptorans (e.g. *Caudipteryx*) is unlikely to have been aerodynamic given the length of the individual feathers; however, their function is unknown. The ontogenetic changes in plumage observed in *Similicaudipteryx*, however, suggest that the feathers are related to sexual maturity and may indicate their function as related to some form of display. The feathers in *J. palmapenis* do not overlap significantly proximally and distally so that no airfoil is formed, and taper distally. Because the tail would

not generate any significant aerodynamic benefit, we suggest the morphology may also have had a display function. Feathers interpreted as for display have been recognised in several other groups of Jehol birds, primarily the Confuciusornithiformes and enantiornithines, some of which preserve a pair of elongate rectrices (Hou et al. 1999; Chiappe et al. 2008; O'Connor 2009). The wide range of 'streamer' morphologies documented within Enantiornithines, as well as a wide range of other known tail morphologies unsuited for optimised flight, suggests these feather morphologies are for display (O'Connor 2009). Within Ornithurae, although feather morphologies are far less common, a new specimen reveals that this clade may have evolved display rectricial patterns early in their history (Zhou et al. in press). The recently described *Schizoura lii* preserves a forked tail, which increases chance of sexual reproduction in living birds while decreasing aerodynamic efficiency (Thomas 1993). However, in a recent cladistic analysis, this taxon is resolved as basal to ornithurines that preserved fan-shaped tails (Zhou et al. In press). The discovery of non-aerodynamic, display-like tail morphologies in the Jeholornithiformes, the most basal group of birds known other than *Archaeopteryx*, and other groups of basal birds (e.g. Confuciusornithiformes) including basal ornithurines, suggests that during the early evolution and Cretaceous radiation of Aves, display was the main evolutionary force driving some feather patterns.

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