

Reduced plumage and flight ability of a new Jurassic paravian theropod from China

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Small feathered theropods were incredibly diverse in the Early Cretaceous Jehol Group of western Liaoning Province, China¹⁻⁴. Recently, however, anatomical distinct non-avian theropods that also preserve feathers have also been discovered in the older Middle-Late Jurassic Tiaojishan Formation in the same area⁵⁻⁷. Phylogenetic hypotheses including these new specimens have challenged the pivotal position of the iconic *Archaeopteryx*, slightly younger than the Tiaojishan specimens, in the phylogeny of birds⁷. Here we describe a new basal troodontid theropod, *Eosinopteryx brevipenna*, from the Tiaojishan Formation that closely resembles *Anchiornis* from the same locality⁵⁻⁶ (regarded here as sister-taxa). The completely preserved plumage of *Eosinopteryx* is much less extensive on the forelimbs, metatarsus, pes and tail than in either *Anchiornis* or *Archaeopteryx*. With a reduced plumage and short uncurved pedal claws, *Eosinopteryx* would have been able to run unimpeded on the ground (with large remiges on its feet, cursorial locomotion was likely impossible in *Anchiornis*, from the same formation and locality). *Eosinopteryx* thus increases the known diversity of small-bodied predatory dinosaurs in Late Jurassic ecosystems, shows that taxa with similar body-plans could occupy different niches in the same ecosystem and implies that cursorial running was likely the precursor to gliding in dinosaurs closely related to *Archaeopteryx*.

Theropoda Marsh, 1881

Maniraptora Gauthier 1986

Troodontidae Gilmore, 1924

Eosinopteryx brevipenna gen. et sp. nov.

Etymology. *Eo*, Greek for daybreak, dawn; *sino*, Latin for Chinese; *pteryx*, Greek for feather, wing; *brevi*, Latin for short; *penna*, Latin for feather.

Holotype. YFGP (Yizhou Fossil & Geology Park)-T5197, a nearly complete and articulated skeleton with associated integumentary structures (Fig. 1; see Supplementary Information for provenance and authenticity of the holotype specimen).

Locality and horizon. Yaolugou, Jianchang, western Liaoning, China; Middle-Late Jurassic Tiaojishan Formation

Diagnosis. A small paravian maniraptoran theropod that possesses the following autapomorphies: a short snout, about 82% the length of the orbit; a lacrimal with a long posterior process participating in about half the length of the dorsal margin of the orbit and a vestigial anterior process; a short tail, composed of 20 caudal vertebrae and 2.7 times the length of the femur; chevrons reduced to small rod-like elements below the proximal 8 or 9th caudals; an ilium with proportionally long, low and distally tapering postacetabular process (ratio 'length / height at mid-length' = 5); pedal unguals shorter than corresponding penultimate phalanges.

The holotype of *Eosinopteryx brevipenna* is 30 cm long (Fig. 1). The skull has a subtriangular lateral profile produced by a shallow snout and expanded postorbital region (Fig. 2, a-b). Unlike in *Anchiornis*⁶, the snout of *Eosinopteryx* is distinctly shorter (about 82 % of orbital length) than the orbit. Both the rostral plate and the maxillary process of the premaxilla are particularly short. The posterior process of the lacrimal is elongated and straight, participating in about half the length of the dorsal margin of the orbit, whereas the anterior process is vestigial. The postorbital process of the jugal is broader than in *Anchiornis*⁶ while the triradiate postorbital is larger than in *Archaeopteryx*⁸ and forms a complete postorbital bar with the jugal. There is no trace of a mandibular fenestra. The dentary has a groove that widens posteriorly and contains a row of foramina as in *Archaeopteryx*, *Anchiornis*, *Xiaotingia*, troodontids, and some basal dromaeosaurids^{6,7}. The teeth of *Eosinopteryx* are unserrated and sharp in contrast to the bulbous teeth of *Xiaotingia*⁷. As characteristic of troodontids⁹, the premaxillary and the dentary teeth in the symphyseal region are more closely packed than are the teeth in the posterior part of the dentary.

There are seven postaxial cervical vertebrae in YFGP-T5197. The cervical ribs are as long as their corresponding centra, contrasting with the shorter cervical ribs seen in *Troodon formosus*⁹ and the much longer ones in *Archaeopteryx*¹⁰. The trunk is about 32% the length of the hindlimb, as in *Mei*¹¹; this region is distinctly longer (42 %) in *Anchiornis*⁶. The middle and posterior dorsals are proportionally elongate as in *Anchiornis*, dromaeosaurids and *Archaeopteryx*¹². As in *Archaeopteryx*, *Anchiornis* and basal deinonychosauroids, the dorsal centra do not have distinct pneumatic foramina just shallow depressions on their lateral surface⁷. Numerous, very slender, abdominal ribs are preserved, as in *Archaeopteryx*¹⁰ and

dromaeosaurids¹³, as well as the basal pygostylian bird *Confuciusornis* and in many enantiornithines (e.g. *Sinornis*¹⁴). The tail of *Eosinopteryx* is particularly short, 2.7 times the length of the femur (contrasting with 3.2 in *Mei*¹¹ and 3.9 in the Eichstätt specimen of *Archaeopteryx*¹⁰), and only composed of 20 caudal vertebrae (contrast with 21-23 in *Archaeopteryx*¹⁰, ca. 30 in *Anchiornis*⁵ and 24-26 in *Microraptor*¹⁵). The anterior caudals are proportionally short, their transverse processes longer than corresponding centra and particularly narrow. The neural spine is developed only on the anteriormost 3 or 4 caudals. As in *Anchiornis* and *Archaeopteryx*⁶⁻⁷, the middle and posterior caudal vertebrae each bear a distinct groove on the lateral surface near the junction of the centrum and neural arch. The chevrons are reduced to small rod-like elements and are only present below the proximal 8 or 9 caudal centra, contrasting with the larger hook-like proximal chevrons of *Anchiornis*⁵ and with the vertically-oriented rectangular proximal chevrons of *Archaeopteryx*¹⁰.

The subrectangular coracoid of *Eosinopteryx* bears a distinct subglenoid fossa and has a wider proximal end than *Xiaotingia*⁷. The arm of this small paravian (0.7 times leg length) is slightly shorter than that of *Anchiornis* (0.8⁶) and *Archaeopteryx* (0.9 – 1.0¹⁰) but is much longer than *Mei* (0.5¹¹). The humerus of *Eosinopteryx* is also shorter (0.8 times) than its femur; the humerus is slightly longer than the femur in *Anchiornis*, distinctly longer (1.1-1.2¹⁰) in *Archaeopteryx*, and is only half the femur length in *Mei*. As in *Anchiornis*, the radius and ulna of *Eosinopteryx* are straight with only a narrow gap between them. The manus is slightly longer than the femur (manus / femur = 1.2), contrasting with the short hand of *Mei* (0.8¹¹) and with the proportionally more elongate hands of *Anchiornis* (1.6⁶) and *Archaeopteryx* (1.4 – 1.6¹⁰). Metacarpal II is about one third the length of metacarpal III; in contrast to *Xiaotingia*⁷, metacarpal IV is shorter and is much more slender than metacarpal III. The phalangeal portion of the manus is also proportionally shorter, relatively to the metacarpus, than in *Xiaotingia*⁷. As in *Anchiornis*⁶, the long manual phalanx II-1 of *Eosinopteryx* is as robust as the radius; this element is much more gracile in *Sinornithoides*¹⁶ and *Archaeopteryx*¹⁰. Contrasting with *Xiaotingia*⁷, phalanx III-2 is shorter than metacarpal III while the manual unguals of *Eosinopteryx*, sheathed by long keratinous claws, are less curved than in *Archaeopteryx*¹⁰, *Anchiornis*⁵, and *Xiaotingia*⁷.

The ilium of *Eosinopteryx* is characterised by a long, low and distally tapering postacetabular process, with a ratio 'length / height at mid-length' of 5 (Fig. 2, c-d). The ischium is particularly short, about 28% the femur length. With its distally displaced obturator process and its long and pointed posterodistal process, this element closely resembles that of *Anchiornis*⁵⁻⁶ (Fig. 2, c and e). The tibiotarsus of *Eosinopteryx* (1.43x femur length) is proportionally shorter than in *Anchiornis* (160 %⁶), while pes proportions (1.34x femur length) are similar to those of *Mei* (1.3¹¹), shorter than *Anchiornis* (1.57⁶). The proximal end of metatarsal III is transversely compressed, suggesting a sub-arctometatarsalian condition. Pedal digit I lies on the medioplantar side of metatarsal II, as in *Archaeopteryx*^{10, 17}, but contrasts with the

position of pedal digit I in *Anchiornis* which is medial to metatarsal II⁵. The phalanges of pedal toes II, III, and IV decrease gradually in length proximo-distally, as in *Archaeopteryx* and terrestrial cursorial birds¹⁸. The pedal unguals of *Eosinopteryx* are much shorter than those of *Archaeopteryx*¹⁰, *Anchiornis*⁵⁻⁶, troodontids⁹, and dromaeosaurids¹³, even shorter than the corresponding penultimate phalanges.

As in *Anchiornis*⁶, the longest remiges of *Eosinopteryx* are at least 150% the length of the humerus (Fig. 2, f) and are symmetrical on the forelimbs. Long, densely-packed and symmetrical pennaceous feathers are present along the posterior part of the thigh and crus, consistent in distribution with the tetrapterygian condition of several other basal paravian taxa^{6, 19}. However, careful preparation of this specimen shows that feathers were absent from the metatarsus and pes of *Eosinopteryx*, contrasting with *Anchiornis*⁶, *Xiaotingia*⁷, *Pedopenna*²⁰ and *Microraptor*¹⁹. Feathers covering other regions of the body (head, neck, thorax, back, and tail) are plumulaceous and 'rachis-like' structures described on the plumulaceous feathers at the base of the tail and on the neck in *Mei*¹¹ are absent in *Eosinopteryx*. The feathers on the tail are short, less than 20 mm long; all are plumulaceous, composed of a bundle of filaments that are joined together proximally and remain nearly parallel as they pass distally. Pennaceous rectrices are absent.

Phylogenetic analysis places *E. brevipenna* sister to *Anchiornis huxleyi* at the base of Troodontidae (Fig. 3). Both taxa share a dorsally curved ilium shaft, a pubis moderately oriented posteriorly and a straight ulna that is not bowed away from the humerus. *Archaeopteryx*, *Wellnhoferia*, and *Xiaotingia* then form an unresolved polytomy at the base of Deinonychosauria in the strict consensus tree, but a monophyletic group at the base of Deinonuchosauria in the 90% majority-rule tree of the 70 most parsimonious trees (Supplementary Information); as a result, this analysis supports the hypothesis that *Archaeopteryx* is a deinonychosaurian theropod instead of a primitive bird⁷ (Fig. 3). However, this phylogeny remains only weakly supported presumably due to the numerous homoplasies widely distributed across coelurosaurian phylogeny^{7, 21}.

The plumage of *Eosinopteryx* is complete but much less developed than that of other known Late Jurassic paravians, including *Anchiornis*, *Archaeopteryx* and *Wellnhoferia*. Indeed, the absence of pennaceous feathers on the lower leg does not reflect a basal phylogenetic position for *Eosinopteryx* among paravians because these are now known to occur on the metatarsus of at least one basal member of each of the three major known lineages in this region of the theropod tree, including the basal troodontid *Anchiornis*⁶, the basal avialan *Pedopenna*²⁰, and the basal dromaeosaurid *Microraptor*¹⁹. Pennaceous rectrices attached to the feet are also present in *Archaeopteryx*, *Wellnhoferia*¹⁰ and some basal Avialae⁴ implying that they were a relatively ubiquitous adaptation amongst maniraptorans. Despite its small size, the holotype of *Eosinopteryx* had reached a late ontogenetic stage (sub-adult or adult): neurocentral sutures are closed on all exposed vertebrae and the astragalus-calcaneum complex is fused to the tibia.

Ontogenetic stage therefore does not account for reduced plumage and although temporary disappearance of rectrices and pennaceous feathers on the metatarsus and pes might be explained by a seasonal molt, more specimens would be needed to test this hypothesis.

It is parsimonious to argue that plumage differences in *Eosinopteryx* can be explained by its mode-of-life. With shorter humerus and manus, and a reduced plumage, *Eosinopteryx* had a much shorter wing span than *Archaeopteryx*, *Wellnhoferia* and *Anchiornis*. The straight and closely aligned ulna-radius of this paravian also means that pronation/supination of the manus with respect to the upper arm would have been limited; combined with the absence of a bony sternum and weakly-developed proximal humerus, these attributes suggest little or no ability to oscillate the arms to produce a wing-beat. The phalanges of the third toe of *Eosinopteryx* decrease proximo-distally and its ungual phalanges are not very recurved and particularly short, suggesting a ground-dwelling, "cursorial" mode-of-life as in living birds^{18, 22}. Reduced plumage on the tail and lower legs likely facilitated this ecology and allowed *Eosinopteryx* to run easily. The plumage of paravian theropods was already diversified during the Late Jurassic and already had different functions: insulation, flight, and visual display²³. Although *Anchiornis* and *Eosinopteryx* are closely similar from an osteological point of view, their external aspect was different and their plumage was adapted to different ecological niches and also implies a much more complex picture in terms of the origin of flight. The diversification of integumental structures therefore facilitated the sympatry of numerous closely-related paravian theropods in the Late Jurassic Tiaojishan Formation and later in the Early Cretaceous Jehol Group of western Liaoning Province.

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Supplementary information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions PG, FE and PC designed the project. HD, PG, GD and DH performed the research. PG, HD and GD wrote the manuscript.

Figure Caption

Figure 1. *Eosipnopteryx brevipenna* YFGP-T5197. **a**, photograph and **b**, line drawing. Abbreviations: cav, caudal vertebrae; cev, cervical vertebrae; dv, dorsal vertebrae; fu, furcula; ga, gastralia; lf, left femur; lh, left humerus; lil, left ilium; lis, left ischium; lm, left manus; lp, left pes; lr, left radius; ls, left scapula; lt, left tibia; lu, left ulna; ma, mandible; rcor, right coracoid; rf, right femur; rh, right humerus; ril, right ilium; ris, right ischium; rm, right manus; rp, right pes; rr, right radius; rs, right scapula; rt, right tibia; ru, right ulna; sk, skull.

Figure 2. Selected skeletal elements and associated feathers of *Eosipnopteryx brevipenna* YFGP-T5197. **a**, photograph of skull and mandible in right lateral view. **b**, line drawing of skull and mandible in right lateral view. **c**, photograph of pelvis in right lateral view. **d**, line drawing of right ilium in lateral view. **e**, line drawing of right ischium in lateral view. **f**, detail of secondary remiges. **g**, detail of plumulaceous feathers under the middle part of the tail. Abbreviations: ac, acetabulum; lpm, left premaxilla; obt, obturator process; postpr, posterodistal process; prac, preacetabular process; ra, right angular; rdt, right dentary; rect, right ectopterygoid; rfr, right frontal; rj, right jugal; rl, right lacrimal; rmx, right maxilla; rna, right nasal; rpa, right parietal; rpal, right palatine; rpm, right premaxilla; rpo, right postorbital; rq, right quadrate; rsq, right squamosal; rsa, right surangular; scl, scleral plate.

Figure 3. Simplified time-calibrated phylogeny of Paraves (Dinosauria: Theropoda), based on the 90% majority-rule tree of the 70 most-arsimonious trees (See Supplementary Information for details.)

Supplementary Information

1. Origin and authenticity of the specimen

As it is the case for most of the paravian specimens known from western Liaoning Province, the holotype and only known specimen of *Eosinopteryx brevipenna* was acquired by the Yizhou Fossil & Geology Park from a Chinese fossil dealer, according to whom the specimen was collected in the Yaolugou locality (Jianchang county, western Liaoning, China) that has also yielded the *Anchiornis huxlei* specimen LPM (Liaoning Paleontological Museum)-B00169¹. The Tiaojishan Formation is widely exposed in this area², though it also has limited outcrops of the Early Cretaceous Yixian Formation³. The *Eosinopteryx brevipenna* specimen is preserved in a shale slab, the sedimentary structures of which closely resemble those of the specimens of *Anchiornis huxlei* and *Xiaotingia zhengi* also described from the Tiaojishan Formation; it is in fact extremely difficult to distinguish between Tiaojishan and Yixian shale slabs on the basis of macro-sedimentary features. It is therefore necessary to study in detail the micro-sedimentary structures and the pollen assemblages within the shale slabs to certify the age of the specimen, as it is also the case for the *Anchiornis huxlei* and *Xiaotingia zhengi* specimens described so far⁴.

The specimen was only partially prepared when it was sold by the Chinese dealer. Careful preparation by the Yizhou Fossil & Geology Park staff and by authors of this paper (FE and PG) did not reveal any trace of forgery, and the probability that the specimen is a composite is accordingly low.

2. Age of the Tiaojishan Formation

The Tiaojishan Formation crops out in the West Liaoning Province and is equivalent to the Lanqi Formation of North Hebei Province⁵. The reason for the abundance of excellently preserved fossils is the presence of interbedded tuffs originating from recurrent volcanic events⁶. In western Liaoning, the Tiaojishan Formation is 130-970 metres thick⁶ and is composed of different types of rocks, including basalts, andesites, rhyolites, tuffs, tuffaceous sandstones and conglomerates⁶⁻⁷. Because of the

complicated stratigraphic pattern in the Tiaojishan Formation, accurate dating of the formation is particularly difficult⁵. Ages between $165 \pm 1,2$ Ma and 153 ± 2 Ma were obtained by SHRIMP U-Th-Pb analysis of samples from the Tiaojishan (= Lanqi) Formation⁷. Zhang *et al.* (2008) concluded that the upper boundary of the Tiaojishan (= Lanqi) formation dates between 156 and 153 Ma⁵. Chang *et al.* obtained Ar-Ar ages of $160.7 \pm 0,4$ Ma and $158.7 \pm 0,6$ Ma for the basal Lanqi Formation in North Hebei Province⁶. These results indicate that the age of the Tiaojishan Formation is between the Callovian (Middle Jurassic) and the Kimmeridgian (Late Jurassic)⁸.

Selected measurements of YFGP-T5197

	Length (mm)	Width middle (mm)
skull	43,2	/
mandible	40,2	/
snout	21,4	/
cervical series	39,6	/
dorsal series	57,9	/
sacral series	25,1	/
caudal series	131,5	/
scapula	23,8	2,5
humerus	37,9	3,7
ulna	42	2
radius	39,5	1,9
manus	56,8	/
ilium	25	/
pubis	35	1,9

ischium	13,4	
femur	48,5	4,8
tibiotarsus	69,5	4,5
pes	65,1	/
forelimb	134,2	/
hindlimb	183,1	/

Measurements of caudal vertebrae:

Nº	Length (mm)	Width middle (mm)	Width caudal end (mm)
1	/	/	/
2	/	/	/
3	/	/	/
4	5,7	3	/
5	5,6	2,8	3,7
6	5,8	2,8	3,7
7	6,4	2,8	4,4
8	6,4	2,8	4,4
9	6,4	2,8	4,4
10	7,6	2,8	3,8
11	9,6	2,5	3,5
12	9,6	1,7	3,3
13	8,8	1,7	3,3
14	8	1,5	2,2
15	7,6	1,5	2,2
16	8	1,5	2,2
17	8	1,5	2,2
18	7,4	1,2	1,8
19	6,3	1,2	1,8
20	9,2	1,2	/

3. Phylogenetic nomenclature

We follow, in this paper, the following definition of higher-level theropod taxa^{4, 11}:

- Coelurosauria, the most inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Allosaurus fragilis* Marsh 1877, *Sinraptor dongi* Currie and Zhao 1993, and *Carcharodontosaurus saharicus* Depéret and Savornin 1927.
- Paraves, the most inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Oviraptor philoceratops* Osborn 1924.
- Avialae, the most-inclusive clade containing *Passer domesticus* Linnaeus 1758 but not *Dromaeosaurus albertensis* Matthew and Brown 1922 or *Troodon formosus* Leidy 1956.
- Deinonychosauria, the most-inclusive clade containing *Dromaeosaurus albertensis* Matthew and Brown 1922 but not *Passer domesticus* Linnaeus 1758.
- Archaeopterygidae, the most inclusive clade including *Archaeopteryx lithographica* Meyer 1861 but not *Dromaeosaurus albertensis* Matthew and Brown 1922 or *Passer domesticus* Linnaeus 1758.
- Scansoriopterygidae, the most inclusive clade including *Epidendrosaurus* Zang *et al.*, 2002 but not *Passer domesticus* Linnaeus 1758 or *Dromaeosaurus albertensis* Matthew and Brown 1922.

4. Phylogenetic analysis

In order to assess likely phylogenetic relationships, *Eosinopteryx brevipenna* was included in the dataset from a recently published analysis of coelurosaurian phylogeny⁴. The data matrix was re-analysed using the TNT software package⁹. The following heuristic search settings were used to generate most-parsimonious trees (MPTs): hold 30,000 trees, 1,000 Wagner builds, retain 10 trees per replication, with tree bisection and reconnection (TBR) as the search strategy. Heuristic searches recovered 70 Most Parsimonious Trees (MPTs) of length 1387 steps, with a Consistency index (CI) excluding uninformative characters = 0.32, and a Retention index (RI) = 0.72. Bremer indices were calculated by re-running the analysis and saving all sub-optimal trees not more than 10 steps longer than the MPTs. Bootstrap proportions were computed using WINCLADA version 1.00.08¹⁰ with 1,000 replications and the 'Max trees' option set to 1,000. The strict consensus tree and the nodal support (Bremer indices and Bootstrap proportions) are shown in Figure S1. For clarity, only paravian taxa are depicted in Figure S1.

The strict consensus tree shows that *Eosinopteryx brevipenna* is the sister taxon of *Anchiornis huxleyi* at the base of the clade Troodontidae. *Xiaotingia*, also from the Tiaojichan Formation of western Liaoning, *Archaeopteryx* and *Wellnhoferia* then form an unresolved polytomy at the base of the clade Deinonychosauria. Scansoriopterygidae, Avialae, and Deinonychosauria form an unresolved polytomy at

the base of Paraves. The results of this phylogenetic analysis therefore support the hypothesis that *Archaeopteryx*, *Wellnhoferia*, *Anchiornis*, and *Eosinopteryx* are all deinonychosauroids rather than primitive Avialae⁴. However, Bremer indices and Bootstrap proportions are relatively low, indicating that this hypothesis remains weakly supported.

In order to clarify the phylogenetic relationships between basal Paraves, a 90% majority-rule consensus tree of the 70 MPTs is presented in Figure 2. This tree suggests that Archaeopterygiidae is a clade composed of *Archaeopteryx*, *Wellnhoferia* and *Xiaotingia* and is the sister-taxon of a clade formed by Troodontidae + Dromaeosauridae. It also confirms the avian status of Scansoriopterygidae^{4, 11}.

Matrix:

This phylogenetic analysis is based on a matrix published in a recently published phylogeny of Coelurosauria⁴ (**doi:10.1038/nature10288**). Several character state have been modified in *Anchiornis huxleyi*, based on direct observations on the specimen LPM-B00169.

Anchiornis huxleyi

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001100?????????????11010??111?00?????0?1?000??1????1?1????????+000??01??1?????00020?+01?
?0?101??+00?0??010?01???01101210??011++011?31110000??1000000010?21?1001102200??11211
2???1?1?000??1?01?000121100010?1000?1??00?0???030010?1101000100100?01?0???0+0?01111
1101?00011020110101000101???0??11?102001011?1011000?20?110001000?12100?00000110101
?0??0000000000100000110
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Eosinopteryx brevipenna

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?011?????????????0?????????0?????????1?????????????????00???01?????????00020++?1??0?
?????????????????01??1?30?0?1?????0??01??1????????0000?000?1??0???022????1??2??0??????
?????????0???1???0?0???00?????0?????3001??11????0?????????0???0+0?0?????0?????1?02
0?0??0100????10100??1???02???01??1??0?????010?010?0?12100????00?1??1?????????00?????
??01??
```

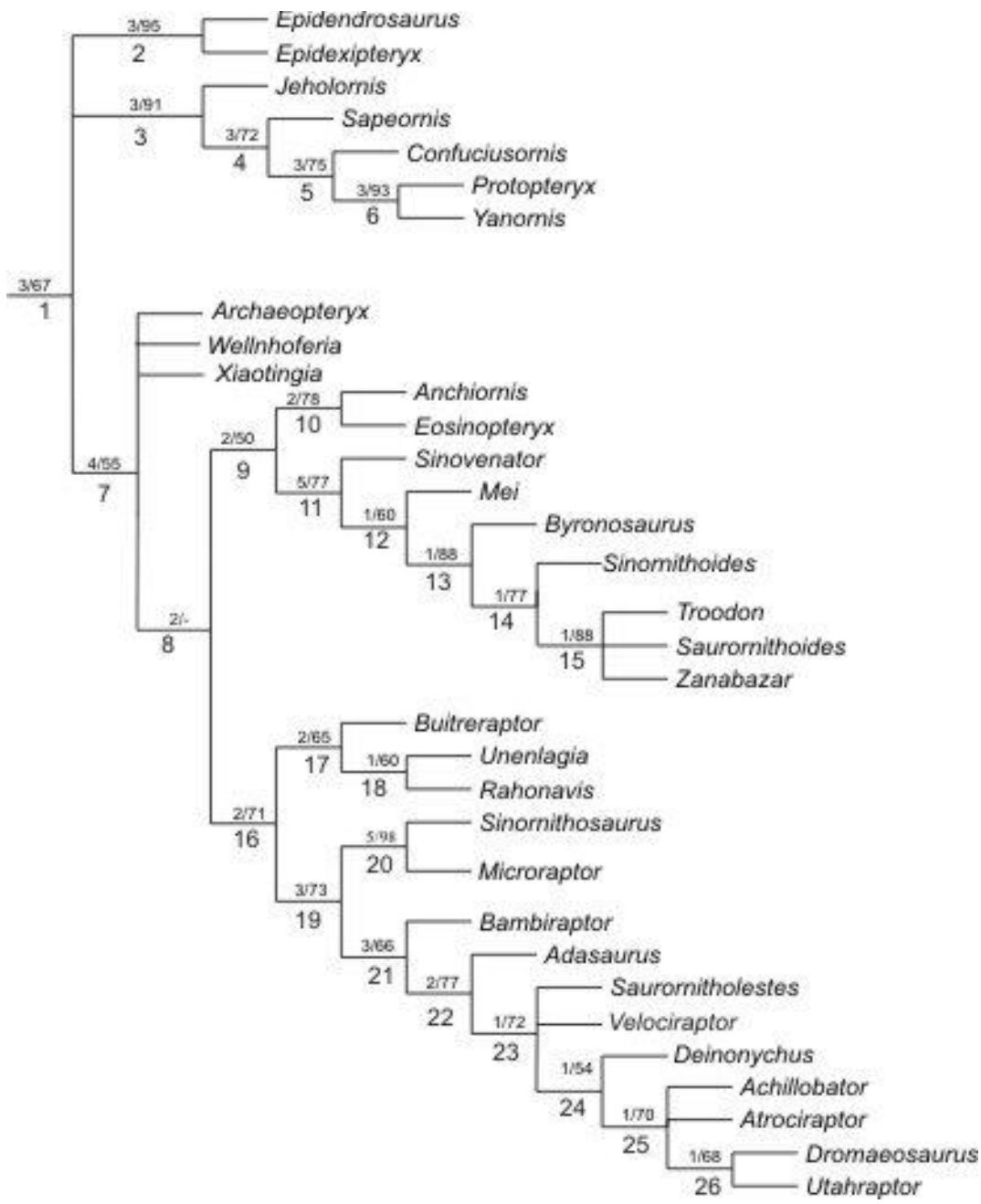


Figure S1. Position of *Eosinopteryx brevipinna* within Paraves, as a result of the inclusion of *Eosinopteryx* in a recently published analysis of coelurosaurian phylogeny⁴. Strict consensus tree of 70 MPT's. Tree Length = 1387; CI excluding uninformative characters = 0.32; RI = 0.72. Nodal support (Bremer indices/Bootstrap proportions) is indicated above each branch. The number below each branch refers to the different clades of the phylogeny.

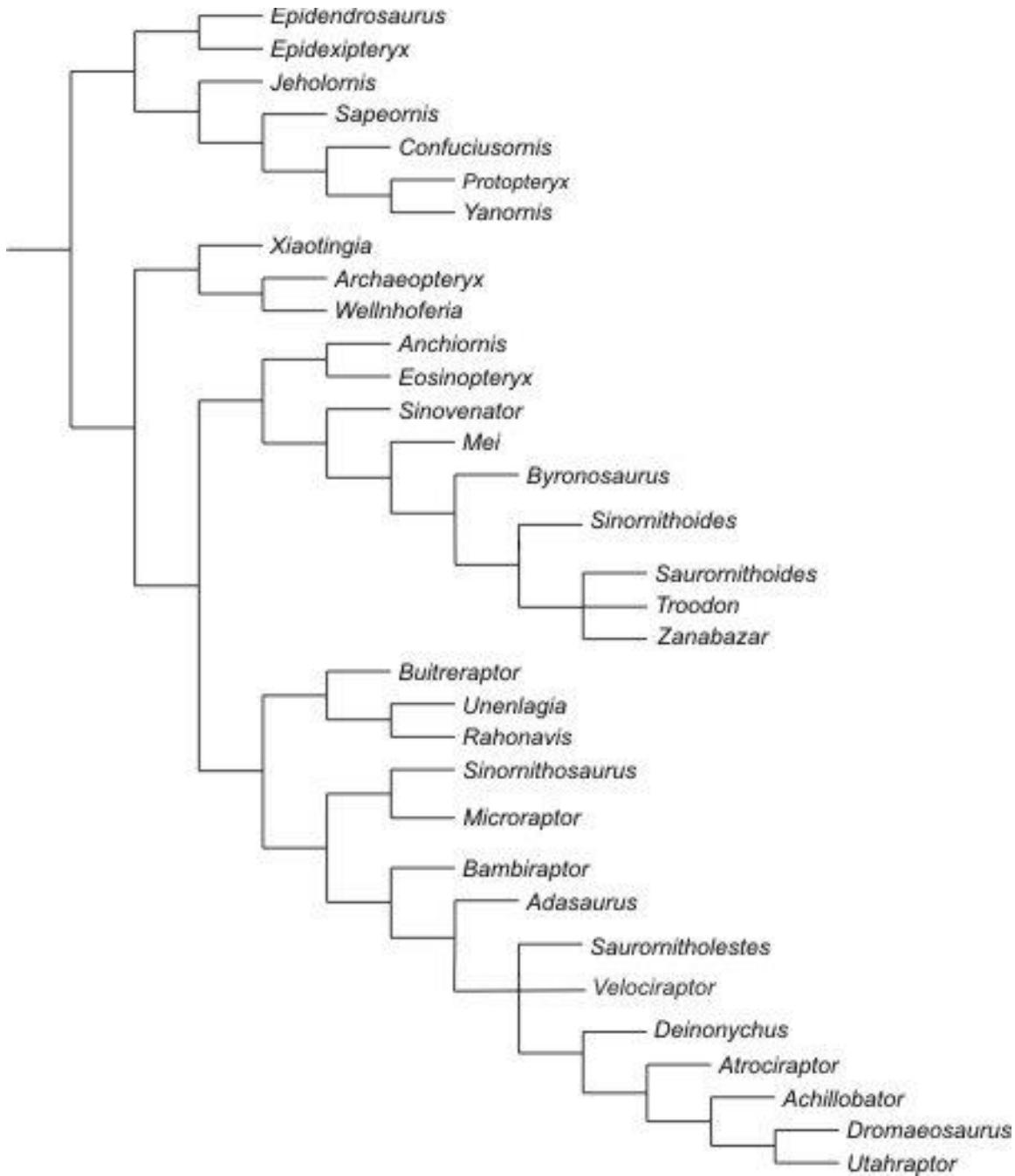


Figure 2. Position of *Eosinopteryx brevipinna* within Paraves, as a result of the inclusion of *Eosinopteryx* in a recently published analysis of coelurosaurian phylogeny⁴. 90% majority-rule tree of 70 MPT's. Tree Length = 1387; CI excluding uninformative characters = 0.32; RI = 0.72.

5. List of the unambiguous synapomorphies supporting the nodes shared by all MPTs

Character numeration refers to the Character list a recently published phylogeny of Coekurosauria⁴ ([doi:10.1038/nature10288](https://doi.org/10.1038/nature10288)). Nodes numerotation refers to Figure 1.

Node 1 (Paraves): 1 (0→1), 20 (0→1), 21 (0→1), 39 (1→0), 65 (1→0), 79 (1→0), 96 (0→1), 97 (0→1), 116 (1→2), 122 (0→1), 137 (0→1), 139 (0→1), 154 (1→0), 155 (0→1), 160 (0→1), 176 (0→1), 179 (0→1), 184 (0→1), 197 (0→1), 202 (0→1), 232 (1→0), 237 (0→1), 267 (0→1), 274 (1→2), 277 (1→2or3), 317 (0→1), 318 (0→1), 320 (0→2), 336 (0→1), 362 (0→1)

Node 2: 171 (1→3), 175 (1→0), 176 (1→2), 217 (0→1), 348 (0→1), 360 (0→1), 361 (0→1)

Node 3: 147 (0→1), 165 (0→1), 175 (1→2), 273 (0→1), 280 (0→1), 285 (0→1), 288 (1→0), 290 (0→1), 291 (0→1), 324 (0→1), 327 (0→1)

Node 4: 121 (1→2), 148 (0→2), 195 (0→1), 278 (0→1), 296 (0→1), 297 (0→1)

Node 5: 125 (0→1), 126 (0→1), 175 (2→3), 176 (1→2), 188 (0→1), 192 (0→1), 371 (1→0)

Node 6: 52 (0→1), 71 (0→1), 244 (0→1), 268 (0→1), 324 (1→0), 368 (1→0)

Node 7 (Deinonychosauria): 29 (0→1), 72 (0→1), 82 (2→0), 85 (2→0), 111 (0→1), 134 (0→1), 171 (1→2), 199 (0→1), 233 (0→1), 238 (1→0), 255 (1→0), 294 (0→1), 297 (0→1), 300 (0→1), 302 (0→2), 323 (0→1), 334 (0→1), 335 (1→2), 359 (1→0), 364 (1→0), 365 (1→0), 366 (0→1), 367 (1→0), 368 (1→0), 371 (1→0), 372 (0→1)

Node 8: 62 (1→0), 64 (1→0), 76 (0→1), 116 (2→1), 122 (1→0), 126 (0→1), 136 (3→1), 179 (1→0), 197 (1→0), 201 (0→1), 228 (1→0), 235 (1→0), 274 (2→1), 302 (2→1), 318 (1→0), 322 (0→1), 333 (0→1)

Node 9 (Troodontidae): 42 (1→0), 89 (0→1), 294 (1→0), 362 (1→0), 373 (0→1)

Node 10: 166 (0→2), 175 (1→2), 276 (1→0), 299 (0→1)

Node 11: 6 (0→1), 85 (0→1), 119 (1→2), 232 (0→1), 297 (1→0), 300 (1→0), 316 (0→1), 374 (0→1)

Node 12: 205 (0→1)

Node 13: 38 (0→2)

Node 14: 23 (1→0), 84 (2→1)

Node 15: 56 (0→1), 66 (0→1), 120 (2→0), 246 (1→0), 252 (1→0), 318 (0→1), 346 (1→0)

Node 16 (Dromaeosauridae): 21 (1→0), 43 (0→1), 88 (0→1), 103 (0→1), 198 (0→1), 296 (0→1),
330 (0→2), 342 (0→1)

Node 17: 165 (0→1), 322 (1→2), 332 (0→1)

Node 18: 106 (0→1)

Node 19: 53 (1→0), 71 (0→1), 72 (1→0), 84 (2→1), 96 (1→0), 107 (1→0), 120 (2→1), 160 (1→0),
175 (1→2), 253 (0→1)

Node 20: 136 (1→2), 176 (1→2), 278 (0→1), 285 (0→1), 288 (1→0), 290 (0→1), 295 (0→1), 308
(0→1)

Node 21: 99 (1→2), 106 (0→1), 171 (2→1), 233 (1→0), 334 (1→0), 335 (2→1), 346 (1→0), 362
(1→0)

Node 22: 200 (1→0), 243 (1→0), 321 (0→1)

Node 23: 256 (0→1)

Node 24: 78 (0→1), 264 (1→0), 333 (1→0)

Node 25: 84 (1→0), 167 (2→1), 254 (0→1), 266 (1→0), 309 (1→0), 330 (2→0)

Node 26: 258 (1→0)

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