

1. Provenance of STM 31-2.

STM 31-2 was collected by Mr. Jianrong Wang, a local farmer from Qinglong County, Hebei Province, China, and later purchased by the Shandong Tianyu Museum of Nature in 2007. According to Mr. Wang, the specimen was collected from a quarry near Mutoudeng Village in Qinglong County, where lacustrine beds of the Tiaojishan Formation are exposed. The formation is widely considered to be Callovian-Oxfordian in age, based on both radiometric dating and its known fossil content ¹.

The Mutoudeng Locality has previously produced several important vertebrate fossils including the salamander *Chunerpeton tianyiensis* ², the 'rhamphorhynchoid' (i.e. non-pterodactyloid) pterosaurs *Changchengopterus pani* ³, *Qinglongopterus guoi* ⁴, and *Dendrorhynchoides mutoudengensis* ⁵, and the haramiyidan mammal *Arboroharamiya jenkinsi* ⁶. Our research team has organized three expeditions to the Mutoudeng Locality (Extended Data Fig. 1) over the last few years. However, the nearby Gangou Locality offers more extensive outcrops of the Tiaojishan fossil-bearing beds, and has produced a nearly identical fossil assemblage. We carried out one excavation at Gangou (Extended Data Fig. 1), which resulted in the discoveries of several vertebrate fossils including a small theropod specimen (IVPP V20796) and a few salamander specimens.

STM 31-2 is preserved in a host matrix similar to that associated with other Mutoudeng and Gangou fossils. For example, most Mutoudeng and Gangou fossils including STM 31-2 and IVPP V20796, are preserved in dark grey shales that have a proportionally high content of fine sand, and are rich in dark plant fragments. Furthermore, STM 31-2 shares with many Mutoudeng and Gangou fossils, including IVPP V20796, an unusual taphonomic signature: the skeletons are articulated but highly compressed, preserving little morphological detail, and some parts of the skeleton are only represented by imprints.

Taken together, our data strongly support the claim that STM 31-2 was collected from the Middle-Upper Jurassic Tiaojishan Formation at the Mutoudeng Locality. Although it will be important in the future to collect more corroborating evidence, it should be noted that the geological age of the specimen is not critical to the focus of the present paper, and has no major effect on the conclusions drawn.

2. Authenticity of STM 31-2.

STM 31-2 is a fully articulated partial skeleton with associated soft tissue impressions, preserved in a slab and counter slab (Extended Data Fig. 2). The slab comprises one continuous block broken into six pieces. The counter slab comprises three isolated pieces, which mainly correspond to parts of the slab. One piece of the counter slab, however, preserves a small part of the specimen that is not present in the slab.

Both the slab and counter slab have undergone preparation by a professional technician (Ms. Xiaoqing Ding) under the supervision of the senior author. Ms. Ding exposed a substantial portion of the specimen, including both skeletal elements and soft tissues, and we can guarantee the authenticity of these newly prepared parts.

It should be noted that some of the skeletal elements and soft tissues are not fully prepared and exposed, for several reasons: 1. some skeletal elements underlie soft tissues, and cannot be exposed completely without damaging the specimen; 2. some regions preserve multiple layers of soft tissue (e.g., membranous tissue overlain by feathers), making it difficult to expose the soft tissue preserved on the lower layer; and 3. preserved soft tissue in Mesozoic fossils from northeast China can typically be exposed with relative ease when a specimen is fresh (within several weeks of collection), but only with difficulty once the matrix is dry. In fact, we have tried to expose more of the membranous soft tissue in the present specimen but have found it extremely difficult to do this in a satisfactory manner, even where membranous tissue is clearly present underneath the matrix.

Many ‘doctored’ specimens from western Liaoning and neighbouring areas are mounted on a supporting back-layer, often composed of pieces of shale combined with cement. No such back-layer is present in the case of the specimen described here, and little man-made cement is present between the six pieces forming the slab. These six pieces all fit perfectly with one another, and all of the skeletal and soft tissue structures that cross fracture lines on the slab do so smoothly and without introducing anatomical anomalies. The skeletal elements and soft tissues preserved on the three isolated pieces from the counter slab closely mirror the corresponding structures preserved on the slab (Extended Data Fig. 3), and this provides the strongest evidence in support of the authenticity of the specimen. Furthermore, we have detected no evidence of forgery despite examining the specimen carefully with both the naked eye and a high-magnification microscope.

In some previous studies⁷, high-resolution X-ray computed tomography (CT) has been used to test the authenticity of fossils or to determine the nature and extent of alterations that have been made to specimens that are known to have been tampered with. We used this technique to further confirm the authenticity of STM 31-2. The scanning was carried out using the 450 kV micro-computerized-tomography apparatus (developed by the Institute of High Energy Physics, Chinese Academy of Sciences (CAS)) at the Key Laboratory of Vertebrate Evolution and Human Origins, CAS. The specimen was scanned using a beam energy of 430 kV, a flux of 1.5 mA, a detector resolution of 160 μm per pixel, a 360° rotation with a step size of 0.25°, and an unfiltered aluminium reflection target. A total of 1,440 transmission images were reconstructed in a 2,048*2,048 matrix of 2,048 slices using two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS. The raw data are available from the Dryad Digital Repository.

As with our observations with the naked eye and microscope, CT analysis shows that the Yi slab is composed of six separate pieces, all containing bone and soft tissue (Extended Data Fig. 4; see also an animation showing the horizontal slices of the slab in a separate supplementary file, “Yi slab horizontal slice animation.avi”). All six pieces fit together naturally, with no sharp discontinuities in either the preserved fossil (both the skeletal elements and the soft tissues) or the matrix. The CT analysis reveals no anomalies, and thus confirms the authenticity of the specimen.

In summary, multiple lines of evidence are consistent in supporting the authenticity of

STM 31-2. We can therefore guarantee the validity of all morphological information extracted from the specimen.

3. Additional osteological features of STM 31-2.

Although the specimen preserves much of the skeleton, many morphological details are not preserved due to the extremely strong compression of the bones, and possibly due to unusual taphonomic influences which appear to have dissolved the majority of the bone material. The skull and mandible are the best preserved parts of the skeleton, showing a degree of three-dimensional preservation. The vertebral column is also slightly three-dimensional, but the remainder of the skeleton is nearly two-dimensionally preserved. However, the soft tissue is well preserved compared to the bones, a preservational pattern that is also seen in some avian specimens from the Lower Cretaceous Jehol Group. Nevertheless, enough morphological information is preserved to permit evaluation of the taxonomic validity and systematic position of the new species to which we assign the specimen.

Table S1. Selected measurements of *Yi qi* holotype (STM 31-2)

Measurement	Value
Skull (snout tip to quadrate ventral end)	44.5
Snout	18.1
Mandible	43.4
Cervicals 2-8	7.3/7.4/7.4/7.6/-/8.2/6.8
Scapula	50*
Scapula mid-shaft width	5.5
Humerus	94.8
Ulna	88.5*
MC II	9.1
MC III	20.1
MC IV	21.2*
Manual phalanx II-1	18.3
Manual phalanx II-2	15.4*
Manual phalanx III-1	14.5
Manual phalanx III-2	19.7
Manual phalanx III-3	15.0
Manual phalanx IV-1	35.2
Manual phalanx IV-2	33.8
Manual phalanx IV-3	23.4
Manual phalanx IV-4	11.6
Styliform element	133.5*(91.3 [#])
Femur	68.0*
Tibiotarsus	81.7
Metatarsal IV	48.9

Feathers over orbit	12.4
Feathers over neck	27.6
Feathers along humerus	35.5-59
Feathers along ulna	>30
Feathers along tibiotarsus	>58

All measurements are lengths in mm unless otherwise noted; * indicates estimated value; the preserved length of the right styliiform element is 91.3 mm, but taphonomic information and morphological comparisons between the right and left styliiform elements lead us to estimate that the total length of the styliiform element is 133.5 mm; femoral length is estimated based on the assumption that *Yi* has the same femur/tibiotarsus length ratio as *Epidexipteryx* (i.e. 0.83).

STM 31-2 is a small, long-armed theropod (see Table S1 for measurements of the major skeletal elements and soft tissue structures of STM 31-2). Additional significant cranial features, beyond those described in the main text, are preserved in STM 31-2. The premaxilla has a deep subnasal portion as in oviraptorosaurs⁸. The posterior portion of the frontal is convex in lateral view, and combines with the long and convex parietal to produce a large, dorsally expanded posterior skull roof. The jugal has a strap-like, dorsoventrally low suborbital ramus and a posterodorsally oriented postorbital process; the quadratojugal has a long jugal process, indicating the presence of a large infratemporal fenestra. The dorsal and ventral margins of the mandible are convex and concave in lateral view, respectively, and a relatively small external mandibular fenestra lies slightly posterior to the mid-length of the mandible⁹. All preserved teeth are slender in lateral view, as in some basal oviraptorosaurs such as *Incisivosaurus*¹⁰.

The vertebrae are in articulation, but only cervicals 1 to 9 are well exposed. The anterior and middle cervical vertebrae are relatively robust, their centra being less than 150% as long as high. In *Archaeopteryx* the cervical vertebrae are more elongate, but STM 31-2 resembles *Archaeopteryx* in that the centra are only slightly oblique in orientation. The neural spines of the exposed cervical vertebrae are relatively short anteroposteriorly (about as long as tall in lateral view). As in other maniraptorans, the prezygapophyseal facets are convex. The dorsal ribs are relatively well preserved, and some gastralia are also present.

The humerus is long and robust (slightly wider mediolaterally than the femur), as in other paravians, and the distal end of the humerus is only slightly expanded transversely. The ulna is relatively long, the ulna/humerus length ratio being 0.93. The equivalent ratio is 0.81 in *Epidendrosaurus*, and 0.84 in *Epidexipteryx*. The ulna has a moderately well developed olecranon process, a straight shaft, and a slightly expanded distal end. The radius is only slightly more slender than the ulna, as in other scansoriopterygids but in contrast to most small paravian theropods. The manual phalangeal formula is 2-3-4 as in most tetanurans. The manual unguals are moderately curved, and bear flexor tubercles of moderate size. The flexor tubercles of digits III and IV are slightly distally displaced. The ungual of digit II is the largest in the manus, and bears a dorsal lip at the proximal end, whereas that of digit IV is considerably smaller.

The tibia has a short cnemial crest, and the thin fibula extends to the ankle. The metatarsus is less than 75% as long as the femur, proportionally shorter than in many other theropods including derived ornithomimosaurs, alvarezsaurs, and troodontids.

Because of their unusual nature, the styliform elements of STM 31-2 warrant special consideration, and are described in some detail below.

4. Additional description of integumentary features and preserved melanosomes.

Soft tissues including feathers are well preserved around the whole skeleton. As in many other feathered dinosaur and early avian specimens, they are preserved in multiple layers. In general, soft tissues are preserved in situ, retaining their original anatomical positions relative to the skeleton, but some isolated feathers are also distributed across the slab and counter slab (Extended Data Fig. 5).

The material that we interpret as the membranous tissue of STM 31-2 occurs in several small patches of varying sizes associated with the hands and the right styliform element. In contrast to the preserved plumage of the specimen, which is made up of discrete filaments, the membranous tissue forms continuous sheets. Two patches of membrane, situated lateral to the distal phalanges of the right manual digits II and IV respectively, are particularly distinctive in that they bear regular, ripple-like striations that may represent either fibres within the membrane or pleats resulting from shrinkage or some other post-mortem effect. The coloured patch of membrane associated with digit II (Fig. 2g) runs along the entirety of the lateral edge of phalanx II-1, extending about 6 mm lateral to the phalanx before disappearing under the sediment. Proximally, the membranous tissue continues onto the dorsal edge of metacarpal II and grows broader. However, the proximal portion of the membranous patch is truncated by breakage dorsally and ventrally, and by phalanx IV-1 proximally. Nearly the entire patch bears the distinctive striations, but they are especially pronounced in the area lateral to the middle part of phalanx II-1. In this region they slant gently distodorsally, and are also concave upward. In the proximal part of the patch they are fainter, straighter, and more steeply inclined. Distally they seem to extend slightly beyond the limits of the coloured area, suggesting that a part of the membrane that was broken or worn away nevertheless left its impression in the sediment. This striated patch of membrane is strikingly different in appearance from the feathers preserved just medial to the right phalanx II-1 (Fig. 2g), implying that the striated patch indeed represents a type of soft tissue distinct from the plumage of STM 31-2.

The striated area of membrane associated with the distal part of the right digit IV (Extended Data Fig. 5g) is spread across two separate sedimentary layers. A subtriangular area lateral to the proximal half of the ungual and the distal half of phalanx IV-3, with a maximum height of about 10 mm, is situated at or just below the level of the bones and bears well developed linear striations that extend dorsodistally relative to the orientation of the digit. An adjacent rectangular area of membrane lateral to the proximal half of phalanx IV-3 is exposed on a deeper layer, and bears only faint, vertical striations.

Striations are absent or weakly developed on the other possible membranous areas of the specimen, which we acknowledge are difficult to distinguish with certainty from sheets of

densely packed, overlapping feathers. A large patch of membrane surrounds at least the distal end of the right styliiform element (Extended Data Fig. 5f, at right of image), and appears to extend beneath the overlying sediment defining the proximal boundary of the exposed membranous area. A few faint, thin dark streaks extend across this patch of membrane roughly parallel to the long axis of the styliiform element, perhaps representing either faint striations or feathers situated on the membrane. Another patch of membranous tissue (visible on both the main slab and a small area of the counterslab) extends along the lateral side of the right phalanx IV-1 (Extended Data Fig. 5f, near top of image), and both membranous tissue and feathers seem to be present in the area between this phalanx and the right styliiform element. The only membranous tissue that appears to be associated with the left hand is a faintly striated patch extending along the lateral margin of the left phalanx IV-3 (Fig. 1e, at upper left), and appearing to continue beneath overlying sediment both dorsally and proximally. In this case a few slender dark filaments that clearly represent feathers are preserved on the surface of the membrane, aligned obliquely to the proximodistally-oriented striations. A small dark area situated just medial to the same phalanx may represent an extension of this membranous region.

These patches of membranous tissue would be difficult to identify in isolation. Were styliiform elements not preserved in STM 31-2, we probably would not have guessed that the small areas of solid, sheet-like, sometimes rippled soft tissue visible on the specimen might represent patches of an aerodynamic membrane. However, this interpretation is highly consistent with the presence of the styliiform elements, for which plausible non-aerodynamic functions are hard to imagine (see below), and with the morphology of the membranous areas themselves. Unfortunately they are not extensive enough to reveal the shape of the aerodynamic membrane, but they do directly support the inference that this membrane was partly anchored by the styliiform elements and manual digits.

STM 31-2 displays an extensive plumage associated with the head, neck, trunk and limbs. Although all of the preserved feathers are filamentous, they were evidently stiff in the living animal because most of them are nearly straight on the slab. Large feathers are present along both the forelimb and the hindlimb, including the metatarsus. The humeral feathers are longer distally than proximally, and the longest exposed ones measure approximately 60 mm. The ulnar feathers are poorly preserved, and are thinner and shorter than the humeral feathers. The tibial feathers are even longer than the humeral feathers, and some large feathers are also preserved near the left metatarsus.

We used scanning electron microscopy (SEM) to investigate the possibility that preserved melanosomes might be present on the soft tissues of STM 31-2. We took small samples of preserved soft tissue from 12 locations on the specimen, including nine on the feathers and three on the sheet-like soft tissue (Extended Data Fig. 6). The uncoated samples were checked and imaged using a Leo1530VP scanning electron microscope with a Variable Pressure Secondary Electron (VPSE) Detector.

All samples from feathers show the presence of melanosomes (Extended Data Fig. 7), but only one sample from the sheet-like soft tissue (sample 11) preserves these structures. We measured short and long axis lengths for the preserved melanosomes based on the SEM images, and calculated the aspect ratio (long:short axis) of the melanosomes. It should be

pointed out that measurements based on two-dimensional images are likely to be erroneous for several reasons. The oblique imaging angle is likely to make the long axis of each melanosome appear shorter, and the short axis appear longer. Furthermore, the preserved melanosomes may have been compressed during fossilization, likely reducing the length difference between the short and long axes. Both factors tend to artificially reduce calculated aspect ratios based on measurements from two-dimensional melanosomes. To mitigate these source of error, we took measurements from those melanosomes that had either the shortest short axes, the longest long axes, or the greatest aspect ratios.

The feathers near the skull contain both phaeomelanosomes (Extended Data Fig. 7a), which are small (maximum diameter about 300 nm) and subspherical (aspect ratio slightly greater than 1.0), and eumelanosomes (Extended Data Fig. 7b, c), which are medium to relatively large in size (long axis 800–1400 nm) with aspect ratios of 1.9 to 3.6. The eumelanosomes preserved in the feathers near the neck (Extended Data Fig. 7d, e) are similar in size and morphology to those in the feathers near the skull; those in the humeral (Extended Data Fig. 7f, g) and ulnar feathers (Extended Data Fig. 7h–j) are medium in size (long axis 800–1200 nm) with aspect ratios of 2.7 to 2.9; and those in the tibial feathers (Extended Data Fig. 7k, l) are large (long axis 1200–2100 nm) compared to previously known melanosomes in both fossil and modern feathers and other integumentary structures^{11,12}, with aspect ratios of 1.5 to 2.2. The phaeomelanosomes preserved in the membranous tissue are small (long axis 300–400 nm), with aspect ratios of slightly greater than 1.0 (Extended Data Fig. 7m).

5. Styliform elements in *Yi* and other tetrapods.

In many volant tetrapods, a neomorphic or highly modified rod-like skeletal element extends from the vicinity of a limb joint and plays a role in supporting an aerodynamic membrane. Although these structures have some clear functional and structural commonalities across the multiple groups in which they have independently evolved, no widely accepted general term for them exists. The word “calcar” has been used in this sense¹³, but is more usually restricted to the specific element associated with the ankle in many bats¹⁴. We propose “styliform element” as a term encompassing all of these bony and cartilaginous structures, both in reference to their characteristic rod-like shape (“styliform” derives from *stilus*, the Latin word for pen) and because the “styliform cartilage” in petauristine flying squirrels is among the best-studied examples^{15–18}.

The structures that we regard as styliform elements in STM 31-2 are a pair of elongate, flattened rods that appear to emanate from the wrists. Their identification is the most obvious, and arguably the central, problem in interpreting the preserved morphology of the specimen. We initially assumed that they were soft tissue structures rather than bones, because of their anomalous position and lack of resemblance to any previously described theropod skeletal elements. However, we realized from the outset that the soft-tissue interpretation had problems of its own, given that the rod-like structures were also very unlike any known integumentary or other soft-tissue structure preserved in theropods (or

other vertebrates) from the lacustrine Mesozoic sediments of northeast China. Furthermore, they closely resembled the unambiguously identified bones of STM 31-2 in their general appearance. These considerations, combined with comparisons to the styliform elements of various other amniotes, eventually led us to accept the styliform elements of STM 31-2 as part of the skeleton. This interpretation was subsequently confirmed by analysis of a sample from the right styliform element using energy dispersive spectrometry (EDS), as explained below.

Like the other bones, the styliform elements are dark grey to black with some lighter patches, although the proximal part of the left styliform element is admittedly among the most lightly coloured portions of the skeleton. The styliform elements also resemble the other bones in having a granular texture, and under magnification it is clear that black particles are interspersed with others in varying shades of grey. The feathers and patches of apparent membranous tissue preserved on the slab are similar in colour to the styliform elements and other bones when viewed at low magnification, but do not show the same degree of fine-scale heterogeneity. For this reason, and because of the EDS results, we are certain that the styliform elements are bones rather than integumentary features or any other form of soft tissue. They seem likely to represent neomorphic ossifications, but we cannot rule out the possibility that they are highly modified carpals.

The left styliform element extends laterally, relative to the orientation of the left hand, from the vicinity of the wrist. The styliform element is overlapped by the distal end of the ulna, but the proximal end of the styliform element is visible medial to the ulna and distal to the radius. This proximalmost part of the styliform element is slightly narrower than the main part of the bone exposed lateral to the ulna. The proximal edge of the styliform element is straight, suggesting that the styliform element could only have been mobile relative to the other distal forelimb bones if it articulated with a convex surface.

Unfortunately, the left wrist joint as a whole is no longer in its natural configuration, and it is not certain how the styliform element articulated with the carpus. The ulna is displaced distally relative to the surrounding bones, protruding well beyond the radius and directly contacting metacarpals III and IV. At least one carpal, tentatively identified as the semilunate, is superimposed on the proximal end of the styliform element, and a second carpal that may be the radiale lies between the putative semilunate and the radius. However, the shapes of these carpals are difficult to confidently discern, and any ossified carpals on the ulnar side of the wrist are obscured by the ulna. As preserved, the left and right styliform elements both appear to be oriented in the ulnar direction, although this is less certain in the case of the right styliform element because the right wrist is missing from the specimen. The preserved alignment of the styliform elements suggests that they extend from the ulnar sides of the wrists, but this inference remains tentative given that the left wrist is so poorly articulated.

The left styliform element curves gently as it extends from the wrist and tapers slightly, its width decreasing from 4.3 mm near the base to 4.0 mm near its distalmost exposed portion. The distal end of the left styliform element is obscured by the left humerus and, beyond the humerus, by an area of matrix that we are reluctant to remove because it is covered in preserved feathers. The total exposed length of the left styliform element,

measuring from the proximal edge exposed on the medial side of the wrist, is 90.8.

The right styliiform element is darker in colour than the left, and its proximal end is broken away. The proximal portion of the preserved shaft is curved, albeit to an even lesser degree than in the left styliiform element, and is 4.1 mm wide at its base. More than two-thirds of the way along its total preserved length of 91.3 mm, the right styliiform element bends sharply through an angle of about 25° and narrows abruptly to a width of 3.1 mm, tapering further to a width of 2.6 mm near its slightly damaged distal end. The right styliiform element is approximately parallel to the distally incomplete right radius and ulna, but opposite in alignment, its distal end protruding well proximal to the elbow. Although the exact length of the right styliiform element is uncertain, its proximal end is directed towards the wrist, and presumably lay close to this joint before the relevant portion of the slab was damaged. If the proximal end of the styliiform element was at the same level as the distal ends of the radius and ulna, and if the ulna was equal in length to its counterpart in the left forearm (88.5 mm long; this is an estimated value based on combining information from the main slab and counterslab, but the error attached to the estimate is unlikely to be large), then the intact styliiform element was about 133.5 mm in length (as noted in Table S1, above).

Styliiform elements in other vertebrates are comparable to that of STM 31-2 to varying degrees. The styliiform cartilage extends from the ulnar side of the wrist in pterosaurines¹⁵, the extant group with a styliiform element that is morphologically and positionally most similar to its equivalent in STM 31-2. This cartilage can be large, reportedly ossifies in old captive individuals¹⁸, and supports part of the leading edge of a large, subrectangular gliding membrane called the plagiopatagium that also attaches to the rest of the forelimb and to the hindlimb. The styliiform cartilage is a mobile structure that can be folded against the forelimb when not in use, or moved to adjust the shape of the gliding membrane.

The pteroid of pterosaurs is an ossified element that forms a seemingly mobile articulation with a wrist bone called the medial carpal¹⁹. In contrast to the pterosaurine styliiform cartilage, however, the pteroid arises from the radial side of the wrist and supports a propatagium.

In extant scaly-tailed flying squirrels (Anomaluridae) and the gliding marsupial *Petauroides volans*, a rod-like cartilage extends from the olecranon process to contribute to support of a plagiopatagium²⁰. A similar structure appears to be present in the Oligocene eomyid rodent *Eomys quercyi*¹³.

In many fossil and extant bats a mobile, variably ossified styliiform element, called the calcar, extends from the calcaneum or the distal part of the gastrocnemius tendon¹⁴. The calcar reinforces and helps to control the trailing edge of the uropatagium, an aerodynamic membrane attached to the hindlimbs. In the hairy-legged vampire bat *Diphylla ecaudata* the small calcar extends beyond the narrow uropatagium and acts as a sixth pedal digit¹⁴, a modification comparable to that of the well known thumb-like radial sesamoid of the giant panda. In connection with this unusual case, it is worth noting that the styliiform element of STM 31-2 is much larger than the manual digits, and appears too

massive and inflexible to be used effectively as a makeshift finger.

6. Composition of styliform elements of STM 31-2.

We used energy dispersive spectrometry (EDS), a well-established technique for analysing the elemental composition of materials, on multiple samples from STM 31-2, primarily in order to test the hypothesis that the styliform elements are composed of bone rather than soft tissue. In EDS, a beam of X-rays or charged particles is used to cause a sample to fluoresce, and the resulting radiation is analysed in terms of the energy distribution of the photons produced. Peaks on a spectrum of photon energies correspond to particular elements present in the sample, as different elements characteristically emit photons of different energy levels.

Samples were taken from the middle of the right styliform element (which appears better-preserved than the left), the right manual phalanx II-1, the preserved feathers associated with the right tibia, and the sedimentary matrix surrounding the specimen. None of the samples was coated prior to analysis. The styliform element sample was analysed using a Zeiss EVO MA 25 scanning electron microscope (SEM) at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), with the following parameters: accelerating voltage 15 keV, working distance 9.0 mm and live time 50 seconds. The other samples were analysed using an SEM of the same model at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), with the following parameters: accelerating voltage 20 keV, working distance 8.4 mm and live time 30 seconds.

The spectra obtained for the manual phalanx (Extended Data Fig. 8a) and styliform element (Extended Data Fig. 8b) are closely similar, and differ from the spectra obtained for the tibial feathers (Extended Data Fig. 8c) and matrix (Extended Data Fig. 8d). In particular, the spectra for the manual phalanx and styliform element both have large peaks corresponding to calcium and phosphorus, key elemental constituents of the bone-forming mineral hydroxyapatite [$3(\text{Ca}_3\text{PO}_4)_2 \cdot \text{Ca}(\text{OH})_2$]. The spectrum for the tibial feathers has a modest calcium peak but no phosphorus peak, a result consistent with the presence of calcium in some previously investigated fossil feathers²¹, whereas the spectrum for the matrix has neither a calcium peak nor a phosphorus peak. These results provide strong confirmation that the styliform elements of STM 31-2 are composed of bone, or possibly of calcified cartilage (which is also mineralized with calcium phosphate). They are clearly hard components of the skeleton rather than soft tissue features.

7. Possible configurations for the aerodynamic apparatus of *Yi*.

Although nearly all skeletal elements of the forelimb and much of the associated soft tissue are preserved, confidently reconstructing the aerodynamic apparatus of *Yi* is difficult because the membranes are very incomplete and the articulation between the styliform element and the carpus is not well-preserved and well-exposed in either

forelimb. We present below three hypothetical configurations that we refer to as the Bat, Frog and Maniraptoran models, essentially labels of convenience that are not intended to imply more than a very general structural and functional similarity between the reconstructed aerodynamic apparatus of *Yi* and that of a bat, a rhacophorid “flying” frog or a more typical volant maniraptoran equipped with a feathered wing, respectively. Each configuration represents a different interpretation of the morphological and taphonomic data provided by the specimen, in the light of aerodynamic principles, the phylogenetic position of *Yi*, and information from other volant tetrapods (Extended Data Fig. 9). Which configuration should be regarded as most plausible depends on how these different considerations are weighted, a theoretical and even philosophical issue regarding which the authors of the present report have divergent opinions. Whereas the evidence preserved in the slab and counter-slab is sufficient to strongly support the presence of an aerodynamic membrane and provide some hints as to its size and shape, any reconstruction of the membrane at this stage is necessarily a result of educated guesswork, and the three configurations described and illustrated here do not exhaust the reasonable possibilities. They are presented in order to demonstrate that the idea of a volant *Yi* is far from implausible, and to emphasize that the aerodynamic apparatus can be reconstructed in many different ways given the currently available evidence.

The different possible reconstructions, including but not limited to the three configurations shown, differ mainly in two respects: whether a large membrane is present lateral to the trunk, and how the styliiform element is oriented. In reconstructions without a membrane lateral to the trunk, the wing is similar in outline to the feathered one of a typical maniraptoran if the styliiform element is medially oriented (Extended Data Fig. 9b), or to the enlarged manual webbing of an extant rhacophorid frog (Extended Data Fig. 9c) if the styliiform element is more laterally oriented. If a membrane is reconstructed lateral to the trunk, the wing is similar in outline to a bat wing if the styliiform element is approximately posteriorly oriented (Extended Data Fig. 9a), or to a pterosaur wing if the styliiform element is approximately laterally oriented (not shown in Extended Data Fig. 9).

In the Bat Model (Extended Data Fig. 9a), the styliiform element protrudes posteriorly from the wrist, and a membrane extends from the styliiform element to the side of the torso. This membrane forms a large aerodynamic surface, lateral to the trunk, which is supplemented by additional membranes between the fingers and between digit IV and the styliiform element. The Pterosaur Model (not shown) differs from the Bat Model in having a laterally oriented styliiform element (which is redundant functionally with the elongated manual digit IV), but otherwise is nearly identical to the Bat Model. A key weakness of the Bat and Pterosaur Models is that no membranous soft tissue is preserved lateral to the body and posterior to the humerus and ulna in the holotype of *Yi qi*, whereas relatively large feathers are clearly present in this region. The feathers may simply have been situated ventrally and/or dorsally on the membrane, for purposes of insulation and/or display, but their large size implies that they might then have increased the drag experienced by the animal to strongly disadvantageous levels. The major strength of the Bat and Pterosaur Models is that the reconstructed wing has a large membranous area and represents a general type of aerodynamic apparatus that is common among volant

tetrapods other than birds and their close relatives^{14–19,22}.

The Maniraptoran Model (Extended Data Fig. 9b) posits a wing that is similar in outline to those of other volant maniraptoran theropods, but with a membrane supported by the styliiform element and fingers partially replacing the large flight feathers present in other taxa. The fingers are directed roughly laterally and the styliiform element is directed medially and slightly posteriorly, allowing space between digit IV and the styliiform element for a large membrane that forms the major flight surface. This membrane is supplemented to some degree by webbing between the fingers, and by an additional aerodynamic surface formed by stiff feathers along the posterior margin of the humerus. This model incorporates the patches of sheet-like soft tissue preserved between the fingers and the styliiform element, the thick, stiff feathers preserved along the posterior margin of the humerus, and the proximal orientation of both styliiform elements as preserved in the holotype of *Yi qi*. Conversely, the Maniraptoran Model avoids postulating membranous tissue attached to the ulna and humerus, in line with the lack of evidence from the fossil to support this possibility. Taken as a whole, the composite wing has a high aspect ratio and is similar in total outline to the pennaceous wings known in other volant maniraptorans, making the model in a sense phylogenetically conservative. The proximal component of the aerodynamic surface is a questionable feature of this model, as it is not clear that the non-pennaceous feathers attached to the humerus could overlap effectively enough to act as a coherent sheet. In extant birds, however, the role of the humeral feathers in flight is comparatively minor, so the forelimb of *Yi* could presumably have functioned adequately as a wing even if the upper arm segment contributed little to its aerodynamic properties (particularly given that this feathered region is small compared to the membranous part of the wing). Furthermore, a postpatagial membrane exists as a fringe along the posterior edge of the entire forelimb in extant birds, and is widest posterior to the humerus²³. An equivalent structure might have been present in *Yi* based on phylogenetic bracketing, given that more basal theropods such as *Caudipteryx* have wings of nearly modern aspect (although a postpatagial membrane is not preserved in any known theropod including *Yi*). If broad enough, such a membrane could have acted as a coherent sheet to supplement the larger membranous surface that the Maniraptoran Model assumes to have been present between the styliiform element and digit IV.

The Frog Model (Extended Data Fig. 9c) is named for its partial resemblance to the forelimbs of rhacophorid “flying” frogs²⁴, which glide down from trees using the expanded interdigital webs on all four feet. In the Frog Model, membranes between the roughly laterally orientated fingers, and between digit IV and the posterolaterally oriented styliiform element, form the major aerodynamic surface. An accessory aerodynamic surface is formed by the feathers along the posterior margin of the forelimb, as in the Maniraptoran Model, but in the Frog Model this accessory feathered surface extends along the ulna as well as the humerus. The combined membranous and feathered wing has a relatively high aspect ratio, another point of resemblance to the Maniraptoran Model. The Frog Model is closely consistent with the soft tissue evidence from the holotype of *Yi qi*. The key disadvantage of the Frog Model is that the main, membranous aerodynamic surface is relatively small and distally placed, resulting in a high wing loading and perhaps poor stability unless the accessory surface formed by the feathers is treated as an

effective part of the wing. However, the aerodynamic efficacy of a surface formed by narrow, non-pennaceous feathers is questionable, as noted above.

8. Preliminary functional analysis of membranous wings of *Yi*.

Assessing the aerial capabilities of extinct animals, even well-studied taxa for which a wealth of fossil material is available, is challenging and fraught with potential controversy^{28–34}. *Archaeopteryx*, for example, has variously been regarded as limited to gliding²⁵, capable of slow flapping at best²⁶, or fully capable of powered flight²⁷. Similarly, the mode of aerial locomotion that might have been used by *Yi* is difficult to reconstruct given the limited evidence currently available. However, the general aerodynamic function of the membranous wings of *Yi*, as opposed to any specific style of flight, is strongly supported by multiple lines of data.

The skeletal proportions of *Yi*, including the relative length and thickness of the forelimb, indicate flight capability. The forelimb is approximately 1.2 times as long as the hindlimb, much longer in relative terms than in non-avian theropods and even some basal birds such as confuciusornithids. The humerus and ulna are as robust as the femur and tibia, in contrast to most theropods but as in flying birds and their close, apparently volant basal paravian relatives²⁸. Additional evidence comes from the styliiform element. All mammalian styliiform elements of which we are aware, and the pterosaurian pteroid, are involved in supporting and controlling an aerodynamic membrane (used for gliding in a variety of mammals, and as an accessory aerodynamic surface in the flapping flight of bats and presumably pterosaurs^{14–19}). These structures are not homologous or even closely analogous across the various taxa that possess them, but their widespread occurrence supports a general inference that rod-like skeletal elements attached to limb joints arise readily in volant taxa when they are needed to help support an aerodynamic membrane. Styliiform elements appear to be highly “evolvable” at least in mammals, and the pterosaurian pteroid provides an example of a comparable structure within Ornithodira.

Conversely, we are aware of no case in which a long, unjointed bony or cartilaginous rod extending from a limb joint has evolved in any vertebrate *without* being associated with an aerodynamic membrane, and plausible alternative functions for such a structure are difficult to conceive. The “thumb” of the giant panda *Ailuropoda melanoleuca*, for example, is a rod-like radial sesamoid used for manipulating bamboo stalks, but this structure is shorter than the manual metacarpals²⁹, whereas the styliiform element of *Yi* is longer than the ulna and could hardly have been used as an improvised sixth digit. Even if no membranous tissue were visible in the holotype of *Yi qi*, the styliiform element would represent a compelling indication that a membranous wing was present, because comparable structures in amniotes are invariably associated with aerodynamic membranes. The membranous tissue preserved in close association with the styliiform element, and elsewhere in the specimen, is best regarded as strong corroborating evidence. Although the membrane is highly incomplete, making its shape and extent impossible to determine, its existence and aerodynamic function can be confidently inferred from the

data at hand.

We estimated the aspect ratio and wing loading for two possible configurations of the flight apparatus of *Yi*, the Maniraptoran and Bat Models presented above, in order to assess their fundamental aerodynamic potential (Table S2). In both models, the wing loading of *Yi* (Table S2) is within the range that is typical among birds (about 0.1 to 2 g/cm²) and much lower than 2.5 g/cm², which represents the upper critical limit for bird flight³⁰. The Maniraptoran Model is comparable in wing loading to living ducks³¹, but has a much higher aspect ratio and considerably smaller wing span³¹; the Bat Model is comparable in wing loading to shore birds³¹, but has a considerably lower aspect ratio and smaller wing span³¹. For comparison, the Berlin *Archaeopteryx* has been estimated to have had a wing aspect ratio of 7.0 and a wing loading of 0.75 g/cm², based on a 388-cm² two-wing-area³² and a body mass of 290 g (from the same equation that was used to estimate the body weight of *Yi*). These values imply that *Archaeopteryx* was intermediate in wing loading between shore birds and ducks, but had a considerably higher aspect ratio and smaller wing span. Consequently, the Maniraptoran and Bat Models are comparable in some aerodynamic parameters to both living birds and the extinct *Archaeopteryx*, suggesting that the wings of *Yi* could have been aerodynamically functional.

Table S2. Dimensions and fundamental aerodynamic parameters for possible configurations of the flight apparatus of *Yi*.

	Maniraptoran model	Bat model
Two forewing area	320 cm ²	638 cm ²
Hind wing area	80 cm ²	80 cm ²
Forewing span	60 cm	60 cm
Membranous wing loading	1.19 g/ cm ²	0.60 g/ cm ²
Total wing loading	0.95 g/ cm ²	0.53 g/ cm ²
Forewing aspect ratio	9.8	4.0

* ‘Two forewing area’ includes the trunk area between the wings, in line with standard practice in measuring wing area; ‘Hind wing area’ includes only the area of the surface formed by the leg feathers.

Whether *Yi* moved through the air by flying, gliding or combining the two modes in some fashion remains an open question. The possibility of combining flapping with gliding is often ignored in discussions of aerial locomotion in extinct taxa, but is well represented in the modern fauna, as the flight of many birds and some bats includes intervals of gliding³³. In bats, this behavior often takes the form of an undulating gliding-fluttering mode of flight that combines a significant gliding component with a minor flapping component³⁴. A similar flight style has been inferred for some early bats, and may even be primitive for the group³⁵.

In the case of *Yi*, we believe that detailed modelling in an effort to reconstruct its mode of aerial locomotion would be premature given that the morphology of the aerodynamic apparatus remains so uncertain. However, a few lines of evidence tentatively suggest that gliding was at least an important component of this taxon’s locomotor behaviour. The

forelimbs of gliding mammals are characteristically elongated, increasing the potential width of the aerodynamic surface, but are delicately constructed because gliding does not involve the production of lift and thrust through muscular work^{22,23}. Similarly, soaring birds that rarely flap after they have launched themselves from the ground have relatively weak flight muscles³⁶. The gracility and weakly developed muscle attachment features of the forelimb in *Yi* suggest that the predominant mode of aerial locomotion was gliding as opposed to flapping flight. Furthermore, the mass of the styliform element may have increased the moment of inertia of the distal forelimb enough to make the rotational movements required by flapping flight difficult, especially if the angle between the styliform element and the long axis of the forearm bones was large. Consequently, *Yi* might have adopted a flight strategy that mainly involved gliding, with a secondary component of low frequency flapping. Among living birds, the parrot *Strigops habroptilus* (the kakapo) is a plausible locomotor analogue for *Yi*. *Strigops habroptilus* “is capable of significant descending glides, during which it may flap its wings occasionally, and (rarely) brief, weak, aerial ascents”³⁷.

This flight strategy would not have required *Yi* to maintain aerodynamic stability to the same degree as typical gliders, in which the centre of mass is close to the anteroposterior level of the centres of lift of the paired wings. However, it bears pointing out that the anteroposterior distance between the centres of lift and mass would probably not have been large even under the Maniraptoran Model. Although this model places the lift centres of the wings relatively far anteriorly, the proportions of *Yi* imply that the centre of mass was also anteriorly positioned as in other basal paravians³⁸, or perhaps even more so given that *Yi* possessed an unusually large forelimb by basal paravian standards. The tail may also have been short, as in *Epidexipteryx*, resulting in an even more anteriorly positioned centre of mass. Furthermore, the large leg feathers might have contributed to producing lift, perhaps in combination with feathers attached to the tail, shifting the overall lift centre posteriorly. It is possible that the relative placement of the centres of mass and lift might have compromised the aerodynamic stability of *Yi*, constraining its aerial capabilities, but a detailed analysis of this potential problem is premature given that the skeleton (particularly the tail) and flight surfaces remain incompletely known. Similarly, more anatomical information is needed to determine whether the wing of *Yi* might have been capable of producing a vortex wake, the hallmark of true flapping flight.

9. Phylogenetic analysis

We carried out a phylogenetic analysis based on a recently published dataset²⁸ with *Yi qi* added in (see below for complete scorings). The data matrix was analyzed using the TNT software package³⁹. The analysis was run using a traditional search strategy, with default settings apart from the following: 10000 maximum trees in memory and 1000 replications. The analysis resulted in 96 equally parsimonious trees, each having a length of 1416 steps. These trees each have a CI of 0.31 and an RI of 0.73. Extended Data Fig. 10 shows the strict consensus of the 96 trees.

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Protarchaeopteryx_robusta ?????????????????0?????????????????
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0????0???0???1????00?10100000002?1??????2200?1?1???00?1???0????????0?
???000?000???10?????0???00?1?101?0?0?????1?0?0????????????010?11?0000?001
111000?010??10?01000100000000001011?1?1?000000?00000?0000100?000000011
010?1??????1000??????10???

Elmisaurus_rarus ?????????????????????????????????
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????????????????????????0?01?1????????????????????????????????100010
??01???0??
??????000010000?0?00?????????01?0?0000000?11?????1?0?00?0?0?1???1????
???????????????????

Rinchenia_mongoliensis ?01?0????0?????????0111?1????1011?10011
??00???000?0?????00?1?221120?01100??111?1?3?????1?????????1???1???1???0???
???1?????????111?1?00000???1?0?00?10?1?0?0?????????????????????0???0???
?0??????0?10?001????00??0?????????10101???01?01110?010?10?????????????
?1????????????????????????0?????1?????????????????????0?????1???1????
1110011????110????10?0

Citipati_osmolskae ?011001001001??2210001111110001011?1001
1210001100000110011000110221120?0110010111?1?3?????1011001100101111001??
20???002100111?011111?010000100?11000001110021100?110220?0?1010010?11010
00000100?0000010000000100100110?000000000?0???01010110101001110101001???
???10????010?001011010010100100000000000100?????1?101?0000000001100100
0001?00000100?10?01?1110??1000-11011?010?0

Ingenia_yanshini ?01?0????????????????11111100010?1?1???11
2???0?1???0?0?0011?????1221120?01100?0111?1?3?????????0?1?1???1???2???01?
???2100???0011111011?000000?10000010100211??11?022000011010?110110100000?
1001000000000000?1100?0?11?000?0?0000?0?101010110?01?01110?010?10??????
???010?001011010010100100010000000110000001011?101?00?????001000100000000
00000101?1010110110011000-11011??10?0

Khaan_mckennai ?0110????????????00111?110?01011?100
1121000110?000?00110?????21120?01?00?0111?????????10110?1?1?1011110?????
1???00210?111001??110110000?00?1100000111002110?1110220001?101??1?110100?0
??10010000000000000100100110?000???000?0?1010101101010011101010?10?????
001110010?00101101001010010000000000110000001011?1011000000000100010000
000000000100?10101?0?10111000?110110010?0

Heyuannia_huangi ??11????????????????????????0???
?????????0????????????1120?011?0?1?????3?????1????????????0?2????????
??0?111?????11??10?00?10??1110?01010021???1?0220?011?1??1??1?010000?0?0??

??0000000?001??01??1????00??0??0??0??1????????????????????0?1?????00?110010?
00?01?01000010010001?0?00?01??00000011?1?1?0?0001000??010?0?00?0000001?
1??0?01?0????1?000????????1???

Byronosaurus_jaffei ?????101???101?1100110101011?00?????201
20????????????1?100?????0000001??11????00021??01?0?0?????010110????????0??
02??1????0?0?0?????
???1?????????0??0??0??100??0?[23]0?100?101100??0100??10?00110?????????????
??11????????????????????0??11????
?0?????????00?00?01?1

Sinornithoides_youngi ?0??0????????????1?000??1??0???0020?2
???????1?0????????????00?0010?????000110101?????11?1001?????????0011?
22102101?????01?11??0?00??10000000?????????0?200?????1?1???11110?????1???
?0001?11001?0??010????0000??00????30110011011??1?0100??1?000?1?0?011???0?0
0??011110100101001100000000000000??0??11?111100011111000010????210000000
001?010110??00?000?0?0?0?00?1?

IGM100/44:unnamedtroodontid ?????012????????????????????????????????
???????????1?0????????????????1??11???????1?0?????0????????????????????
????????????????????????10000000????????????????????????????????????01
?1?001???00?????0?0?1??????3????????????????????1??0????????????????????
1?0101001?000???00000????????????1??0?1111???0?????????0??0????0?0?????
???000????????????

Troodon_formosus ???1?1112?1101000001???0?010100?????2
0120000210?00?1?01100????0?10??001?????????011010100???11110010110111?10
00?1020??11????????????010????0????????1????????????????1?0?011?100?????
?0100001210?01????0?0???0?01000??0?30?????0?1???????10?000???1?10??111?
????????1?01?0????????????????????????11?10101110?????0?101?0?000??
0????10??0?0001???????0111

Saurornithoides_mongoliensis ?01??1?1??1101???0?110001?10?00???????1?
????????????????1?010?100?0010??1???0001101010???????1???0?0????100??1?
???0????????????????????????????????002000?0101?10??11110?????????0
0??211?01?????0??1?0????00?00?30?0001101100100000??1?0??1?010??1?0?0????
????????????????????????0011??1???1?01011110????100?0??0?0??0?01??
??000?0???0100000??0111

Zanabazar_junior ?01101?12?110100?001?000??10??000????20
12000?21?0?0???11100?????100?001???1????00011010100????????????1?1000
?1020??01?
????????????00?00??1100??0?30?1001101?001000001010000?110?0????0????
????????????????????????????????????1????????????1?????????0??01?1??
?0?0??????-00000?0111

Unenlagia ???
??1111?01????0?????
0?????????0?0?1?01?????????????01221110?111020102???1112011?01????0?????????
?1????0???????11???????????0?0??101?0?0?11?
???????????????????1?0???02???011???????????1?????1221?1?0?00???????????1????
????00?????????0???

Buitreraptor_gonzalezorum ?0110????????????????00001011?000?????????
?100?10?0011?0?????????00?001?????????021??100?0010111100111?010???10001
1012?021???????01101111010?1?100?0???????11?101??122??1?111?110???11?0?0?0?1?
011?011110000???????1?00?0????000??[23]?0???????1001001?0?01?0?????0?0?11
1?00?10011120????????????????????????????0?101?1????1?0???0?2?????12011021??000?
0??1??1?1?0??0?00001?0?0?0?0?0?

Rahonavis_ostromi ???
??01111?0?1?11?011012
?02?????????0????11?000?????????01121100111102?002?101??00111?10000?1?100
011010000???????1????0?????0?0??1111??3?0??
?130????????????????????????0211?011?101?01?10021?????11?1111100?01?????1?1
1?????0?00?????????0???

Bambiraptor_feinbergi ?0110?????0?0?1??1?0000?01110000??10?01
??10?1?????0?01?0?????????00??010??1?0000?0101-100?????0?120011??10??0??001
1??110?????001100101110?001?1010000010?21?001110020001?1021100?1?110000??
10010001111?0?000?00?0?1?0000???000?0000000?1013001??100101?10?011100011
011000?00111201011010011000001011001010201101101?100001001100?0012001011
00000100001011110???0000001001?0000100

Sinornithosaurus_millenii ?011?????0???????0?01???11100???10001?1
100?1???0?01???????????00?00100??1????010[12]010[01]00???????1??1???????0???
00?1??1???????011?01031110?00???0?0000010?211?0??10?2?0?211022?0????1????
??1?0100011110?0?000?1001??0000???0?00?[02]001001101300?0?100101?1?00110
?0?????00010011121?00101101001000111100001?211111??1?10000120110000012??1
12?000001000110101?0?????001100100000100

Microraptor_zhaoianus
1?1???????????????0?01?????1?????????????????????????????????????0?010?0?1???
?0?0[12]00000?????001?1??01?1000?01???0110?11?2111?01?100?131?10100?1101000
011012110?011002?0?211022100?11111?00?1001?1011110?00??010?11?000?????0?
?00?[23]0?100?1?????????00??1?1?0???0?0?11110001001112110?011010010001111
001000211110?1?100001201110000020?11210000010001?0101?0???00?001?0010000
0?0?

NGMC91:unnameddromaeosaurid ?011????????????????000????111?00?????0
01????0????????????????????0000100??1?0?0?010??[01]0??0????????????????????

701???1????1????10?031?10?00??1?100001????????????????????????????1???0??
 ?????????11????0???10????000????10????0010011013?01?1100??1?1?0?1?0?00????
 ?0?0?001112110?011010?1000110100100?????1??1?1?001201110000??????21?000
 0100011010??0????0001?00100000?0?

[illegible][illegible]

Velociraptor_mongoliensis ?01100100100001201120000101110000111000
12111?100010001000011101010000010011110000101010100001100012001111101111
1000110111021110011100111111010011100000010022110011100200011112110011110
00000010010101101001000000?00110000000000000000000010013000010000010100
1010000110100001001111010010100110000010110010202001011?0011000001110000
01200101100000100001010110000?00000100000?00100

Saurornitholestes_langstoni ?????????????????????01110????????????11
1????????????11????0????010????00???010101000?11000120011111011011100?101
1??11????????01?1??????10??000100221?0?11?????????????????????????????
???????0???00?0????00?000?0???0000?????013?????0???00??10?1?1000011????00100
?????1????????????????11001?0????????????????????1?00?1?0?010?0?0???0?0?0?01
?0???0???01???????????

Deinonychus_antirrhopus ?0110????1???????11?0000?0111100001110001
2??????0?1?????00?11010?000?0100111?1000?010101000?1100012001?111011????0
0110110?21?10???1?010111101001110000001002211001110020001110?010011111000
00010010001101000000?00?001100000?0?000?0000?00?0013000?000????000?1?110
001001?????0111101001010011000001011001020000101100011000101110000012?00
00100000100001010110000000000100000?00100

Achillobator_giganticus ??????????????????????01110?????????????
 ?????????????????????????????????000101?????0?01200?111100?????????011?
 ?1?????????0101????????????00?010220?0111100100?011010?00?11110?0???00?000
 ?101?????0???????1?????0???????0?000?????013?????????????????10?00000?00?0?
 ??1????????????0?????01?0????0000100100?1?????11?????1000000?0?????????0??1

????0?0?01?????????

Dromaeosaurus_albertensis ?0?001000000000010?0?0?0?0?01110??
?1111????10001?1001100??000001001111000?000101000?????????????????
??
????1?????00?????00?0?0000???0?00?000?00????0?00?0010010100000?????????
??0111????????????????0?01????
000???0???00000?0???

Utahraptor_ostrommaysi ?????????????????0?0????????00????
????????????????????????????????01???101??0???00??101111?0?????0?101
1????????????01????????????????2????11001?0?0?0????1???000???00?0??
????????????????0???????0???????0?0????????????????0????000?????????
????????????????????????001?00????????????10???0????????0????????
?0????????????????

Atrociraptor_marshalli ?????????????????1110????????????
????????????????????0?1???1???01000101?00????????????????????
??
????????????0?????0???0?00?00?00?3?????0????010?0110????????????
??
?1??????????

Archaeopteryx_lithographica
101?0010?000??112011010??11100?011?00012100010?0000?0??100111?1000000110
0002?0000020?00000?1?1??100?0??010?0???0021012111000????001031110000?110
00000101121?0001?102000221011101?111100000?10010010?1010?000000100110000
0?0?0000102001011101000100100101?0?00?0001?11110?3?0121130110?0100110001
010010010202010011?1011011120010000010000121000000000110101?000000000110
0100100100

Wellnhoferia_grandis ?0????????????110?0????????????
????????????????00?01????????00020?-0020????????????0????02?0?2
31?000????01031110?0???0?0000001?1????1?0?0?2?1?11?01?1?0100?0???010
01??1010?000?010???00?0???1000?0200101?1?????0?00???0???0?0?0?11?1?03
10?21130?10?0110110001010010010202???011?1?1101112001000001?001210000000
001?0101?????0?001100100?00??

Jeholornis_prima
10????????????1????0????????0????0????????????100?010?0020
0???022?00?0?0????????1???1???02???211?1???1?1?0003?110?00??110000000
1221?0???10?0?0???21?0????1?000??1?01011?0010?000?0010?0???1000???00?010
2?0?0?1????0?10?1???01?0110????01?1111?031012113011?011010?11001100000000
2???01?1?1?0111200?100101?0??11000000000110101?0??1?01001?1?011011???

Sapeornis_chaoyangensis ?011????????????11011????00001?00001
2??0011???00????????????000?000?00?00002?20?????0???????0?00?010?2???0??
????21?1001????100011110?00??1120000?011?1??01??100?0?1?1021101???010000??
0??1110000???000?0010?1???000???1010?02?0?0?1111?00100?0?01?0??0?????1?111
?003101211311?1011110?1110011100?1?02???011?1?110111????1??101?00?01?0000
00000110?0110??1?01001?110?10110?0

Confuciusornis_sanctus
10110????????????11010?0??00001???0??2??0?01??0?0???01???????000010000?10
?0001?1-3??????0???1??1????01110?2???0?????2??111?1101000131114000111110000
10112101????100?0012103210111??10??11?1121111010010?000000100110?000???001
??0??0011?????00100000?01?0?10?????1111?000101211211101010010010102011001
0002???011?1?1101112000101101??0001?000000000?10?01?0??10?1001?110110?0???

Protopteryx_fengningensis
10????????????110????????????0????????????01????????????000??1???????0
?0??2???0?0?????????0?????1??2?????????2??111?11?11?031?10000??1120000001?
????????????0?1?1?????????1???1?????????1110010?0?0?0101????00?????0???2?01
?111???00?10?00?01?0??????01?????1?3?012113111??011010?1100-0110001???????1
1?1?1?0111200?0??10?????1??00000000110?01?0?????001???0?0?00???

Yanornis_martini ?01????????????111?0?????0?????0???
?????????0?1?0???????????000?010?00???00021??0000????11?????????0?2???????
?????111?1???0?0031?10?00??1120?00????????????00???121?32?01???0100?1???11??
112?00010?000??010????00?????101?1?200001?1???00110?00??1?00?00?0001111??1?
??012113111??0110?0011?0-1111101?????01??1?1101??20000???0?????1??0000000
0110?0??0??10?001?11-00?-0???

Hagryphus_giganteus ?????????????????????????????????
??
????????????????????????10000001????????????????????????????????????
?????????0???0?
0111000000010001?00100? ??????????????????????0?11?????????????0?0?0?0?????
???????????????????

Microvenator_celer ?????????????????????????????????
????????????????????21?10?0?????????????????011?0?11000111100???0???1002
?????????????0000?01000?????0??1002???0111????0?????10110?0101100?0010010?
?????0?0?0?0??11?0?0????00?0?0?????????????????????00???????0?111?????01
1110?0?????????????0?0??0???011?????????????????0???00000?1???0????
????0?1???????11?01?0?

Avimimus_portentosus ?01?0???10001?00?0??1?1???????1???1??
???00?11?0?00100110?????2?1???00?0?0110????3?????011011110101?0?00??100?
?????????????????01?000100???110????00?211?01??022000???010100001100?0???1

0011110020???00?0???01?0?00000?00?0????0??????1????1011???0???001???
??????111??1?????0??????????????00?011?101?0???00000????1000002?0000?0??
???????10?01??000??????1???

Oviraptor_philoceratops ?0110?????????1??00????111?0?011???0112?
?0?1?0???0?100????1????1120?01100?01?1?1?3?????0??1???1?????1?0?????????
??????1????11?1?0?000001?110?0001???21?00?????????????????????????????
????????00100100????00?0000??????01?1?010??1??1?00?010?10????0?11?010?00
?11?01??101001000000000000100????????????????????1000????????00??100?10?
01?0?10??1?00-11011?010?0

Conchoraptor_gracilis ?0110?????????1???00111?1100?1011?100112
1000110?000?????1?0????221120?010?0?0111?1?3????????????????010??1?012?110??1
???0?0111???1?11?11000010??????011?00210001?102???0???01001??11010?0???0
??000000?0?0???00?0110?0?000000?0???0101011?101001110101?????????????
0?????1?1???010?0???0?00?0000111000?????1???110?????0?0001000000????0??
?0?10?0??011011?00?-11011??1000

Chirosstenotes_pergracilis ???????01?01101??0???1?11?0?????????????
?????????01110????0?????????????????1?????????????1101?11????1?12?????????
?????????001????????????000110021?0001?0220001110?00?0????0????10?100?00
100000????0???1???0?000????????????????????1????????1?1???????0????
???0?????000010?0?1001000?001?1??101?0000000?0001110000?1?000000?0?0???
?????01???????????????

Incisivosaurus_gauthieri ?0110???1??01????1000101010001001?0?011?
?00011000?0101011010111211100001001?1?02022?0002?????????????????????
??
????????????00?00?00?0?000?00020?00010110?010010010110010?001?????????
??0?11???
?0110??1???----11??10?0

IGM100/42:unnamedoviraptorid ?0110????????????001111110?01011?1001
12100?11??000??01100?111221120?01100??111?1?3?????10?0??1??1?1?1???1???0
1??00?10?1??01?1110110000?0???100000011002110?1110220??1?1010?1??1?01000?
??????0000?0000000100?001?0??00?0?00?0?1010101101001110101??10?????0
01010010?001011?100?010011?000000000010000001011?10110???00000110010?0001
0001000100?101011110111??????????1???

Anchiornis_huxleyi
0011?0????????????101???111?00????0?1?000??1????1?1????????-000?01??1??
???00022?-01??0?101??-00?0?010?01???01101210??011---011111110000??10000000
10?21?1001102200?2?112112???1?1?000??1?01?000110100010?0000?1?00?0???0???
?020110?1101000100100?01?0?0?0-0?01111101?000111201001010011010100011001
01020?0011?1011000?20?1100001000?021000?00000110101?0??000000110010000011

0

Xiaotingia_zhengi ?01????????????????1?1???1111000???0?1?
????????01?1?????-----?001001??1???00??022?-01??0?-0???1?0???000?01?????1??
---10?1---01?03101?10???10200001011?1110?12012?????103?12?????????10?????
?1?010001010000?0??0?10???0???102?110111?1??0110100?01?1100?-0?0?111?013?1
?111211001010111??0001011001020201????0??1?00100011100012?0?1??000?00000?
?0??1????00?000110?10010011?

Sinovenator_changii ?0???1002?000011120010101?11100???1???
1?000011???011?10100?????000?001?????00000111101?????1?11100011010000100
01102???1?????????010111?0?????????000?0?21?0111002000211011100?11110000?
??0010001011?000?????0?1?000011?0??0??301100?10?000??010?1?1100??0?000?11
11??00100?????????011?0???0000000???2011011?101?1???0011?0??1000112?00?
?000??1?0??110??0??000100100000111

Mei_long ?0????????????????1010?????00?01?000
012100001?10?010??100?????00010010??1?0000?021?01?0011011110010?1010?01?
??011022??11011????101?11?10?0?1?10000000?0?2111?1???020??21101110?0111100?
0101101?0001111011?0?0000???00000???0????3?110011???001?0100101?????????1
111??00010011110?0?0?0?0?0?????00000?????1??1?1?11100?0?11?000?10??1121?
000000?01?010110???000000???10000011?

Similicaudipteryx
00110?????????????00010??1000000??00011210001100??0?????????????21110000?1
0??1002022??00?20?????10010??1?0?0??01??00210?111010??000010001?001?1000
000010021?????02200?111?1?????1??0??00?????0??00001000?00000010???00?0???0
???021100010110001?01001?0?0?10??1?0001110010?001111010??010110??01000000
010100001011?1011000000000001010000010000000000110101?????0?1000-11011?01
000

Caudipteryx
00110?????????????0?110?010000011?00011210001?00?00?????????????21110?00??
??10021?3?????00?????0?100?????????0???01?????210?111000??000010001?00??100000
0010020???11?02200?111?10?10?11?01??0???01000001000000000010?110?000???0?
00?0??10001011000110100110?0010?????001110?10?0001110100?01011000010?0000
001?00001011?1011000000000??010000010000000000110101?0??0001000-11011?01
0?0

Haplocherius ?0110??000010?????0110100?11110101?000
0101100210000011?0000?010010001010011010000?0-11010?00?100??0-0111101??0?1
000000???0?0001???0?0102000??210?00100210?000???10?200100?111001100?00000?
00?0?00?000?000???001100100?100100001100?001001000000100100100001?0001??0
0000???1??2?1001010100010010100010000001001?0001011010110??000000000000?
00100000?0000111?10000000000000000000?00??0

Patagonykus_puertai ???
 ???111????????1?2?????
 ??????????0020?30210?110??110???????1?????0?????10?00?11?1?00???10011?0??
 0?????01?0?0??1??0?????010????????????????????????????????????1?1?????????0
 0?0??????0????00?1??????????11??1???0????????????????????1??????1?????????
 0???0?????????0?

Mononykus_olecranus ??????00??????112?????????????????????
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