Sci Nat (2017) 104: 74
DOI 10.1007/s00114-017-1496-y

ORIGINAL PAPER

A new Jurassic theropod from China documents a transitional step in the macrostructure of feathers

Ulysse Lefèvre[1,2] · **Andrea Cau**[3,4] · **Aude Cincotta**[2,5] · **Dongyu Hu**[6,7] · **Anusuya Chinsamy**[8] · **François Escuillié**[9] · **Pascal Godefroit**[2]

Received: 13 April 2017 / Revised: 13 April 2017 / Accepted: 3 August 2017 / Published online: 22 August 2017

Abstract Genuine fossils with exquisitely preserved plumage from the Late Jurassic and Early Cretaceous of northeastern China have recently revealed that bird-like theropod dinosaurs had long pennaceous feathers along their hindlimbs and may have used their four wings to glide or fly. Thus, it has been postulated that early bird flight might initially have involved four wings (Xu et al. Nature 421:335–340, 2003; Hu et al. Nature 461:640–643, 2009; Han et al. Nat Commun 5:4382, 2014). Here, we describe *Serikornis sungei* gen. et sp. nov., a new feathered theropod from the Tiaojishan Fm (Late Jurassic) of Liaoning Province, China. Its skeletal morphology suggests a ground-dwelling ecology with no flying adaptations. Our phylogenetic analysis places *Serikornis*, together with other Late Jurassic paravians from China, as a basal paravians, outside the Eumaniraptora clade. The tail of *Serikornis* is covered proximally by filaments and distally by slender rectrices. Thin symmetrical remiges lacking barbules are attached along its forelimbs and elongate hindlimb feathers extend up to its toes, suggesting that hindlimb remiges evolved in ground-dwelling maniraptorans before being co-opted to an arboreal lifestyle or flight.

Keywords Paraves · Birds · Feathers · Barbules · Jurassic · Flight evolution

Abbreviation

PMOL	Palaeontological Museum of Liaoning
YFGP	Yizhou Fossil and Geology Park

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-017-1496-y) contains supplementary material, which is available to authorized users.

✉ Ulysse Lefèvre
ulysse.lefevre@naturalsciences.be

Pascal Godefroit
pascal.godefroit@naturalsciences.be

[1] Department of Geology, University of Liège, allée du 6 Août B18-B20, 4000 Liège, Belgium

[2] Earth and Life History O.D, Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium

[3] Earth, Life and Environmental Sciences Department, Alma Mater Studiorum, Bologna University, via Zamboni 67, 40126 Bologna, Italy

[4] Geological and Palaeontological Museum "G. Capellini", via Zamboni 63, 40126 Bologna, Italy

[5] Department of Geology, University of Namur, rue de Bruxelles 61, 5000 Namur, Belgium

[6] Paleontological Institute, Shenyang Normal University, 253 North Huanghe Street, Shenyang 110034, China

[7] Key Laboratory for Evolution of past Life in Northeast Asia, Ministry of Land and Resources (Shenyang Normal University), Shenyang 110034, China

[8] Department Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa

[9] Eldonia, Avenue des Portes Occitanes 9, 3800 Gannat, France

Introduction

The Late Jurassic-Early Cretaceous formations of northeastern China are well known for the extraordinary abundance and diversity, and the exceptional preservation of feathered dinosaurs that shed light on the origin and early diversification of birds (Han et al. 2014; Sullivan et al. 2014). Several small non-avian paravians (e.g. *Microraptor*, *Pedopenna*, *Anchiornis*, *Changyuraptor*, *Xiaotingia*, *Jianianhualong*) are characterized by long pennaceous feathers attached to both their tibia and metatarsus, suggesting that early bird flight might initially have involved four wings (Xu and Zhang 2005; Xu et al. 2003, 2017; Hu et al. 2009; Han et al. 2014). However, because deinonychosaurian theropods and earliest birds show a similar distribution of long pennaceous feathers along their forelimbs, hindlimbs and tail, and because different hypotheses of paravian phylogenies have recently been proposed (Hu et al. 2009; Xu et al. 2011; Godefroit et al. 2013a, b), the origin and early evolution of feather-based flight within Paraves remains controversial. Moreover, the morphology and internal structure of the feathers in the earliest paravians is poorly documented, so their real aerodynamical capacities remain conjectural. For example, the presence or absence of interlocked barbules, commonly considered as a criterion for determining whether a feather can produce useful aerodynamic lift (Zhang et al. 2006), remains unclear in the Late Jurassic basal paravians from China described so far.

Here we report a new paravian theropod, *Serikornis sungei* gen. et sp. nov., from the Late Jurassic Tiaojishan Formation of Linglongta (Jianchang County, Liaoning Province, China), based on a complete articulated skeleton, PMOL-AB00200, with associated integumentary structures. The plumage of this new specimen brings new information on the structure and function of the feathers in basal paravians and consequently on the early evolution of flight.

Materials and methods

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank life science identifiers can be resolved and the associated information viewed by appending the life science identifiers to the prefix http://zoobank.org/.

The life science identifiers for this publication are urn:lsid:zoobank.org:pub:65432F68-4DF9-4CC2-BE86-F366B858893A.

Results

Systematic palaeontology

Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Paraves Sereno, 1997; Avialae Gauthier, 1986
Serikornis sungei gen. etsp. nov.

Etymology

Serikos, ancient Greek for silk, because the body is almost covered with plumulaceous-like feathers; *Ornis*, ancient Greek for bird; named in honour of Sun Ge, for his contribution to our knowledge of Jurassic and Cretaceous ecosystems in Asia.

Holotype

PMOL-AB00200 is a single complete articulated skeleton with associated integumentary structures preserved on a slab. The counterpart is missing, but most of the skeleton is preserved on the main slab.

Locality and horizon

PMOL-AB00200 was collected in the Tiaojishan Formation (Oxfordian, Upper Jurassic; Chu et al. 2016) from Daxishan village, Linglongta (Jianchang County, Liaoning Province, China).

Diagnosis

Serikornis is characterized by the following combination of characters (autapomorphies are marked with an asterisk): four anterior maxillary teeth twice as long as the others regarding the crown height*; coracoid tuber well-developed and laterally projected from the lateral margin of the coracoid and forming a subglenoid shelf along the caudoventral margin of the bone; the distal end of the lateral process of the coracoid is thicker than the proximal part and forms a ventral rounded bump; ventrodistal process of ischium narrow, hook-like, strongly deflected caudodorsally and set at the distal end of the ischium*; smooth ventral side of coracoid devoid of small pits.

Osteological description

PMOL-AB00200 is about 49 cm long (Fig. 1). Although most of the cranial bones are shattered, the rostral part of the skull is almost well-preserved. The maxillary process of the premaxilla is short and does not exclude the maxilla from the ventral margin of the external naris, as in *Archaeopteryx*, *Anchiornis*,

Fig. 1 Photograph and drawing of the basal bird *Serikornis sungei* sp. nov. from the Middle-Late Jurassic of north-eastern China. **a** PMOL-AB00200 photograph. **b** Line drawing. Abbreviations: *cev* cervical vertebrae, *co* coracoids, *cv* caudal vertebrae, *fu* furcula, *il* ilium, *is* ischium, *lf* left femur, *lfi* left fibula, *lh* left humerus, *lma* left manus, *lpes* left pes, *lr* left radius, *ls* left scapula, *lt* left tibia, *lu* left ulna, *pu* pubis, *ra* radiale, *rf* right femur, *rh* right humerus, *rma* right manus, *rpes* right pes, *rr* right radius, *rt* right tibia, *ru* right ulna, *sk* skull

and most of theropods (e.g. *Saurornithoides*, *Zanabazar*, *Velociraptor*, *Caudipteryx*, *Haplocheirus*, *Monolophosaurus*, but not in Ornithomimosauria) (Barsbold 1974; Choiniere et al. 2010; Godefroit et al. 2013a; Ji et al. 1998; Makovicky et al. 2004; Norell et al. 2009; Osborn 1924; Wellnhofer 2009; Zhao and Currie 1993) (Fig. 2). The rostral plate and the maxillary process of the premaxilla are short and robust as in *Eosinopteryx* (Godefroit et al. 2013b). Only the ventral margin of the maxilla is well-preserved with partial shattered portions of the interfenestral bar. The left lacrimal is mostly completely preserved in *Serikornis*, and only the proximal part of the right lacrimal is located posteriorly to the left one. The left lacrimal has a long and slender anterior process (= rostral process), while the posterior process is shortened. It is impossible to know whether the anterior process contacts the nasal and forms the entire dorsal border of the antorbital fenestra as in all paravians where this bone is known (e.g. *Aurornis*, *Anchiornis*, *Deinonychus*, *Sinornithosaurus*, *Byronosaurus*) (Hu et al. 2009; Makovicky and Norell 2004; Norell and Makovicky 2004; Xu and Wu 2001). Anterior teeth are closely packed as in troodontids (Makovicky and Norell 2004; Wellnhofer 2009; Xu et al. 2011). A posteriorly widening groove extends along the labial surface of the dentary, as in many paravians (Agnolin and Novas 2013; Godefroit et al. 2013a, b; Hu et al. 2009; Makovicky and Norell 2004; Xu et al. 2011). The vertebral column is almost complete, although most details of the vertebrae are poorly preserved. Nine cervical vertebrae can be confidently identified. The second, the third and the fourth cervical vertebrae have ossified cervical ribs as long as their corresponding centra. Most of the dorsal portion of the vertebral column is covered by the left humerus, and its posterior part is shattered at the junction between two slabs. Only six dorsal centra can be identified. Details of the sacral portion is poor due to the junction of four slabs, but they appear to be fused. The tail is formed by 27 vertebrae (20 in *Eosinopteryx*, 30 in *Aurornis*, 21–23 in *Archaeopteryx*, 24 in *Anchiornis* YFGP-T5199 (pers. obs.), 22 in *Jeholornis*, at least 26 in *Velociraptor* IGM 100/986) and is 3.9 times the length of the femur (Godefroit et al. 2013a, b; Lindgren et al. 2015; Norell and Makovicky 1999; Wellnhofer 2009; Zhou and Zhang 2002). The scapula is 64% the length of the humerus (selected relative proportions are given in Table S4). This bone is thin and ribbon-shaped with a pointed distal end. It is gently convex caudoventrally whereas it is straight in *Aurornis*, *Eosinopteryx*, *Xiaotingia*, *Microraptor*, *Mei*, and *Anchiornis* (Gao et al. 2012; Godefroit et al. 2013a, b, Xu et al. 2003, 2011). The acromion process is not as strongly laterally everted as it is in *Xiaotingia* and oviraptorosaurs (e.g. *Caudipteryx*) (Osmolska et al. 2004; Xu et al. 2011), more closely resembling the moderately developed and cranially everted acromion in dromaeosaurids (Ostrom 1969; Norell and Makovicky 2004). The coracoid is subrectangular as in most basal paravians (e.g. *Eosinopteryx*, *Aurornis*, *Anchiornis*, *Archeopteryx*). The biceps tuber of the coracoid is better developed and projects further laterally in *Serikornis* than in other basal paravians and dromaeosaurids; it forms a subglenoid shelf along the caudoventral margin of the coracoid as in dromaeosaurids (Norell and Makovicky 2004, 1999,). The lateral process of the coracoid is thickened distally, forming a ventral rounded

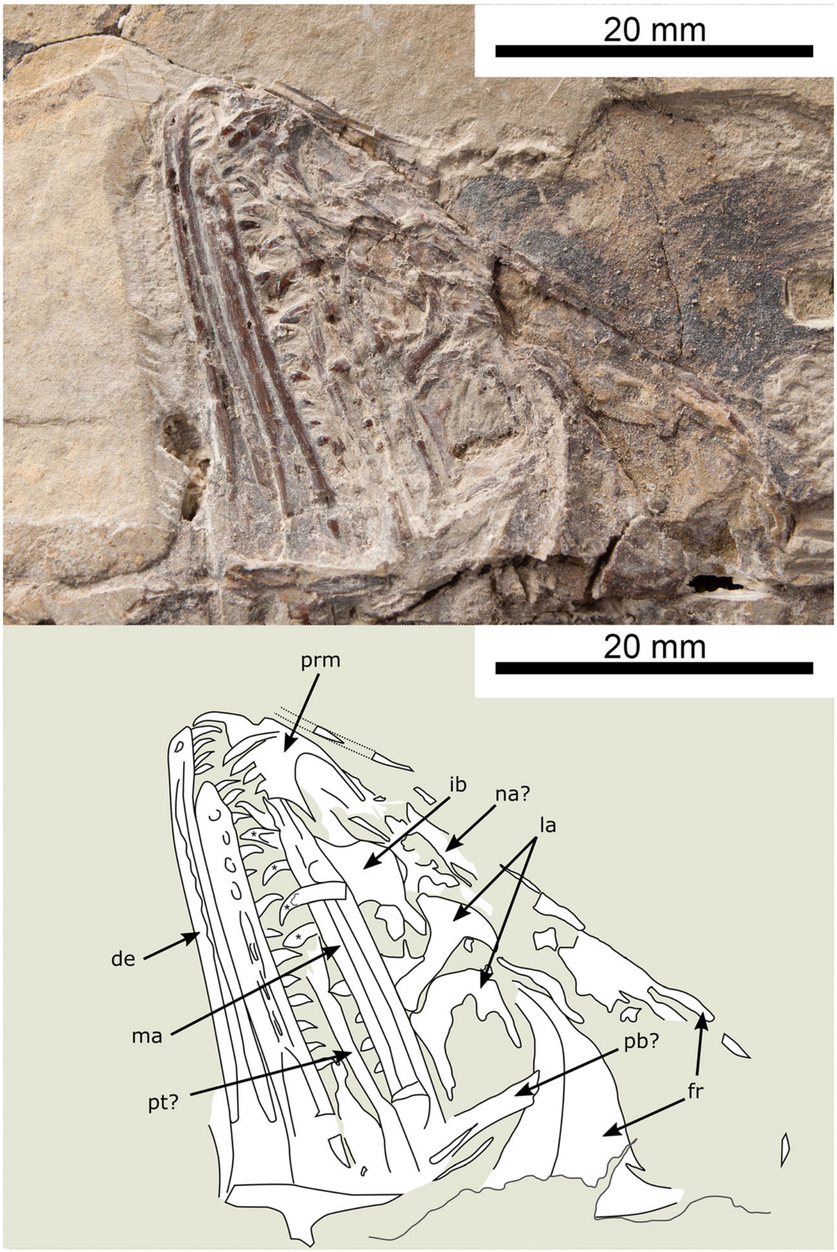


Fig. 2 Photograph and line drawing of the skull region of *Serikornis*. Abbreviations: *de* dentary, *fr* frontal, *ib* interfenestral bar, *la* lachrymal, *ma* maxillary, *na* nasal, *pb* postorbirtal bar, *prm* premaxillary, *pt* pterygoid

bump. The boomerang-shaped furcula is robust as in most other non-avialan theropods (Xu et al. 2011). The humerus of *Serikornis* is slightly shorter than the femur (0.9). Its deltopectoral crest is about one quarter the length of the humerus, as in other Late Jurassic basal paravians (Table S1). The radius and ulna are straight in dorsal view, as in scansoriopterygids, *Anchiornis*, *Eosinopteryx*, and *Aurornis* (Godefroit et al. 2013a, b; Zhang et al. 2002). The distal end of the radius lacks the distinct flange shared by deinonychosaurians and avialans (Zheng et al. 2010). Metacarpals II and III, although partially incomplete, are not fused proximally. The dorsal margin of the ilium is gently convex as in other paravians (Xu et al. 2011) except in *Aurornis*, in which the dorsal margin is subhorizontal (Godefroit et al. 2013a). The obturator process of the ischium is blunt, and its ventrodistal process is strongly deflected caudorsally (Fig. 3). The femur is slightly bowed anteriorly as in *Aurornis*, *Anchiornis*, and *Archaeopteryx* (Godefroit et al. 2013a; Hu et al. 2009; Wellnhofer 2009). The tibia is proportionally shorter (1.41 the length of the femur) than in *Anchiornis* (Table S4). The metatarsals are not fused proximally, and metatarsal III is transversely compressed as in *Aurornis*, *Eosinopteryx*, *Anchiornis*, *Microraptor*, unenlagiines and all troodontids (Gao et al. 2012; Godefroit et al. 2013a, b; Hu et al. 2009; Makovicky and Norell 2004; Snively et al. 2004; Xu and Norell 2004). Metatarsal V is one third the length of metatarsal IV. Pedal digit II lacks the proximo-dorsally expanded

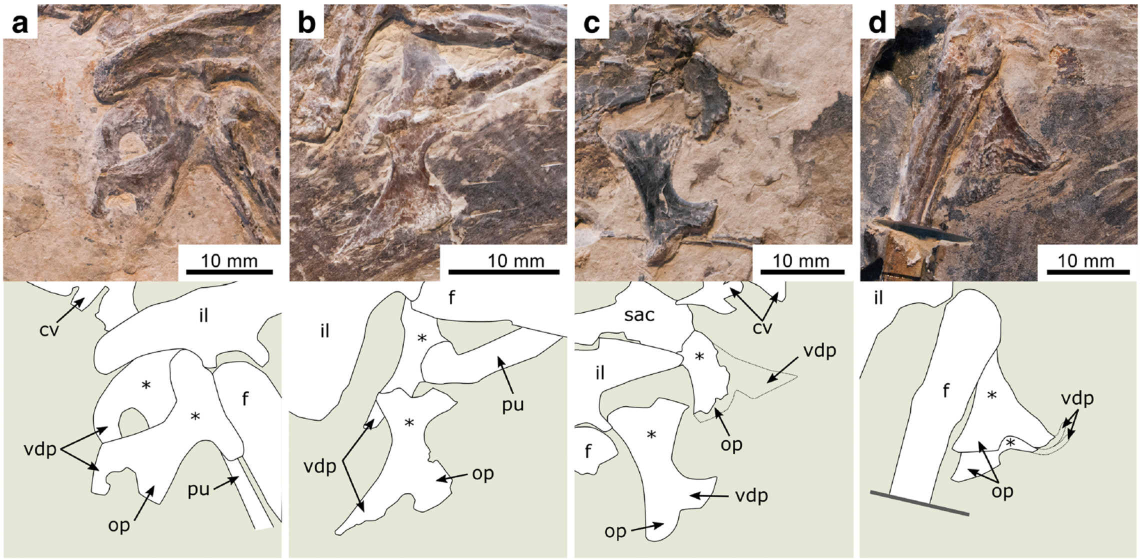


Fig. 3 Photographs and line drawings of the ischial region among several paravian theropods. **a** *Aurornis*. **b** *Eosinopteryx*. **c** *Anchiornis*. **d** *Serikornis*. Abbreviations: *cv* caudal vertebrae, *f* femur, *il* ilium, *op* obturator process, *pu* pubis, *sac* sacral vertebrae, *vdp* ventrodistal process. Ischia are labelled with an *asterisk*

articular trochlea of deinonychosaur-grade paravians (e.g. *Deinonychus*, *Velociraptor*) and possibly also the Eichstätt specimen of *Archaeopteryx* (Mayr et al. 2005; Norell and Makovicky 1999; Ostrom 1969). Pedal phalanges of digits III and IV are slender, and successive phalanges do not significantly increase in length proximodistally (see supplementary files for a complete description).

Osteological comparisons

Serikornis differs from other paravians in the following osteological features: the first four maxillary teeth that are twice as large as the others (Fig. S3 and Fig. S4). This anisodonty does not reflect taphonomic factors (i.e. a partial extrusion of first teeth from maxillary sockets) as the maxillary rim recovering the tooth is erased, allowing to observe that the roots are not displaced. X-ray analysis of the skull shows that the posterior maxillary teeth were completely erupted at the moment of the dead (Fig. S4). The biceps tuber of the coracoid is strongly developed and well detached from the lateral margin of the coracoid; the lateral process of the coracoid forms a rounded bump (Fig. S5). The ventrodistal process of the ischium is narrow, hook-like, strongly deflected caudodorsally and placed at the distal end of the bone, a unique feature in basal paravians (Fig. 3). The shape of the ventrodistal process of the ischium is not the result of a local deformation during the diagenesis because other long bones (humerus, ulna, radius, femur and tibia) remain straight along their entire length.

Although they share relatively close bone proportions (Table S4), several characters clearly distinguish *Serikornis* from *Anchiornis*, also from the Tiaojishan Formation. The ventral side of the coracoid in PMOL-AB00200 is not sculptured by the numerous small pits, regarded as autapomorphic for *Anchiornis* (Fig. 4) (Lindgren et al. 2015; Makovicky and Norell 2004; Xu et al. 2009). As this character is present both in the smaller holotype (femur length 43 mm; Xu et al. 2009) and in a larger referred specimen (YFGP-T5199, femur length 70 mm, as in the holotype of *Serikornis*; Lindgren et al. 2015) of *Anchiornis*, the ornamentation of the coracoid is clearly not ontogenetic. The ischium of *Serikornis* differs from that of *Anchiornis* by its blunt obturator process located more distally than the midpoint of the ischial shaft (Figs. 3c, d and S6). In *Anchiornis*, the posterodorsal margin of the ischium is gently concave in lateral view (Hu et al. 2009) (pers. obs. on YFGP-T5199). This is the plesiomorphic paravian condition, also shared by *Eosinopteryx* (Godefroit et al. 2013b). The ischium of *Serikornis* is also unique among basal paravians because of its hook-like process on the apical end of its dorsal margin; this process is clearly visible on the left ischium, and as an impression on the slab above the damaged end of the right ischium that closely resembles the process on the left ischium (Fig. 3d). In both ischia, the process is more expanded dorsoventrally than anteroposteriorly, resulting in a narrow 'hooked' apex of the bone. *Serikornis* also differs from *Anchiornis* in having a tibiotarsus/femur ratio smaller than 1.5 (1.41 in YFGP-T5199, > 1.55 in all known *Anchiornis* specimens regardless of body size (Hu et al. 2009; Xu et al. 2009; pers. obs. on YFGP-T5199, Table S3)). This ratio is shared by *Anchiornis* specimens smaller than *Serikornis* (pers. obs., on YFGP-T5199) and individuals subequal in size to the latter (femur length 66 mm; ratio = 1.60; LPM-B00169) (Hu et al. 2009). Therefore, different proportions of the tibia in

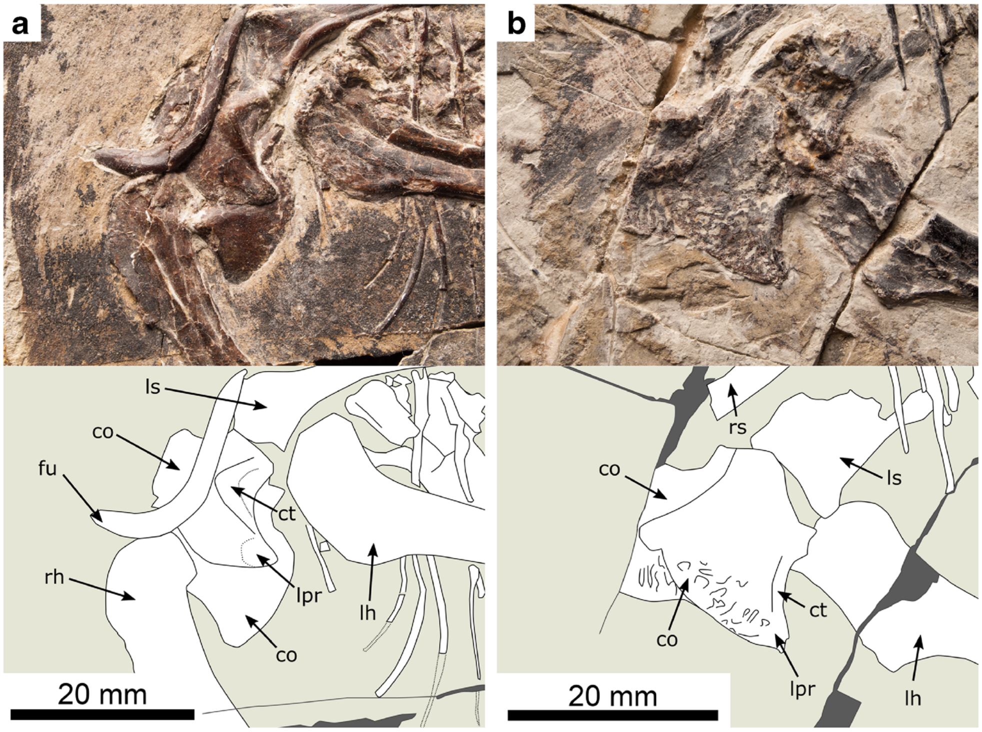


Fig. 4 Comparison of the scapular girdle in *Serikornis sungei* and *Anchiornis huxleyi* (YFGP-T5199). **a** *Serikornis sungei*. **b** *Anchiornis huxleyi.* Numerous pits are present on the anterior surface of the coracoid of *Anchiornis* that are completely absent in *Serikornis*. Abbreviations. *co* coracoids, *ct* coracoid tuber, *fu* furcula, *lh* left humerus, *lpr* lateral process of the coracoid, *ls* left scapula, *rs* right scapula

Serikornis and *Anchiornis* likely do not reflect ontogenetic variations.

Serikornis differs from *Aurornis* in the morphology of its ischium: the postacetabular process tapers distally and the dorsal margin is gently convex, whereas it is not markedly deflected ventrally with a horizontal dorsal margin in *Aurornis*. The ischium also lacks the ventrally expanded, hook-like ventral process on the distal end that delimits a prominent distal obturator notch in *Aurornis* (Godefroit et al. 2013a).

Serikornis differs from *Eosinopteryx* in the longer rostral plate and larger maxillary process of the premaxilla (although this latter difference may be biased by the different ontogenetic stages of the type of individuals). It also differs by the presence of an anterior process of the lacrimal (the latter is vestigial in *Eosinopteryx*). This feature is likely not an ontogenetic feature as *Serikornis* is a subadult specimen whereas *Eosinopteryx* is thought to be an earlier juvenile (Godefroit et al. 2013b).

Serikornis differs from *Pedopenna* in its relatively longer metatarsal I, its metatarsal III longer than metatarsals II and IV, and in the more robust first phalanx of pedal digit I (Xu and Zhang 2005).

Serikornis differs from *Xiaotingia* in the posterior process of its maxilla that does not exceed in depth the dentary at mid-length, in having a metacarpal III as long as and not more robust than metacarpal II, in the interclavicular angle of its furcula wider than 75° with a slender omal end, and in lacking a strongly laterally everted acromial process on its scapula that overhangs a groove along the lateral surface of the scapular blade (Xu et al. 2011).

Limb element ratios used to differentiate *Serikornis* may be affected by allometric effects as in other theropods (Houck et al. 1990; Gatesy 1991; Christiansens 1999; Currie 2003). In order to demonstrate that the difference in proportions is due to taxonomy rather than ontogeny, a plot of the limb ratios presented in Table S4 versus the femur length (taken as a body size proxy) is presented in Fig. 5. Trend lines indicate that there is no relationship in regard of each limb proportion ratio. Therefore, the differences in limb proportion ratios are due to taxomony rather than to ontogeny and they can be used in order to discriminate *Serikornis* from other paravian species.

Pneumaticity

Without the presence of recognizable foramina in *Serikornis* due to the crushing of bones during diagenesis, it is impossible to determine whether the bones are pneumatized. Thanks to a X-ray technique called laminography (see supplementary files), the skull and the four anteriormost cervical vertebrae were digitally sliced with high resolution (Fig. 6). At least the anteriormost cervical vertebrae are pneumatized and form numerous small internal chambers (camellate vertebrae). This pattern suggests that a cervical air sac system invades those vertebrae (Sereno et al. 2008) as it is also the case in many theropods (e.g. *Aerosteon*, *Archaeopteryx*, *Rahonavis*, *Deinonychus*, *Velociraptor*, *Anchiornis*) (Britt et al. 1998;

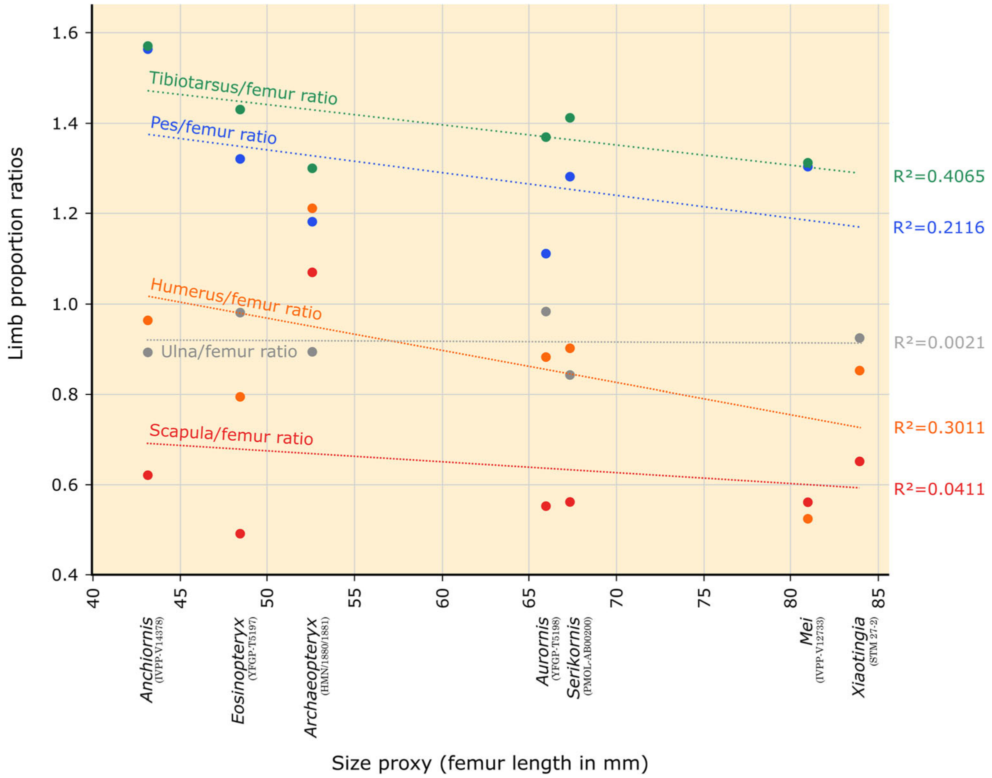


Fig. 5 Plot of limb proportion ratios versus the length of the femur as a body size proxy in seven paravians. *Trendlines* and R^2 indicate an absence of relationship between species in regard of each limb proportion ratio

Forster 1998; Norell and Makovicky 1999; Ostrom 1969; Sereno et al. 2008; Xu et al. 2009).

Plumage description

Feather impressions are present around the entire skeleton, extending onto the pedal phalanges (except the unguals), as also described in *Anchiornis* (Hu et al. 2009) and *Xiaotingia* (Xu et al. 2011) (Fig. 7). It is not possible to observe whether the long and thin filaments that cover the top of the skull remain isolated or are bundled proximally. Feathers similar to those previously identified in the dromaeosaurid theropod *Sinornithosaurus* (Ji et al. 2001) cover the neck of *Serikornis* and consist of bundles of filaments that are joined together proximally and remain nearly parallel as they extend distally (down-like feathers) (Fig. 7a). The back of *Serikornis* is entirely covered by contour-like feathers with well-defined rachis and transversely inserted barbs (Fig. 7b). As in *Anchiornis*, the forelimb wings appear to be formed by multiple layers of relatively short, slender, symmetrical and poorly differentiated feathers inserted on a large propatagium; unlike in *Archaeopteryx*, *Microraptor*, *Confuciusornis* and modern birds, remiges and coverts cannot be distinguished (Fig. 7c) (Brown et al. 1994; Chiappe et al. 1999; Li et al. 2012; Longrich et al. 2012). The number of pennaceous feathers attached to the forelimb cannot be accurately estimated. As in *Anchiornis* (Hu et al. 2009) and *Eosinopteryx* (Godefroit et al. 2013b), the longest forelimb feathers are attached near the distal end of the forearm and the proximal end of the manus, and are about 150% the humeral length. A large number of undifferentiated forelimb feathers are arranged in several rows in *Serikornis*, suggesting the presence of a large propatagium, a fleshy structure made of skin filling the angle between the humerus and the forearm (Baumel 1993; Brown et al. 1994; Feduccia and Czerkas 2015), in life. In modern birds, the propatagium is mainly responsible for the aerodynamical profile of the wing (Brown et al. 1994; Lucas and Stettenheim 1972), but this structure is also necessary for the insertion of numerous covert feathers responsible for the cambered dorsal surface of the wing (Brown et al. 1994). The development of a large propatagium in basal paravians is therefore supported by the presence of numerous layers of feathers along the forearm in *Serikornis* but also in *Anchiornis* (Longrich et al. 2012; Wang et al. 2017), although this character could be inherited from a common ancestor with oviraptorosaurs as this character is also present in *Caudipteryx* (Feduccia and Czerkas 2015). In *Serikornis*, the vanes of the remiges obviously lack barbules, as observed in both optical and electronical microscopy (Fig. S8 and Fig. S9), and confirmed by the absence of basal expansions along the barbs that mark the insertion of barbules in modern feathers (Lucas and Stettenheim 1972); however, those basal expansions have not been observed either in early bird specimens assumed to have barbules (see supplementary files). Of course, it cannot be excluded that this apparent absence of barbules is a taphonomic bias. However, thin integumentary structures, with a mean

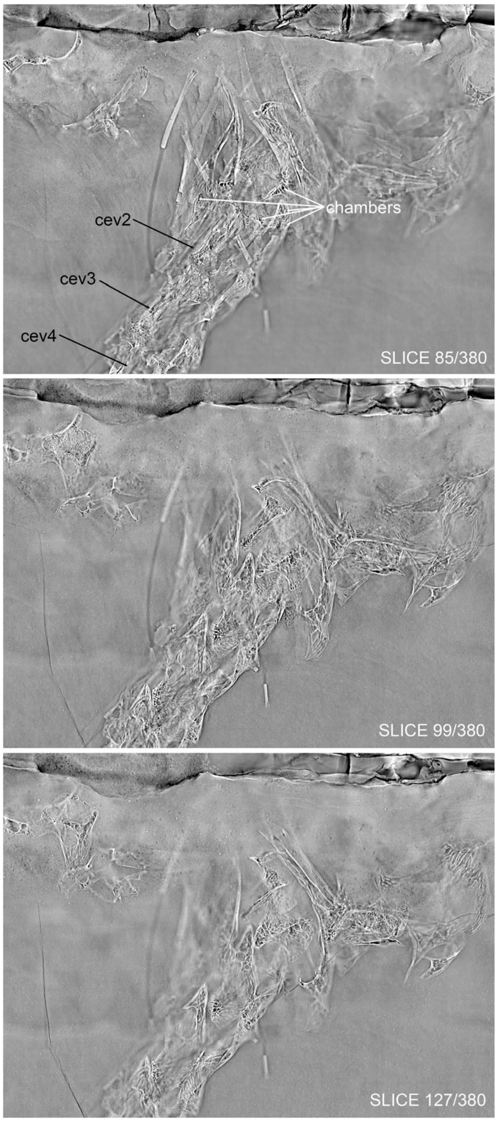


Fig. 6 Pneumaticity in *Serikornis sungei* under laminography. At least the most proximal portion of the cervical column is highly pneumatized as shown by numerous small chambers revealed under laminography. Abbreviation: *cev* cervical vertebra

width of 43 ± 0.002 μm, similar to the range of modern barbule widths (e.g. 23 μm in the shelduck up to 80 μm in the single comb chicken; Lucas and Stettenheim 1972; D'Alba et al. 2014), are preserved in the neck region indicating that the absence of barbules does not reflect preservation conditions. If barbules were really missing, the pennaceous feathers of *Serikornis* did not form an efficient aerial surface for supporting the air pressure during a wing-propelled flight (Lucas and Stettenheim 1972). Ji et al. (1998) argued that the presence of a well-formed vane in fossilized feathers, as observed in *Serikornis*, is an indirect evidence for the presence of barbules. However, the distal part of the covert feathers of the cassowary (*Casuarius casuarius*) does not form a loose tangle of barbs although they are devoid of barbules (Fig. S10). Moreover, the proximodistal distances between the proximal barbs in this bird are sometimes insufficient to allow interlocking barbs. It is therefore conceivable that complete interlocked vanes evolved later in paravian evolution, when the main role for feather changed from a social/thermoregulatory display to a flight function.

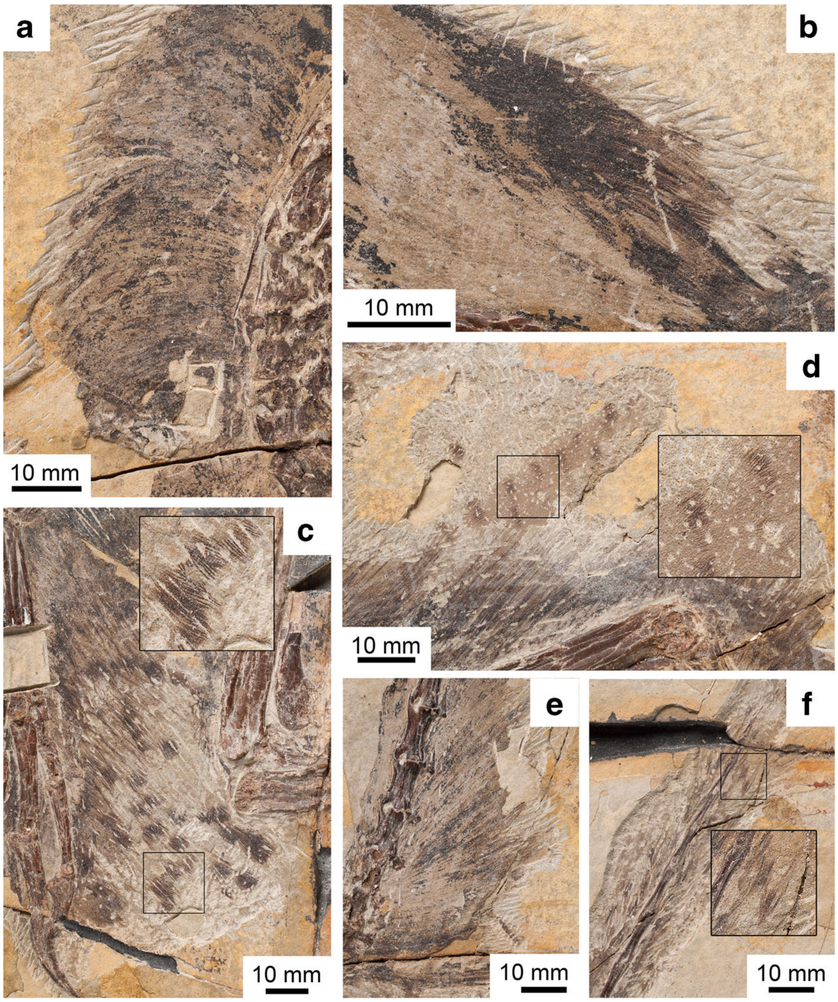
Densely packed integumentary filaments that are joined together proximally are present along the posterior part of the hindlimbs—from the femur up to the penultimate pedal phalanges—contrasting with *Eosinopteryx* in which the lower leg is devoid of any integumentary structures (Godefroit et al. 2013b), although it cannot be excluded that this character reflects taphonomical conditions. Besides the down-like feathers, meticulous preparation of PMOL-AB00200 reveals the presence of tibial and of short metatarsal remiges (Fig. 7d and Fig. S11), as in *Anchiornis, Archaeopteryx* and *Sapeornis* (Foth et al. 2014; Xu et al. 2003; Xu and Zhang 2005; Zheng et al. 2013b). *Serikornis* can be viewed as a tetrapterygian paravian (= four-wing biplan made of elongated feathers), although its forewing is composed of undifferentiated contour and flight feathers, and its hindwing includes both pennaceous and plumulaceous-like feathers (both wings may lack barbules). As in *Anchiornis*, the presence of both plumulaceous-like feathers and pennaceous feathers on the hindwing of PMOL-AB00200 represents a transitional stage between the fully plumulaceous leg of basal coelurosaurians (e.g. *Sinocalliopteryx* and *Yutyrannus*) and a fully pennaceous hindlimb recovered in more derived Avialae (e.g. *Archaeopteryx* and *Sapeornis*) (Godefroit et al. 2013a; Hu et al. 2009; Zheng et al. 2013b).

The tail of *Serikornis* is proximally covered by numerous down-like feathers (Fig. 7e), while short pennaceous symmetric feathers with a slender rachis are inserted along the distal end of the tail (Fig. 7f). The distal tail feathers of *Serikornis* cannot be considered as true rectrices (that is, large-sized asymmetrical feathers of the tail) but more closely resemble tectrices (upper tail coverts) in Avialae (O'Connor et al. 2013). As in the hindlimb, the tail feathers of *Serikornis* therefore represent a transitional condition between the fully plumulaceous tail filaments of more basal coelurosaurs and the longer rectrices inserted all along the tail of *Anchiornis* (see YFGP-T5199 specimen in Lindgren et al. 2015) and basal Pennaraptorans (Foth et al. 2014; Hu et al. 2009).

Phylogenetic analysis

The data matrix consists of 1732 informative characters, including 9 characters describing the plumage, and has been scored for 130 operational taxonomic units (OTUs) (see supplementary files). In order to recover the position of *Serikornis*, the data matrix has been analysed with the TNT software (Goloboff et al. 2008). One hundred 'New Technology search' runs with default settings

Fig. 7 Integumentary structures of *Serikornis sungei* sp. nov. **a** 'Down' feathers from the neck region. **b** 'Contour' feathers from the back region. **c** Symmetric feathers of the left wing where the remiges and the contour feathers cannot be distinguished. **d** Tibial feathers on the posterior face of the right femur. **e** Metatarsal feathers recovered after a second preparation. **f** Distal part of the tail covered by numerous 'down' feathers. **g** Upper part of the tail where pennaceous symmetric feathers are inserted. *Scale bars*: **a**–**d**, **f**, **g** = 10 mm and **e** = 5 mm



have been computed. Then the shortest tree islands found were explored by the tree-bisection-reconnection algorithm to only hold the shortest trees. Our analysis recovered 96 shortest trees with each a length of 5743 steps. The consensus tree focused on the paraves clade (Fig. 8) shows that the scansoriopterygid lineage is placed at the base of the clade. Here, *Xiaotingia* is recovered as a basal member of Scansoriopterygidae but its position is highly unstable (Foth et al. 2014; Godefroit et al. 2013a, b; Xu et al. 2011) and further investigations are required to fix its position. Several taxa (*Pedopenna*, *Aurornis*, *Eosinopteryx* and *Anchiornis*) previously regarded as basal members of Avialae are now placed in a more basal position outside Eumaniraptora. As in numerous studies, Troodontidae and Dromaeosauridae are grouped within the Deinonychosauria, which is the sister group of Avialae.

Our phylogenetic analysis places *Serikornis* among basal paravians, outside the Avialae-Deinonychosaurian node (Eumaniraptora) (Fig. 8 and Fig. S11), as the sister taxon of *Eosinopteryx*, and closely related to *Aurornis* and *Pedopenna* (Foth et al. 2014; Godefroit et al. 2013a; Hu et al. 2009; Lefèvre et al. 2014). Our analysis also recovers *Anchiornis* as the sister taxon of Eumaniraptora.

Discussion

Our results are consistent with the presence of four wings as the primitive condition for Eumaniraptora (Fig. 8) and inherited by basal birds or, in other words, that the flapping flight of modern birds was preceded by a four-winged gliding stage (Godefroit et al. 2013a, b; Longrich et al. 2012; Xu et al. 2003, 2011; Xu and Zhang 2005; Zheng et al. 2013b). Fully developed hindlimb wings, implying the presence of elongated remiges along both the tibia and the metatarsus, are present in *Microraptor* (Xu et al. 2003), *Pedopenna* (Xu and Zhang 2005), *Anchiornis* (Xu and Zhang 2005), *Changyuraptor* (Han et al. 2014) and *Sapeornis* (Zheng et al. 2013b). Although the hindlimbs of *Serikornis* are covered both by bundles of filaments joined proximally and by fully developed pennaceous feathers, this pattern remains consistent with the tetrapterygian condition of basal birds. *Eosinopteryx* seems to

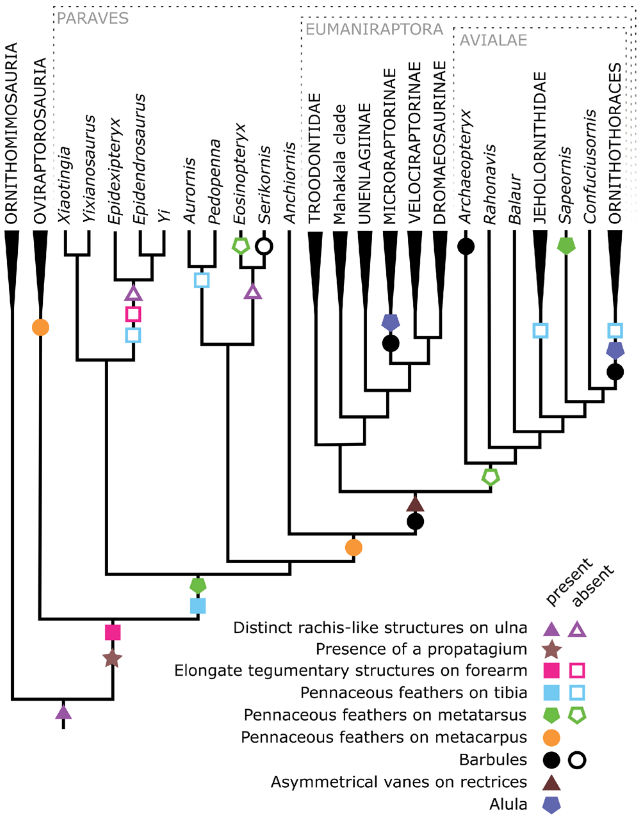


Fig. 8 Strict consensus tree resulting from the phylogenetic analysis (length = 5743, consistency index = 0.2614, retention index = 0.7386). Major evolutions in the history of birds are mapped on the paraves clade. The complete tree is presented as supplemental fig. S11

be devoid of hindlimb wings: pennaceous feathers are only present along the posterior part of the thigh and crus, but this absence can be the result of a taphonomic bias. This apparent reduction of the hindlimb plumage may be regarded as a secondary loss in *Eosinopteryx* (Godefroit et al. 2013b) or as an ontogenetically controlled feature.

The symmetrical vanes on the hindwing feathers of *Serikornis*, *Anchiornis* and *Pedopenna* (Xu and Zhang 2005) seem to be less efficient from an aerodynamic perspective than those of more derived paravians, so these taxa may have used their hindwing feathers for other functions, such as visual display or mate recognition. The high plasticity in the development of metatarsal plumage in paravians can still be observed in modern birds, with the recurrent development of feathered feet in birds of prey (e.g. *Aquila chrysaetos*, *Asio flammeus*, *Bubo scandiacus*) or in chicken breeds such as Silkies (Barrows 1981; Bartels 2003). Although their small size suggests that these animals were probably not top predators, they would have needed fast movements to escape predation. In this way, the development of hindwing feathers remains disadvantageous and should be regarded as a sign of sexual selection (Chiappe et al. 1999; O'Connor and Chang 2015).

Although elongated rectrices are present along the distal half of the tail in Oviraptorosauria (Ji et al. 1998; Xu et al. 2010) and *Microraptor* (Li et al. 2012), they seem to be absent in *Serikornis*, *Aurornis* and *Eosinopteryx*, which may suggest that the tail of those basal paravians had no aerodynamic function in increasing the total lift of the animal while gliding as in *Archaeopteryx* (Longrich et al. 2012), nor any display function as well. The long bony tail was completely covered by elongated pennaceous rectrices in both *Anchiornis* (Hu et al. 2009) and *Archaeopteryx* (Foth et al. 2014), whereas *Jeholornis* had both proximal and distal tail fans (O'Connor et al. 2013). The tail plumage is highly variable in pygostylian birds: a pair of elongate rectrices in *Confuciusornis* male specimens (Chinsamy et al. 2013) and, in some Enantiornithes (Wang et al. 2014), a graded fan of pennaceous feathers in *Sapeornis*, a forked tail of pennaceous feathers in *Schizooura* and a fan-shaped tail of pennaceous feathers in *Hongshanornis* and in most modern birds (Lucas and Stettenheim 1972; Wang et al. 2014). Rectrices are secondarily absent in *Confuciusornis* females (Chinsamy et al. 2013) and some enantiornithine female birds (Foth et al. 2014; Zheng et al. 2013a).

Although they extensively covered both arms and hands, the forelimb feathers of the Middle-Late Jurassic basal paravians *Anchiornis*, *Eosinopteryx* and *Serikornis* remained unspecialized and undifferentiated into elongated remiges and shortened coverts, unlike in *Archaeopteryx*, *Microraptor* and modern birds (Foth et al. 2014; Longrich et al. 2012): all were rather short, slender, symmetrical and, at least in *Serikornis* and *Eosinopteryx*, devoid of barbules, contrasting with the more elongated and asymmetrical wing feathers with well-developed barbules in *Archaeopteryx* (Carney et al. 2012; Foth et al. 2014) and modern birds (Lucas and Stettenheim 1972). Based on these results, the forelimb feathers in Late Jurassic basalmost paravians were obviously not adapted for active flight (although glide flight cannot be excluded) and were therefore more likely related to other biological phenomena, including visual display and sexual selection (Foth et al. 2014; Ji et al. 1998; Li et al. 2010; O'Connor et al. 2013; Prum and Brush 2012; Xu and Guo 2009).

The supposed limited flight capabilities of *Aurornis*, *Eosinopteryx* and *Serikornis*, as evidenced by the study of their preserved plumage, is also reflected in their osteology. Their forelimbs are proportionally shorter and more gracile than in *Anchiornis* and *Archaeopteryx* (Table S1-S2), resulting in a reduced wing surface. All these specimens also have a relatively straight ulna and radius (thus limiting the pronation and supination movements necessary for producing a wing beat), lack a bony sternum for attachment of powerful pectoral muscles and have proximodistally decreasing pedal phalanges, together with small pedal unguals that are poorly recurved

(Pike and Maitland 2004). Moreover, the relatively high ratio of tibiotarsus length to femur length can be regarded as a good evidence of cursoriality (Boles 1997). All these characters suggest that basal paravians were primarily ground-dwelling animals with good cursorial abilities (Foth et al. 2014; Hu et al. 2009). However, the manual digits of *Serikornis* are long and slender with strongly curved unguals I and III. This supposed that they could have been effective for climbing trees as in *Archaeopteryx* (Feduccia 1993; Manning et al. 2009; Wellnhofer 2009). In this way, the hindlimbs can be regarded as less specialized than the forelimbs for grasping.

The recent discovery of a patagium in scansoriopterygids (a lineage found among basalmost paravians in our phylogenetic analysis, and lacking evidence of remiges) (Xu et al. 2015) suggests that the earliest adaptation to an arboreal/gliding lifestyle among paravians did not involve exaptation of the plumage as an aerodynamic surface. This is particularly true as the insertion of several rows of forelimb feathers requires a large propatagium. The absence of true flying adaptation in the 'tetrapterygian' *Serikornis* and the gliding membrane of scansoriopterygids both challenge an aerodynamic function as earliest driver of plumage elaboration in basalmost Paraves.

Birds and, by extension, some other archosaurs are characterized by a pneumatic postcranial skeleton with invasion of bones by the pulmonary air-sac system (Benson et al. 2012; Britt et al. 1998; O'Connor and Claessens 2005). This system allows a flow-through ventilation and exceptionally efficient gas exchanges (Duncker 1971), and has two evident additional functions: weight reduction in large-bodied or flying taxa and density reduction by energetic savings during foraging and locomotion (Benson et al. 2012; Bramwell and Whitfield 1974; Britt 1993; Cope 1877; Currey and Alexander 1985). The latter function is widely accepted as the main reason for skeletal pneumatization because body size has no significant influence on the proportion of pneumatized skeletal compartments (O'Connor 2004).

Pneumatic foramina (that is, the opening that allows an air sac to enter bone) are proportionally much larger than the primitive nutriment foramina in non-pneumatic vertebrae (including apneumatic bird vertebrae) (Britt et al. 1998). Pneumatic foramina are present in most tetanuran theropods (Benson et al. 2012; Britt et al. 1998), dromaeosaurs (Makovicky et al. 2005; Ostrom 1969), oviraptorosaurs (Osmolska et al. 2004), birds (Apostolaki et al. 2015; Baumel 1993; O'Connor 2004), sauropods (Cope 1877; Marsh 1877; Upchurch et al. 2004; Wedel 2003) and pterosaurs (Bonde and Christiansen 2003; Butler et al. 2009; Claessens et al. 2009; Eaton 1910; Seeley 1870). The character distribution of pneumaticity shows that although axial pneumaticity may lighten the skeleton, its evolution cannot be considered to be an adaptation for flight (Britt et al. 1998). The pneumaticity of cervical and anterior dorsal vertebrae occurred early in theropod evolution (Benson et al. 2012), and the presence of pneumatic foramina in vertebrae of non-avialan and avialan theropods indicates that some components of the avian air-sac lung system was already, to some degree, in place (Britt et al. 1998).

Britt (1993) proposed several osteological correlates of vertebral pneumaticity, based on osteological study of extant ratites (*Struthio camelus* and *Dromaius novaehollandiae*) (e.g. large external foramina, external fossae with a crenulate surface texture, thin outer bone walls) (Benson et al. 2012). However, O'Connor (2006) noted that several of these features are present in crocodilians, which lack postcranial pneumaticity. Thus, the presence of internal chambers (called camerate or camellate based on the number and size of internal chambers) opening externally via large (and thus not simply vascular) foramina is the only unambiguous evidence of skeletal pneumaticity (Britt et al. 1998; O'Connor 2006; Wedel 2007). The presence of a high pneumaticity of the anteriormost cervical vertebrae and the limited flight capacities of *Serikornis* suggest that high pneumatization in small maniraptorans reflects the demands of an increasingly high-performance metabolic regime rather than a prerequisite for flight (Benson et al. 2012; Britt et al. 1998; Cubo and Casinos 2000; Currey and Alexander 1985; Fajardo et al. 2007; O'Connor 2004). Further analyses are required to explore the pneumaticity of the whole specimen. The laminography technique is promising as it allows to investigate the proportion of pneumaticity without external traces of foramina or pneumaticity.

Acknowledgments This work was supported by a grant (BL/36/62) to P.G. from the SPP Politique scientifique (Belgium), by FRIA Grants to U.L. and A.Ci. from the F.R.S.-FNRS and by grants to H.D. from the National Natural Science Foundation of China (41172026) and the Natural Science Foundation (201102199). Photographs were taken by Thierry Hubin (RBINS). The use of TNT was kindly permitted by the Willi Hennig Society. The genus name was found after the preliminary expertise of the specimen by Danielle Dhouailly (Université Joseph Fourier). We thank each reviewer that spent time and made efforts in order to improve the final version of our paper. We would also like to thank Emily Willoughby who painted the life reconstruction of *Serikornis sungei.*

References

Agnolin FL, Novas FE (2013) Avian ancestors. In: Lohmann G, Mysak LA, Notholt J, Rabassa J, Unnithan V (eds) A review of the phylogenetic relationships of the theropods unenlagiidae, microraptoria, anchiornis and scansoriopterygidae. Springer, Netherlands

Apostolaki NE, Rayfield EJ, Barrett PM (2015) Osteological and soft-tissue evidence for pneumatization in the cervical column of the ostrich (*Struthio camelus*) and observations on the vertebral columns of non-volant, semi-volant and semi-aquatic birds. PLoS One 10:e0143834

Barrows CW (1981) Roost selection by spotted owls: an adaptation to heat stress. Condor 83:302–309

Barsbold R (1974) Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. Paleontol Pol 30: 5–22

Bartels T (2003) Variations in the morphology, distribution, and arrangement of feathers in domesticated birds. J Exp Zool 298B:91–108

Baumel JJ (1993) Handbook of avian anatomy: nomina anatomica avium, 2nd ed. ed, Publications of the Nuttall Ornithological Club. The Nuttall Ornithological Club

Benson RB, Rich TH, Vickers-Rich P, Hall M (2012) Theropod fauna from Southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. PLoS One 7:e37122

Boles WE (1997) Hindlimb proportions and locomotion of *Emuarius gidju* (Patterson & Rich, 1987) (Aves: Casuaridae). Mem Qld Mus 41:235–240

Bonde N, Christiansen P (2003) The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications. Geol Soc Lond Spec Publ 217:217–232

Bramwell CD, Whitfield GR (1974) Biomechanics of *Pteranodon*. Philos Trans R Soc B 267:503–581

Britt BB (1993) Pneumatic postcranial bones in dinosaurs and other archosaurs (PhD thesis). University of Calgary

Britt BB, Makovicky PJ, Gauthier J, Bonde N (1998) Postcranial pneumatization in *Archaeopteryx*. Nature 395:374–376

Brown RE, Baumel JJ, Klemm R (1994) Anatomy of the propatagium: the great horned owl (*Bulbo virginianus*). J Morphol 219:205–224

Butler RJ, Barrett PM, Gower DJ (2009) Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs. Biol Lett 5:557–560

Carney RM, Vinther J, Shawkey MD, D'Alba L, Ackermann J (2012) New evidence on the colour and nature of the isolated *Archaeopteryx* feather. Nat Commun 3. doi:10.1038/ncomms1642

Chiappe LM, Grimaldi DA, Wang X, Tedford RH, Nguyen T, Taylor BE (1999) Anatomy and systematics of the Confuciusornithidae (Theropoda, Aves) from the Late Mesozoic of northeastern China. American Museum of Natural History

Chinsamy AT, Chiappe LM, Marugán-Lobón J, Gao C, Zhang F (2013) Gender identification of the Mesozoic bird *Confuciusornis sanctus*. Nat Commun 4:1381

Christiansens P (1999) Long bone scalin and limb posture in non-avian theropods: evidence for differential allometry. J Vertebr Paleontol 19:666–680

Choiniere JN, Xu X, Clark JM, Forster CA, Guo Y, Han F (2010) A basal Alvarezsauroid theropod from the Early Late Jurassic of Xinjiang, China. Science 327:571–574

Chu Z, He H, Ramezani J, Bowring SA, Hu D-Y, Zhang L, Zheng S, Wang X, Zhou Z, Deng C, Guo J (2016) High precision U/Pb geochronology of the Jurassic Yanliao biota from Jianchang (western Liaoning Province, China): age constraints on the rise of feathered dinosaurs and eutherian mammals. Geochem Geophys Geosyst 17: 3983–3992

Claessens LPAM, O'Connor PM, Unwin DM (2009) Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. PLoS One 4:e4497

Cope ED (1877) On a gigantic saurian from the Dakota Epoch of Colorado. Paleontol Bull 25:5–10

Cubo J, Casinos A (2000) Incidence and mechanical significance of pneumatization in the long bones of birds. Zool J Linnean Soc 130:499–510

Currey JD, Alexander RM (1985) The thickness of the walls of tubular bones. J Zool 206:453–468

Currie PJ (2003) Allometric bgrowth in tyrannosaurids (Dinosauria: TTheropod) from the Upper Cretaceous of North American and Asia. Can J Earth Sci 40:651–665

D'Alba L, Van Hemert C, Spencer KA, Heidinger BJ, Gill L, Evans NP, Monaghan P, Handel CM, Shawkey MD (2014) Melanin-based color of plumage: role of condition and of feathers' microstructure. Integr Comp Biol 54:633–644. doi:10.1093/icb/icu094

Duncker HR (1971) The lung air-sac system of birds. Adv Anat Embryol Cell Biol 45:1–171

Eaton GF (1910) Osteology of *Pteranodon*. Conn Acad Arts Sci Mem 2: 1–38

Fajardo RJ, Hernandez R, O'Connor PM (2007) Postcranial skeletal pneumaticity: a case study in the use of quantitative microCT to assess vertebral structure in birds. J Anat 211:138–147

Feduccia A (1993) Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. Science 259:790–793

Feduccia A, Czerkas SA (2015) Testing the neoflightless hypothesis: propatagium reveals flying ancestry of oviraptorosaurs. J Ornithol 156:1067. doi:10.1007/s10336-015-1190-9

Forster CA (1998) The theropod ancestry of birds: new evidence from the late cretaceous of Madagascar. Science 279:1915–1919. doi:10.1126/science.279.5358.1915

Foth C, Tischlinger H, Rauhut OWM (2014) New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. Nature 511:79–82. doi:10.1038/nature13467

Gatesy SM (1991) Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. J Morphol 209:83–96

Gao C, Morschhauser EM, Varricchio DJ, Liu J, Zhao B (2012) A second soundly sleeping dragon: new anatomical details of the Chinese Troodontid *Mei long* with implications for phylogeny and taphonomy. PLoS One 7:e45203. doi:10.1371/journal.pone.0045203

Godefroit P, Cau A, Hu D, Escuillié F, Wenhao W, Dyke GJ (2013a) A Jurassic avialan dinosaur from China resolves the early phylogenetic history if birds. Nature 498:359–362. doi:10.1038/nature12168

Godefroit P, Demuynck H, Dyke GJ, Hu D, Escuillié F, Claeys P (2013b) Reduced plumage and flight ability of a new Jurassic paravian theropod from China. Nat Commun 4. doi:10.1038/ncomms2389

Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786

Han G, Chiappe LM, Ji S-A, Habib M, Turner AH, Chinsamy A, Liu X, Han L (2014) A new raptorial dinosaur with excetpionally long feathering provides insights into dromaeosaurid flight performance. Nat Commun 5:4382

Houck MA, Gauthier JA, Strauss RE (1990) Allometric scaling in the earliest fossil bird *Archaeopteryx lithographica*. Science 247:195–198

Hu D, Hou L, Zhang L, Xu X (2009) A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. Nature 461:640–643

Ji Q, Currie PJ, Norell MA, Ji S-A (1998) Two feathered dinosaurs from the northeastern China. Nature 393:753–761

Ji Q, Norell MA, Gao K, Ji S (2001) The distribution of integumentary structures in a feathered dinosaur. Nature 410:1084–1088

Lefèvre U, Hu D, Escuillié F, Dyke G, Godefroit P (2014) A new long-tailed basal bird from the Lower Cretaceous of north-eastern China. Biol J Linn Soc 113:790–804. doi:10.1111/bij.12343

Li Q, Gao K-Q, Meng Q, Clarke JA, Shawkey MD, D'Alba L, Pei R, Ellison M, Norell MA, Vinther J (2012) Reconstruction of *Microraptor* and the evolution of iridescent plumage. Science 335: 1215–1219

Li Q, Gao K-Q, Vinther J, Shawkey MD, Clarke JA, D'Alba L, Meng Q, Briggs DEG, Prum RO (2010) Plumage color patterns of an extinct dinosaur. Science 327:1369–1372

Lindgren J, Sjövall P, Carney RM, Cincotta A, Uvdal P, Hutcheson SW, Gustafsson O, Lefèvre U, Escuillié F, Heimdal J, Engdahl A, Gren JA, Kear BP, Wakamatsu K, Yans J, Godefroit P (2015) Molecular composition and ultrastructure of Jurassic paravian feathers. Sci Rep 5. doi:10.1038/srep13520

Longrich NR, Vinther J, Meng Q, Li Q, Russell AP (2012) Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. Curr Biol 22:2262–2267. doi:10.1016/j.cub.2012.09.052

Lucas AM, Stettenheim PR (1972) Avian anatomy: integument, parts I. U.S. Agricultural Research Service, Washington D.C.

Makovicky PJ, Apesteguía S, Agnolin FL (2005) The earliest dromaeosaurid theropod from South America. Nature 473:1007–1011

Makovicky PJ, Kobayashi Y, Currie PJ (2004) Ornithomimosauria. In: Weishampel DB, Dodson P, Osmólska (eds) The Dinosauria, 2nd edn. University of California Press, California, pp 135–150

Makovicky PJ, Norell MA (2004) Troodontidae. In: Weishampel DB, Dodson P, Osmolska H (eds) The Dinosauria, 2nd edn. University of California Press, California, pp 184–195

Manning PL, Margetts L, Johnson MR, Withers PJ, Sellers WI, Falkingham PL, Mummery PM, Barrett PM, Raymont DR (2009) Biomechanics of Dromaeosaurid dinosaur claws: application of X-ray microtomography, nanoindentation, and finite element analysis. Anat Rec 292:1397–1405

Marsh OC (1877) Notice of new dinosaurian reptiles from the Jurassic formation. Am J Sci 14:514–516

Mayr G, Pohl B, Peters SD (2005) A well-preserved *Archaeopteryx* specimen with theropod features. Science 310:1483–1486

Norell MA, Makovicky PJ (2004) Dromaeosauridae. In: Weishampel DB, Dodson P, Osmolska H (eds) The Dinosauria, 2nd edn. University of California Press, California, pp 184–195

Norell MA, Makovicky PJ (1999) Important features of the dromaeosaur skeleton. II. Information from newly collected specimens of *Velociraptor mongoliensis*. Am Mus Novit 3215:1–28

Norell MA, Makovicky PJ, Bever GS, Balanoff AM, Clark JM, Barsbold R, Rowe TB (2009) A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). Am Mus Novit 3654: 1–63

O'Connor J, Wang X, Sullivan C, Zheng X, Tubaro P, Zhang X, Zhou Z (2013) Unique caudal plumage of Jeholornis and complex tail evolution in early birds. Proc Natl Acad Sci 110:17404–17408. doi:10.1073/pnas.1316979110

O'Connor JK, Chang H (2015) Hindlimb feathers in paravians: primarily "wings" or ornaments? Biol Bull 42:616–621. doi:10.1134/S1062359015070079

O'Connor PM (2006) Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. J Morphol 267:1199–1226

O'Connor PM (2004) Pulmonary pneumaticity in the postcranial skeleton of extant Aves: a case study examining Anseriformes. J Morphol 261:141–161

O'Connor PM, Claessens LPAM (2005) Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. Nature 436:253–256

Osborn HF (1924) Three new theropoda, protoceratops zone, Central Mongolia. Am Mus Novit 144:1–12

Osmolska H, Currie PJ, Barsbold R (2004) Oviraptorosauria. In: Weishampel DB, Dodson P, Osmólska (eds) The Dinosauria, 2nd edn. University of California Press, California, pp 165–183

Ostrom JH (1969) Osteology of *Deinonychus antirrhopus*, an usual theropod from the Lower Cretaceous of Montana. Bull Peabody Mus Nat Hist 30:1–165

Pike AVL, Maitland DP (2004) Scaling of bird claws. J Zool 262:73–81

Prum RO, Brush AH (2012) The evolutionary origin and diversification of feathers. Q Rev Biol 77:261–295

Seeley HG (1870) Remarks on Professor Owen's monograph on *Dimorphodon*. Ann Mag Nat Hist 4:129–152

Sereno PC, Martinez RN, Wilson JA, Varrichio DJ, Alcober OA, Larsson HCE (2008) Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. PLoS One 3:e3303

Snively E, Russel AP, Powell GL (2004) Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric and phylogenetic approaches. Zool J Linnean Soc 142:525–553

Sullivan C, Wang Y, Hone DWE, Wang Y, Xu X, Zhang F (2014) The vertebrates of the Jurassic Daohugou Biota of northeastern China. J Vertebr Paleontol 34:243–280

Upchurch P, Barrett PM, Dodson P (2004) Sauropoda. In: The Dinosauria, 2nd edn. California, pp 259–322

Wang X, Michael P, Zheng X, Kaye TG, Falk AR, Hartman SA, Xu X (2017) Basal paravian functional anatomy illuminated by high-detail body outline. Nat Commun 8:14576

Wang X, O'Connor JK, Zheng X, Wang M, Hu H, Zhou Z (2014) Insights into the evolution of rachis dominated tail feathers of a new enantiornithines (Aves: Ornithothoraces). Biol J Linn Soc 113:805–819

Wedel MJ (2003) The evolution of vertebral pneumaticity in sauropod dinosaurs. J Vertebr Paleontol 23:344–357

Wedel MJ (2007) What pneumaticity tells us about "prosauropods", and vice versa. Spec Pap Palaeontol 77:207–222

Wellnhofer P (2009) Archaeopteryx: the icon of evolution. Verlag Dr. Friedrich Pfeil, München

Xu X, Currie PJ, Pittman M, Xing L, Meng Q, Lü J, Hu D, Yu C (2017) Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. Nat Commun 8:14972

Xu X, Guo Y (2009) The origin and early evolution of feathers: insights from recent paleontological and neontological data. Vertebr Palasiat 47:311–329

Xu X, Norell MA (2004) A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431:838–841

Xu X, Qi Z, Norell M, Sullivan C, Hone D, Erickson G, Wang X, Han F, Guo Y (2009) A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. Chin Sci Bull 54:430–435

Xu X, Wu X-C (2001) Cranial morphology of *Sinornithosaurus millenii* Xu et al. 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. Can J Earth Sci 38:1739–1752

Xu X, You H, Du K, Han F (2011) An *Archaeopteryx*-like theropod from China and the origin of Avialae. Nature 475:465–470. doi:10.1038/nature10288

Xu X, Zhang F (2005) A new maniraptoran dinosaur from China with long feathers on the metatarsus. Naturwissenschaften 92:173–177

Xu X, Zheng X, Sullivan C, Wang X, Xing L, Wang Y, Zhang X, O'Connor JK, Zhang F, Pan Y (2015) A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. Nature 521:70–73

Xu X, Zheng X, You H (2010) Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature 464:1338–1341

Xu X, Zhou Z, Wang X, Kuang X, Zhang F, Du X (2003) Four winged dinosaurs from China. Nature 421:335–340

Zhang F, Zhou Z, Dyke G (2006) Feathers and 'feather-like' integumentary structures in Liaoning birds and dinosaurs. Geol J 41:395–404

Zhang F, Zhou Z, Xu X, Wang X (2002) A juvenile coelurosaurian theropod from China indicates arboreal habits. Naturwissenschaften 89:394–398

Zhao X-J, Currie PJ (1993) A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. Can J Earth Sci 30:2027–2036

Zheng X, O'Connor JK, Huchzermeyer F, Wang X, Wang Y, Wang M, Zhou Z (2013a) Preservation of ovarian follicles reveals early evolution of avian reproductive behaviour. Nature 495:507–511. doi:10.1038/nature11985

Zheng X, Xu X, You H, Zhao Q, Dong Z (2010) A short-armed dromaeosaurid from the Jehol group of China with implications for early dromaeosaurid evolution. Proc R Soc Lond B 277:211–217

Zheng X, Zhou Z, Wang X, Zhang F, Wang Y, Wei G, Wang S, Xu X (2013b) Hind wings in basal birds and the evolution of leg feathers. Science 339:1309–1312

Zhou Z, Zhang F (2002) A long-tailed, seed-eating bird from the Early Cretaceous of China. Nature 418:1754–1756