Two feathered dinosaurs from northeastern China

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Current controversy over the origin and early evolution of birds centres on whether or not they are derived from coelurosaurian theropod dinosaurs. Here we describe two theropods from the Upper Jurassic/Lower Cretaceous Chaomidianzi Formation of Liaoning province, China. Although both theropods have feathers, it is likely that neither was able to fly. Phylogenetic analysis indicates that they are both more primitive than the earliest known avialan (bird), *Archaeopteryx*. These new fossils represent stages in the evolution of birds from feathered, ground-living, bipedal dinosaurs.

Dinosauria Owen 1842
Theropoda Marsh 1881
Maniraptora Gauthier 1986
Unnamed clade
Protarchaeopteryx robusta Ji & Ji 1997

Holotype. National Geological Museum of China, NGMC 2125 (Figs 1, 2 and 3).
Locality and horizon. Sihetun area near Beipiao City, Liaoning, China. Jiulongsong Member of Chaomidianzi Formation, Jehol Group[1]. This underlies the Yixian Formation, the age of which has been determined to be Late Jurassic to Early Cretaceous[3,4].
Diagnosis. Large straight premaxillary teeth, and short, bulbous maxillary and dentary teeth, all of which are primitively serrated. Rectrices form a fan at the end of the tail.
Description. The skull of *Protarchaeopteryx* is shorter than the femur (Table 1). There are four serrated premaxillary teeth (Fig. 1c), with crown heights of up to 12 mm. Premaxillary teeth of coelophysids[5], compsognathids[6,7] and early birds lack serrations, but premaxillary denticles are present in most other theropods. Six maxillary and seven dentary teeth are preserved (Fig. 1), all of which are less than a quarter the height of the premaxillary teeth. They most closely resemble those of *Archaeopteryx*[8] in shape (Figs 1b, c and 2b, c), but have anterior and posterior serrations (7–10 serrations per mm).

The amphicoelous posterior cervicals are the same length as the posterior dorsals, which have large pleurocoels. If the lengths of missing segments of the tail are accounted for, there were fewer than 28 caudals. Vertebrae increase in length from proximal to mid-caudals, as in most non-avian coelurosaurs.

There are two thin, flat, featureless sternal plates. The clavicles are fused into a broad, U-shaped furcula (interclavicular angle is about 60°) as in *Archaeopteryx*, *Confuciusornis* and many non-avian theropods. The forelimb is shorter than the hindlimb. The arm is shorter (compared to the femur) than it is in birds, but is longer than those of long-armed non-avian coelurosaurs such as dromaeosaurids and oviraptorids (Table 2). The better preserved right wrist of NGMC 2125 has a single semilunate carpal capping the first two metacarpals. The hand has the normal theropod phalangeal formula of 2-3-4-x-x. The manus is longer than either the humerus or radius. Compared to femur length, the hand is more elongate than those of any theropods other than *Archaeopteryx*[9] and *Confuciusornis* (Table 2). More advanced birds such as *Cathayornis* have shorter hands[10]. Phalanges III-1 and III-2 in the hand of *Protarchaeopteryx* are almost the same size, and are about half the length of III-3. The unguals are long and sharp, and keratinous sheaths are preserved on two of them.

The preacetabular blade of the ilium is about the same length as the postacetabular blade. The pubic boot expands posteriorly. Anteriorly, the pubis is not exposed.

The tibia is longer than the femur, as it is in most advanced theropods and early birds. It is not known if the fibula extended to the tarsus.

The metatarsals are separate from each other and the distal tarsals. Metatarsal I is centred halfway up the posteromedial edge of the second metatarsal. In perching birds such as *Sinornis*[9], metatarsal I is positioned near the end of metatarsal II and is retroverted. Its condition in *Archaeopteryx* is intermediate. Pedal unguals are smaller than manual unguals.

A clump of at least six plumulaceous feathers is preserved anterior

Table 1 Lengths of elements in *Protarchaeopteryx* and *Caudipteryx*

Element	NGMC 2125	NGMC 97-4-A	NGMC 97-9-A
Body length	690	890	725
Skull	70	76	79
Sternal plates	25	36	–
Humerus	88	69	70
Arm (humerus to end of phalange II-2)	297	214	220
Ilium	95	101	–
Ischium	–	77	–
Leg (femur to end of phalange III-4)	450	550	540
Femur	122	147	149
Tibia	160	188	182
Tibia	160	188	182
Metatarsal III	85	115	117

Length measurements are given in millimetres. NGMC 2125, *Protarchaeopteryx*; NGMC 97.4-A and NGMC 97-9-A, *Caudipteryx*.

Table 2 Relative proportions of elements in relevant avian and non-avian theropods

Element	Drom	Ov	Tro	Cx	Px	Ax	Con
Arm/F	1.8–2.6	1.5–1.8	1.8	1.5	2.4	3.7	3.9
S/H	0.8	1.0–1.2	–	1.1	–	0.6	0.8
R/H	0.7–0.8	0.8–0.9	0.6–0.7	0.9	0.8	0.9	0.8
Manus/H	0.9–1.2	1.2–1.4	1.3	1.2	1.6	1.2	1.3
Manus/F	1.0	0.7–1.0	0.8	0.6	1.2	1.5	1.6
McI/McII	0.4–0.5	0.4–0.6	0.3	0.4	0.4	0.3	0.4
T/F	1.1–1.4	1.2	1.1–1.2	1.2	1.3	1.4	1.1
Leg/F	3.6	3.3	3.8	3.7	3.7	3.8	3.3
Leg/arm	1.4	1.7	2.1	2.5	1.5	1.1	0.8

All data were collected from original specimens by P.J.C. Ax, *Archaeopteryx*; Con, *Confuciusornis*; Cx, *Caudipteryx*; Drom, dromaeosaurids; F, femur; H, humerus; L, length; Mc, metacarpal; Ov, oviraptorids; Px, *Protarchaeopteryx*; R, radius; S, scapula; T, tibia; Tro, troodontids.

to the chest, with some showing well-developed vanes (Fig. 3a). Evenly distributed plumulaceous feathers up to 27 mm long are associated with ten proximal caudal vertebrae. Twenty-millimetre plumulaceous feathers are preserved along the lateral side of the right femur and the proximal end of the left femur.

Parts of more than twelve rectrices are preserved[11] attached to the distal caudals. One of the symmetrical tail feathers (Fig. 3b) extends 132 mm from the closest tail vertebra, and has a long tapering rachis with a basal diameter of 1.5 mm. The well-formed pennaceous vanes of *Protarchaeopteryx* show that barbules were present. The vane is 5.3 mm wide on either side of the rachis. At midshaft, five barbs come off the rachis every 5 mm (compared with six in *Archaeopteryx*), and individual barbs are 15 mm long. As in modern rectrices, the barbs at the base of the feather are plumulaceous.

Maniraptora Gauthier 1986
Unnamed clade

Diagnosis. The derived presence of a short tail (less than 23 caudal vertebrae) and arms with remiges attached to the second digit.

Caudipteryx zoui gen. et sp. nov.

Etymology. '*Caudipteryx*' means 'tail feather', '*zoui*': refers to Zou Jiahua, vice-premier of China and an avid supporter of the scientific work in Liaoning.

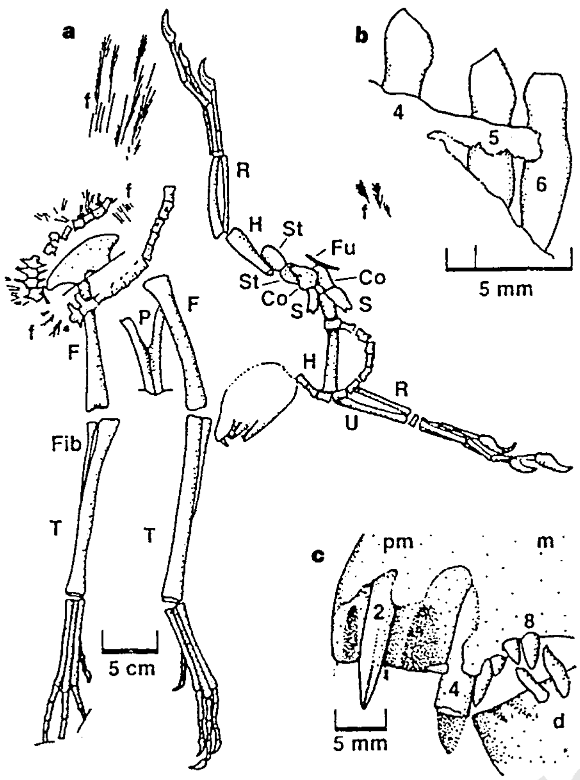
Holotype. NGMC 97-4-A (Figs 4 and 5b).

Paratype. NGMC 97-9-A (Fig. 5d).

Locality and horizon. Sihetun area, Liaoning. Jiulongsong Member of the Chaomidianzi Formation.

Diagnosis. Elongate, hooked premaxillary teeth with broad roots; maxilla and dentary edentulous. Tail short (one-quarter of the length of the body). Arm is long for a non-avian theropod; short manual claws. Leg-to-arm ratio, 2.5.

Description. The skulls of both specimens of *Caudipteryx* are shorter than the corresponding femora because of a reduction in the length of the antorbital region. The relatively large premaxilla (Figs 6 and 7) borders most of the large external naris. The maxilla and nasal are short, but the frontals and jugals are long. The lacrimal of NGMC 97-4-A is an inverted L-shaped, pneumatic bone. Scleral plates are preserved in the 20-mm-diameter orbits of both specimens. The tall quadratojugal seems to have contacted the squamosal and abutted the lateral surface of the quadrate. The single-headed quadrate is vertical in orientation. The ectopterygoid has a normal theropod hooklike jugal process. There is a broad, beak-like margin at the symphysis of the dentaries. Posteriorly, the dentary bifurcates around a large external mandibular fenestra as in oviraptorids. A



◀ **Figure 2** *Protarchaeopteryx robusta*. **a**, Outline of the specimen shown in Fig. 1a. **b**, Outline of the left dentary teeth shown in Fig. 1b. **c**, Drawing of the front of the jaws, showing the large size of the premaxillary teeth compared with maxillary and dentary ones. Abbreviations: Co, coracoid; d, dentary; F, femur; f, feathers; Fib, fibula; Fu, furcula; H, humerus; m, maxilla; P, pubis; pm, premaxilla; R, radius; S, scapula; St, sternal plate; T, tibia; U, ulna. Numbers represent tooth positions from front to back.

Figure 1 *Protarchaeopteryx robusta*. **a** (facing page), NGMC 2125, holotype. Scale bar, 5 cm. **b**, Fourth to sixth left dentary teeth. Scale bar, 1 mm. **c**, Premaxillary teeth showing small serrations. Scale bar, 5 mm.

well-developed, sliding intramandibular joint is present between dentary and surangular.

There are four teeth in each premaxilla. They have elongate, needlelike crowns, and the roots are five times wider than the crowns (Fig. 7b). The lingual wall of the root of the third right tooth has been resorbed for the crown of a replacement tooth. The teeth seem to have been procumbent, with an inflection at the gumline. *Caudipteryx* had no maxillary or dentary teeth.

There are ten amphicoelous cervical vertebrae and five sacrals as in most non-avian theropods and *Archaeopteryx*[8,12]. The tail of NGMC 97-4-A is articulated and well-preserved, and includes 22 vertebrae, as in *Archaeopteryx*. It is shorter than the 30-segment tails of oviraptorids. Most other non-avian theropods have much longer tails. Caudals do not become longer posteriorly, as they do in most non-avian theropods and *Archaeopteryx*. Almost two-thirds of the tail of NGMC 97-4-A is preserved as a straight rod, but the vertebrae are not fused. The first six haemal spines are elongate, rodlike structures. More posterior haemal spines decrease in height, but expand anteriorly and posteriorly (Fig. 5a).

Each segment of gastralia is formed by two pairs of slender, tapering rods, as in all non-avian theropods, *Protarchaeopteryx* and early birds[8,9,13,14].

The paired sternals are similar to those of dromaeosaurids and oviraptorids. *Confuciusornis* had a relatively larger, unkeeled sternum. Some short bones with slight expansions at each end are found near the sternal plates of NGMC 97-9-A, and may be sternal ribs.

The scapula is longer than the humerus, whereas the scapula-to-humerus ratio is less than 1.0 in flying birds (Table 2) because of humerus elongation. The clavicles are fused into a broad, U-shaped furcula in NGMC 97-9-A as in *Archaeopteryx*, *Confuciusornis* and many non-avian theropods.

Compared to the humerus, forearm length is similar to that in oviraptorosaurs (Table 2), *Archaeopteryx* and *Protarchaeopteryx*. In more advanced birds[15,16], the radius is longer than the humerus. The external surface of the ulna, as in *Archaeopteryx*[8], lacks any evidence of quill nodes.

There are three carpals preserved in NGMC 97-4-A, including a large semi-lunate one that caps metacarpals I and II as in dromaeosaurids, oviraptorids, troodontids, *Archaeopteryx*, *Confuciusornis* and other birds. Four carpals have been recognized in *Archaeopteryx*[12]. A large triangular radiale sits between the semilunate and the radius. A small carpal articulates with the third metacarpal. A thin wedge of bone at the end of the ulna is probably a fragment of gastralia.

The unfused metacarpals and digits of both specimens are well preserved. The third metacarpal is almost as long as the second, but is more slender. The hand has the normal theropod phalangeal

Figure 3 *Protarchaeopteryx robusta*, NGMC 2125. **a**, Contour and plumulaceous feathers. Scale bar, 10 mm. **b**, Rectrices. Scale bar, 5 mm.

formula of 2-3-4-x-x. The manus is longer than either the humerus or the radius, which is a primitive characteristic shared with most non-avian coelurosaurs, *Archaeopteryx*[9] and *Confuciusornis*. In contrast with *Archaeopteryx*, *Confuciusornis*, *Protarchaeopteryx* and many non-avian theropods (ornithomimids, troodontids, dromaeosaurids and oviraptorids), the manus is relatively short compared with the femur.

The curved second manual ungual is about two-thirds the size of the same element in *Protarchaeopteryx*, and is less than 70% the length of the penultimate phalanx.

Pelvic elements are unfused, as they are in all non-avian theropods (except some ceratosaurs) and the most primitive birds[16]. The acetabulum is large, comprising almost a quarter of the length of the ilium (the ratio of acetabulum-to-ilium length is less than 0.11 in birds[17]). It has a deeper, shorter, more squared-off preacetabular region than that of *Protarchaeopteryx*, and closely resembles the ilium of dromaeosaurids[18]. The tapering postacetabular region is lower and longer than the preacetabular. The pubic penduncle is anteroposteriorly elongated, and has a notch (Figs 4 and 5b) in the ventral margin that divides the suture into two surfaces. This notch and the deep pubic peduncle of the ischium are characteristic of opisthopubic pelves. The ischium has no dorsal process such as that found in *Archaeopteryx* and *Confuciusornis*, and the shaft curves down and back. A well-developed ventromedial flange is present, perhaps indicating contact between elements. In general appearance, the ischium most closely resembles those of non-avian coelurosaurs.

The ratio of hindlimb-to-forelimb length is higher than in other coelurosaurs (Table 2) except alvarezsaurids[19], which had exceptionally short arms. The greater trochanter is separated from the

Figure 6 *Caudipteryx zoui*, skull of NGMC 97-9-A in right lateral view. Scale bar, 1 cm.

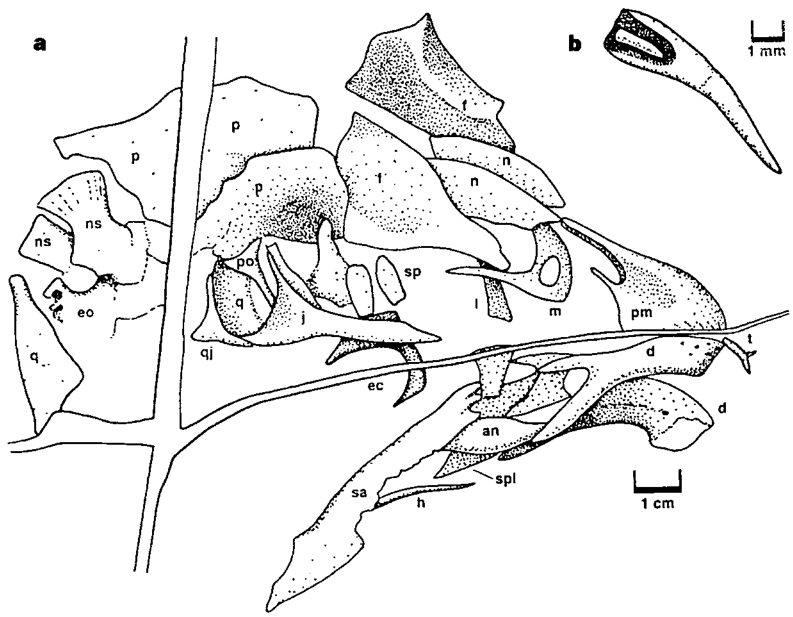


Figure 7 *Caudipteryx zou*. **a**, Sketch of skull shown in Fig. 6. **b**, Premaxillary tooth of NGMC 97-4-A, showing resorption pit and germ tooth. Abbreviations: an, angular; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; h, hyoid; j, jugal; l, lacrymal; m, maxilla; n, nasal; ns, neural spine; p, parietal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sp, scleral plate; spl, splenial; t, premaxillary teeth.

lesser trochanter of the femur by a shallow notch, and forms a raised, semi-lunate rim that is similar to the trochanter femoris of birds, troodontids and avimimids.

None of the fibulae is complete, but NGMC 97-9-A has a socket for the distal end of the fibula formed by the calcaneum, astragalus and tibia. The astragalus is not fused to the tibia. The ascending process of NGMC 97-9-A (Fig. 5e) extends 22% of the distance up the front surface of the tibia, compared with 12% in *Archaeopteryx*[12]. As in *Archaeopteryx*[8], *Confuciusornis*[10] and most non-avian theropods, the calcaneum is retained as a separate, disk-like element. Two distal tarsals are positioned over the third and fourth metatarsals, as in *Archaeopteryx*, *Buluochia*[20] and all non-avian theropods that lack fused tarsometatarsals.

The metatarsals of *Caudipteryx* are not fused; this is the plesiomorphic condition expressed in most non-avian theropods. Metatarsal I is centred about a quarter of the way up the posteromedial corner of the second metatarsal. The third is the longest of the metatarsals, and in anterior view completely separates the second and fourth metatarsals, unlike in the arctometatarsalian condition of many theropods[21]. Nevertheless, at midshaft the third metatarsal is thin anteroposteriorly and is triangular in cross-section. The pedal unguals are triangular in cross-section and are about the same size as the manual unguals.

At least fourteen remiges are attached to the second metacarpal, phalanx II-1, and the base of phalanx II-2 of NGMC 97-4-A (Fig. 8a). Each remex has a well-preserved rachis and vane. The most distal remex is less than 30 mm long. The second most distal remex is 63.5 mm long, is symmetrical, and has 6.5-mm-long barbs on either side of the rachis. The fourth most distal primary remex is 95 mm long and is longer than the humerus. Unfortunately, the distal ends of the remaining remiges are not preserved. In flying birds (even *Archaeopteryx*[12]), each remex is longer than they are in *Caudipteryx*, and the most distal remiges are the longest. For example, the remiges of *Archaeopteryx*[22] are more than double the length of the femur. The barbs on either side of the rachis are symmetrical, contrasting with *Archaeopteryx* and modern flying birds[23].

The holotype preserves ten complete and two partial rectrices. Eleven are attached to the left side of the tail, and were probably paired with another eleven feathers on the right side (only the terminal feather is preserved). Two rectrices are attached to each side of the last five or six caudal vertebrae, but not to more anterior ones. NGMC 97-9-A preserves most of nine retrices. In *Archaeopteryx*, rectrices are associated with all but the first five or six caudals[12,22]. Each rachis has a basal diameter of 0.74 mm and tapers distally. All the feathers appear to be symmetrical (Fig. 8b), although in most cases the tips of the barbs of adjacent feathers overlap. The vane of the sixth feather is 6 mm wide on either side of the rachis.

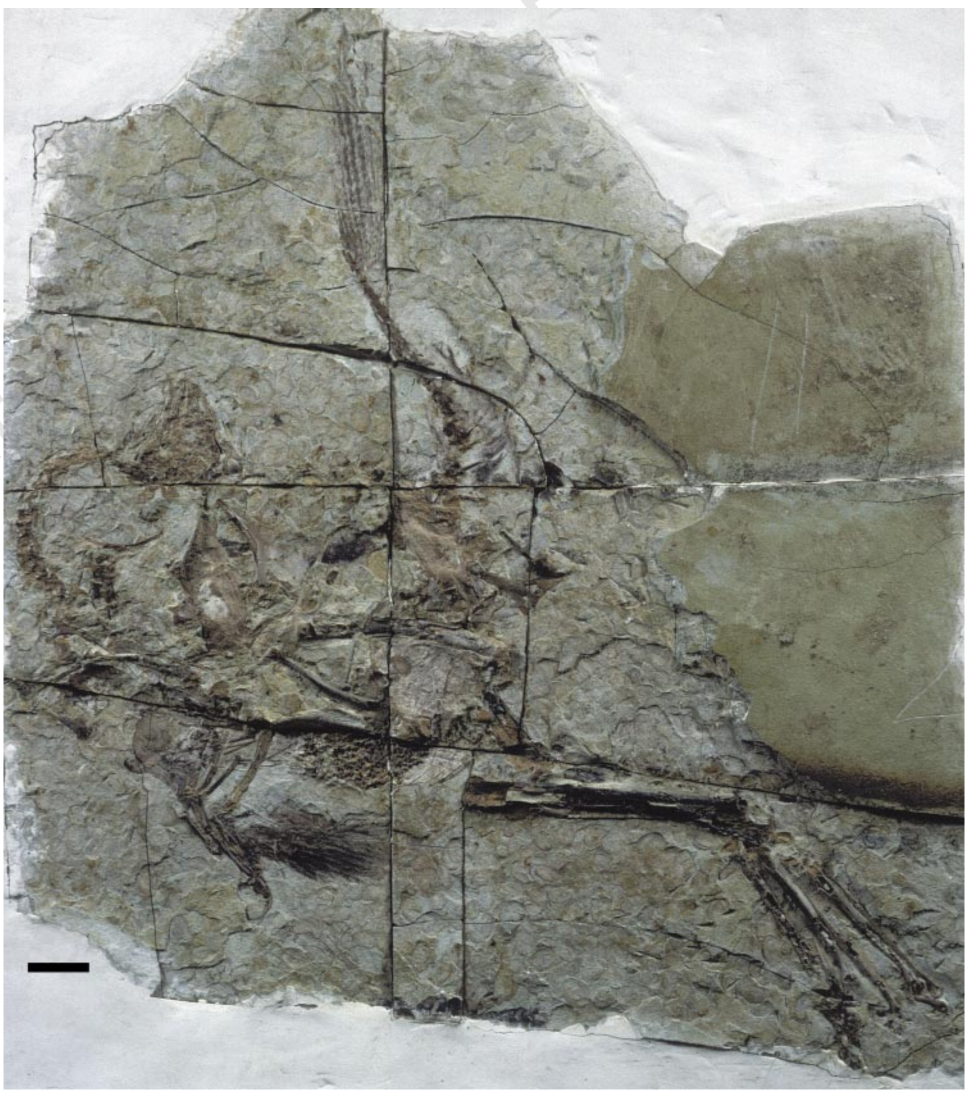


Figure 4 *Caudipteryx zoui*, holotype, NGMC 97-4-A. Scale bar, 5 cm.

The body of NGMC 97-4-A, especially the hips and the base of the tail, is covered by small, plumulaceous feathers of up to 14 mm long.

Both specimens have concentrations of small polished and rounded pebbles in the stomach region. These gastroliths are up to 4.5 mm in diameter, although most are considerably less than 4 mm wide.

Phylogenetic analysis

We examined the systematic positions of *Protarchaeopteryx* and *Caudipteryx* by coding these specimens for the 90 characters used in an analysis of avialan phylogeny[24] (for a matrix of these characters, see Supplementary Information). Characters were unordered, and a tree was produced using the branch-and-bound option of PAUP[25]. We rooted the tree with Velociraptorinae[26,27]. A single tree resulted with a length of 110 steps, a retention index of 0.849 and a consistency index of 0.855. Analysis shows *Caudipteryx* to be the sister group to the Avialae, and *Protarchaeopteryx* to be unresolved from the Velociraptorinae root (Fig. 9). The placement of *Protarchaeopteryx* as the sister group to *Caudipteryx* + Avialae, as the sister group to Velociraptorinae, or as the sister group to Velociraptorinae + (*Caudipteryx* + Avialae) are equally well supported by the data. Characters that define the *Caudipteryx* + Avialae clade in the shortest tree include unambiguous (uninfluenced by missing data or optimization) characters 2 and 12 and several more ambiguous ones (characters 4, 5, 10, 11, 15, 19, 24, 37, 85 and 86). *Caudipteryx* is separated from the Avialae by three unambiguous characters (7, 8 and 71) and additional ambiguous ones (characters 5, 6, 9, 10, 11, 18, 24, 39, 40, 56 and 69). The important characteristic of this phylogeny is that the Avialae (not including *Protarchaeopteryx* and *Caudipteryx*) is monophyletic; this placement is supported by the unequivocal presence of a quadratojugal that is joined to the quadrate by a ligament[17] (character 7), the absence of a quadratojugal squamosal contact (character 8) and a reduced or absent process of the ischium (character 71).

As characters dealing with feathers cannot be scored relative to outgroup conditions, they were not used in the phylogenetic analysis. However, our analysis indicates that feathers can no longer be used in the diagnosis of the Avialae.

Discussion

The three *Protarchaeopteryx* and *Caudipteryx* individuals were close to maturity at the time of death. The neural spines seem to be fused to cervical and dorsal centra in *Protarchaeopteryx*. Sternal plates ossify late in the ontogeny of non-avian theropods, and are present in both *Caudipteryx* and *Protarchaeopteryx*. Well-ossified sternal ribs, wrist bones and ankle bones in *Caudipteryx* also indicate the maturity of the specimens.

The remiges of *Caudipteryx* and the rectrices of both

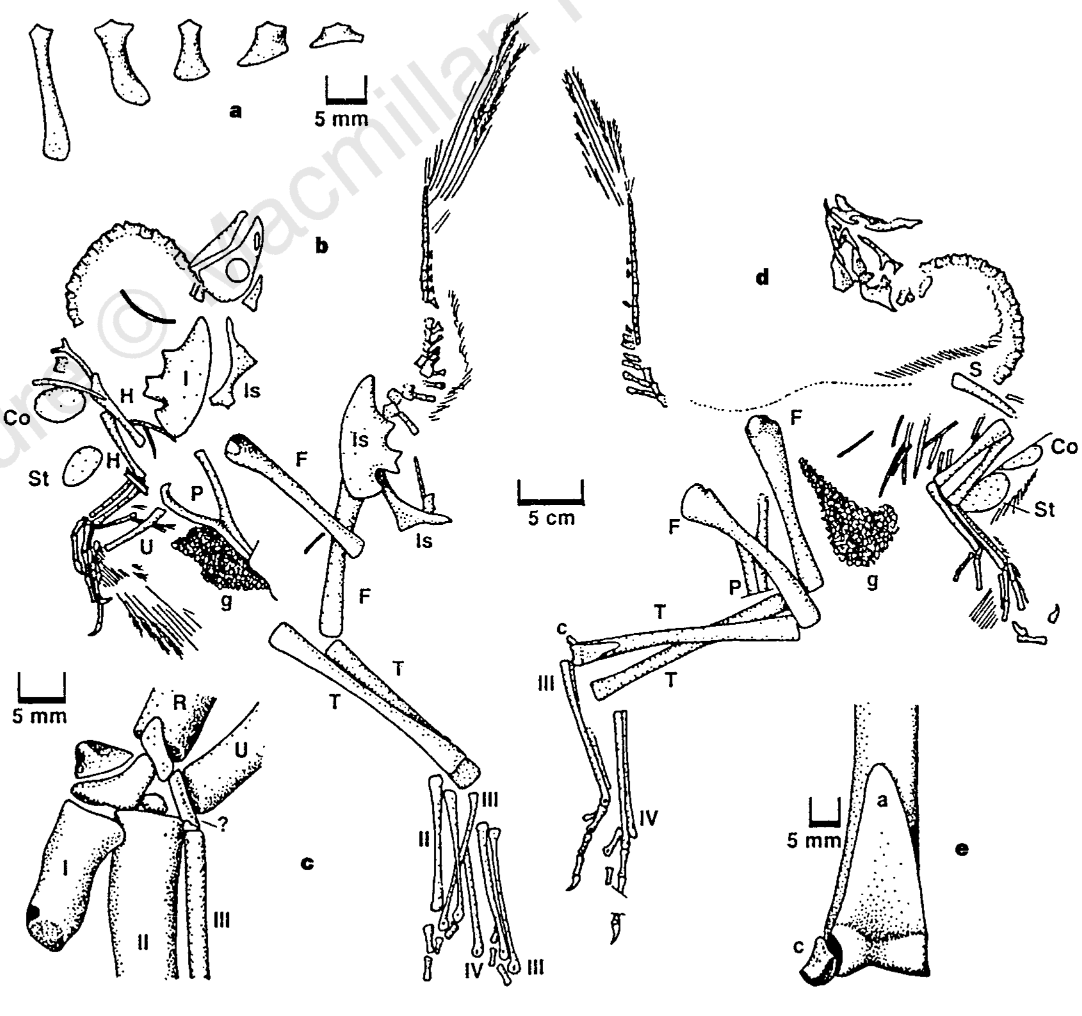


Figure 5 *Caudipteryx zoui*. **a**, Haemal spines from the fourth, sixth, eighth, eleventh and thirteenth caudal vertebrae (from left to right) of NGMC 97-4-A in left lateral view. **b**, Drawing of the specimen shown in Fig. 4a. **c**, Wrist of NGMC 97-4-A. **d**, Drawing of NGMC 97-9-A. **e**, Proximal tarsals of NGMC 97-9-A. Abbreviations: a, astragalus; c, calcaneum; Co, coracoid; F, femur; g, gastroliths; H, humerus; I, ilium; Is, ischium; P, pubis; R, radius; S, scapula; St, sternal plate; T, tibia; U, ulna;?, possibly fragment of gastralia. Roman numerals represent digit numbers.

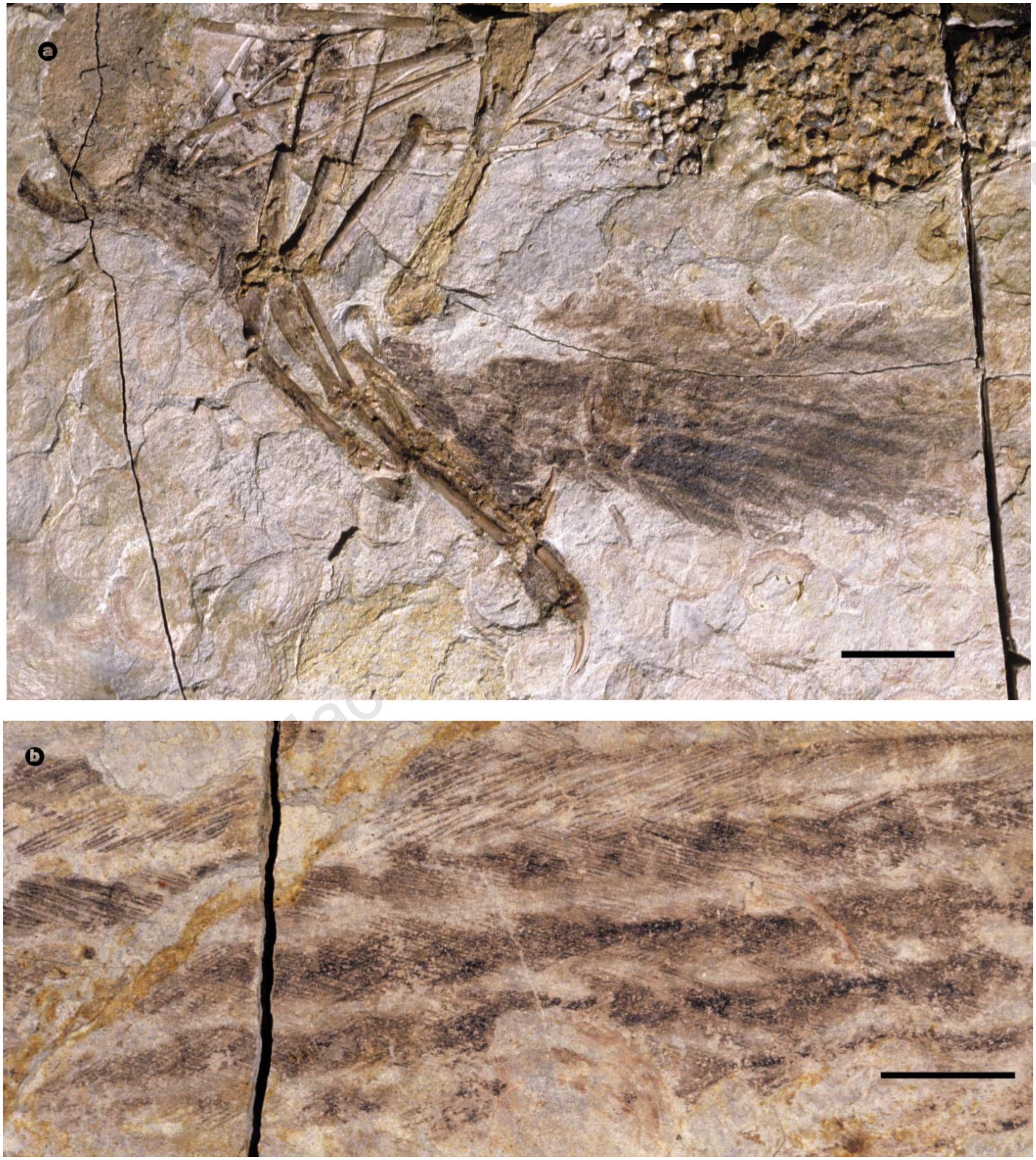


Figure 8 Feathers of *Caudipteryx zoui*, NGMC 97-4-A. **a**, Remiges of left arm. Scale bar, 1.75 cm. **b**, Rectrices, showing colour banding. Scale bar, 1 cm.

Protarchaeopteryx and *Caudipteryx* have symmetrical veins, whereas even those of *Archaeopteryx* are asymmetrical. Birds with asymmetrical feathers are generally considered to be capable of flight[23], but it is possible that an animal with symmetrical feathers could also fly. Relative arm length of *Protarchaeopteryx* is shorter than that of *Archaeopteryx*, but is longer than in non-avian coelurosaurs. The arms of *Caudipteryx*, in contrast, are shorter than those of most non-avian coelurosaurs; the remiges are only slightly longer than the humerus; and the distal remiges are shorter than more proximal ones. It seems unlikely that this animal was capable of active flight. The relatively long legs of *Protarchaeopteryx* and *Caudipteryx*, both of which have the hallux positioned high and orientated anteromedially, indicate that they were ground-dwelling runners.

Paired rectrices of *Protarchaeopteryx* and *Caudipteryx* are restricted to the end of the tail, whereas in *Archaeopteryx* they extend over more than two-thirds the length of the tail[12]. Wherever preservation made it possible, we found semi-plumes and down-like feathers around the periphery of the bodies, suggesting that

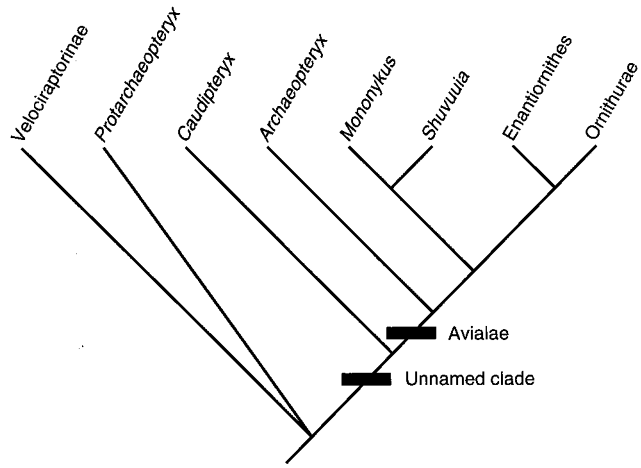


Figure 9 Cladogram of proposed relationships of *Protoarchaeopteryx* and *Caudipteryx*. This tree is based on 90 characters and has a length of 110 steps.

most of the bodies were feather-covered, possibly like *Archaeopteryx*[28]. Feathers found with *Otogornis*[29] were also apparently plumulaceous. Plumulaceous and downy feathers cover the bodies of *Protarchaeopteryx* and *Caudipteryx*, and possibly that of *Sinosauropteryx* as well[7]. This suggests that the original function of feathers was insulation.

Phylogenetic analysis shows that both *Caudipteryx* and *Protarchaeopteryx* lie outside Avialae and are non-avian coelurosaurs. This indicates that feathers are irrelevant in the diagnosis of birds. It can no longer be certain that isolated down and semi-plume feathers[30–33] discovered in Mesozoic rocks belonged to birds rather than to non-avian dinosaurs. Furthermore, the presence of feathers on flightless theropods suggests that the hypothesis that feathers and flight evolved together is incorrect. Finally, the presence of remiges, rectrices and plumulaceous feathers on non-avian theropods provides unambiguous evidence supporting the theory that birds are the direct descendants of theropod dinosaurs. □

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