

# An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China

Pei-ji Chen\*, Zhi-ming Dong† & Shuo-nan Zhen‡

\* Nanjing Institute of Geology and Palaeontology, Academia Sinica, 39 East Beijing Road, Nanjing 210008, People's Republic of China

† Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, PO Box 643, Beijing 100044, People's Republic of China

‡ Beijing Natural History Museum, 126 Tien Qiao Street, Beijing 100050, People's Republic of China

**Two spectacular fossilized dinosaur skeletons were recently discovered in Liaoning in northeastern China. Here we describe the two nearly complete skeletons of a small theropod that represent a species closely related to *Compsognathus*. *Sinosauropteryx* has the longest tail of any known theropod, and a three-fingered hand dominated by the first finger, which is longer and thicker than either of the bones of the forearm. Both specimens have interesting integumentary structures that could provide information about the origin of feathers. The larger individual also has stomach contents, and a pair of eggs in the abdomen.**

The Jehol biota<sup>1</sup> was widely distributed in eastern Asia during latest Jurassic and Early Cretaceous times. These freshwater and terrestrial fossils include macroplants, palynomorphs, charophytes, flagellates, conchostracans, ostracods, shrimps, insects, bivalves, gastropods, fish, turtles, lizards, pterosaurs, crocodiles, dinosaurs, birds and mammals. In recent years, the Jehol biota has become famous as an abundant source of remains of early birds<sup>2,3</sup>. Dinosaurs are less common in the lacustrine beds, but the specimens described here consist of two nearly complete skeletons of a small theropod discovered by farmers in Liaoning. The skeletons are from the basal part of the Yixian Formation, from the same horizon as the fossil birds *Confuciusornis* and *Liaoningornis*<sup>3</sup>. Both are remarkably well preserved, and include fossilized integument, organ pigmentation and abdominal contents. One of the two was split into part and counterpart, and the sections were deposited in two different institutions. One side (in the National Geological Museum of China, Beijing) became the holotype of *Sinosauropteryx prima*, a supposed bird<sup>4</sup>. The counterpart and the second larger specimen are in the collections of the Nanjing Institute of Geology and Palaeontology.

The Yixian Formation is mainly composed of andesites, andesite-

breccia, agglomerates and basalts, but has four fossil-bearing sedimentary intercalations that are rich in tuffaceous materials. The Jianshangou (formerly Jianshan<sup>5,6</sup>) intercalated bed (60 m thick) is the basal part of this volcanic sedimentary formation, and is made up of greyish-white, greyish-yellow and greyish-black sandstones, siltstones, mudstones and shales. These sediments are rich in fossils of mixed Jurassic-Cretaceous character. The primitive nature of the fossil birds of the Jianshangou fossil group has led to suggestions that the beds could be as early as Tithonian in age<sup>2</sup>. But although *Confuciusornis* and the other birds<sup>3</sup> are more advanced than *Archaeopteryx* in a number of significant features, we can only conclude that the beds that the fossils came from are probably younger than the Solnhofen Lithographic Limestones (Early Tithonian). The presence of *Psittacosaurus* in the same beds is more consistent with an Early Cretaceous age<sup>7</sup>, as are the palynomorphs<sup>8</sup> and a recent radiometric date of the formation<sup>9</sup>, but other radiometric dating attempts have indicated older ages<sup>10</sup>.

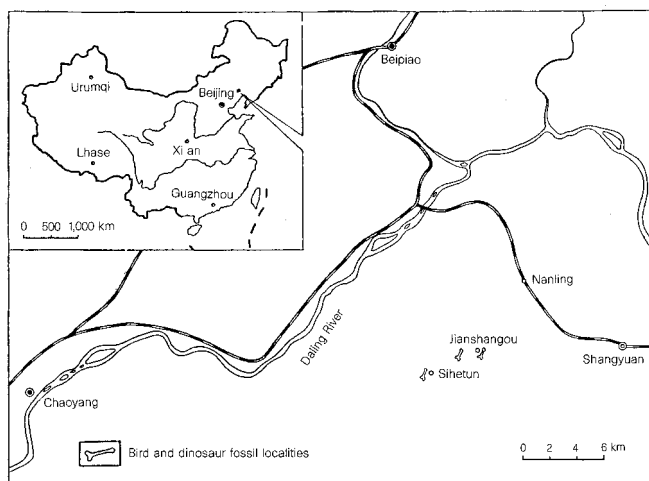
Dinosauria OWEN 1842  
 Theropoda MARSH 1881  
 Coelurosauria VON HUENE 1914  
 Compsognathidae MARSH 1882  
*Sinosauropteryx prima* JI and JI 1996

**Holotype.** Part (National Geological Museum of China, GMV 2123) and counterpart (Nanjing Institute of Geology and Palaeontology NIGP 127586) slabs of a complete skeleton.

**Referred specimen.** Nanjing Institute of Geology and Palaeontology NIGP 127587. Nearly complete skeleton, lacking only the distal half of the tail.

**Locality and horizon.** Jianshangou-Sihetun area of Beipiao, Liaoning, People's Republic of China. Yixian Formation, Jehol Group, Upper Jurassic or Lower Cretaceous (Fig. 1).

**Diagnosis.** Compsognathid with longest tail known for any theropod (64 caudals). Skull 15% longer than femur, and forelimb (humerus plus radius) only 30% length of leg (femur plus tibia), in contrast with *Compsognathus* where skull is same length as femur, and forelimb length is 40% leg length. Within the Compsognathidae, forelimb length (compared to femur length) is shorter in *Sinosauropteryx* (61–65%) than it is in *Compsognathus* (90–99%). In contrast with all other theropods, ungual phalanx II–2 is longer than the radius. Haemal spines simple and spatulate, whereas those of *Compsognathus* taper distally.



**Figure 1** Map showing the localities of *Sinosauropteryx* and *Confuciusornis* in western Liaoning, northeastern China.

**Description**

*Sinosauropteryx* is comparable in size and morphology to known specimens of *Compsognathus*<sup>11,12</sup> from Germany and France. The smaller Chinese specimen (Fig. 2) is 0.68 m long (snout to end of tail) and has a femur length of 53.2 mm, whereas the second specimen (Fig. 3) has a femur length of 86.4 mm. The former is smaller than the type specimen of *Compsognathus longipes* (femur length about 67 mm) and the latter is smaller than the second specimen of *Compsognathus* from Canjuers (France), which has a femur length of 110 mm and an estimated length of 1.25 m. Although size and body proportions indicate that the smaller specimen was younger when it died, well-ossified limb joints and tarsals suggest that it was approaching maturity.

*Sinosauropteryx* and *Compsognathus* share several characteristics that indicate close relationship. These can be used to diagnose the Compsognathidae and include unserrated premaxillary but serrated maxillary teeth, a powerful manual phalanx I–1 (shaft diameter is

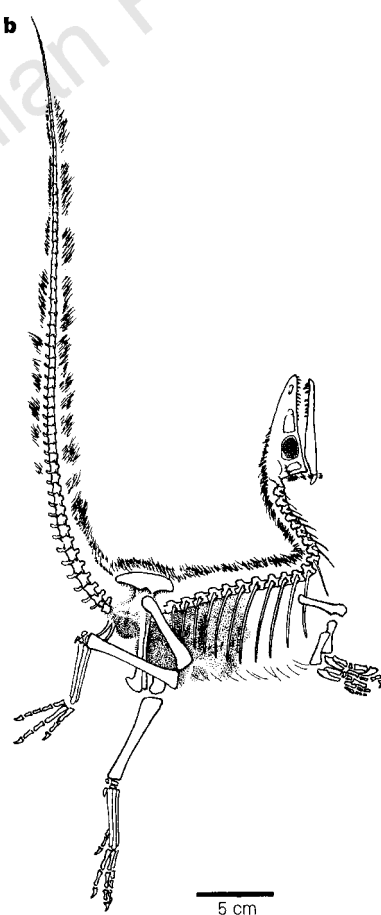
greater than that of the radius), fan-shaped neural spines on the dorsal vertebrae, limited anterior expansion of the pubic boot and a prominent obturator process of the ischium.

Other characteristics were used to diagnose *Compsognathus*, including the presence of a relatively large skull and short forelimbs. In *Compsognathus*, skull length is 30% of that of the presacral vertebral column, whereas this same ratio is 40% in the new specimen NIGP 127586 and 36% in NIGP 127587. Unfortunately, relative skull length is highly variable in theropods. Comparing skull length with femur length, which is less variable than vertebral length, most theropods have skulls 100–119% the length of the femur<sup>13</sup>. The *Compsognathus* skulls are 99–100% and *Sinosauropteryx* skulls are 113–117%. Compsognathids have short forelimbs<sup>11</sup>, 40% of the length of the hindlimb in *Compsognathus*. In *Sinosauropteryx*, the lengths of humerus plus radius divided by the sum of femur and tibia lengths produces a figure of less than 30% (Table 1). Unfortunately, such ratios are dependent on the absolute

**Table 1 Comparison of size and proportions of *Sinosauropteryx* and *Compsognathus***

Species	Specimen	Skull	Humerus	Radius	Femur	Tibia	Skull/femur	Arm/leg
<i>Compsognathus</i> sp.	BSPASI	70	39	24.7	71	87.6	0.99	0.40
<i>Compsognathus</i> sp.	MNHN	110	67	42	110		1.00	
<i>Sinosauropteryx primus</i>	NIGP127586	62.5	20.3	12.4	53.2	61	1.17	0.29
<i>Sinosauropteryx primus</i>	NIGP127587	97.2	35.5	21	86.4	97	1.13	0.31

Length measurements are given in millimetres. Data about *Compsognathus* are from ref. 11.



**Figure 2** *Sinosauropteryx prima* Ji and Ji. **a**, NIGP 127586, the counterpart of holotype (GMV 2123). **b**, Skeletal reconstruction of NIGP 127586. The integumentary structures are along the dorsal side and tail and dark pigmentation in the abdominal region might be some soft tissues of viscera.

size of the animal, mostly because of negative allometry experienced by the tibia during growth or interspecific size increase. Comparing the lengths of humerus plus radius with femur length produces more useful results. The resulting figures fall within the range of most theropods (60–110%). The abelisaurid *Carnosaurus* and all tyrannosaurs have relatively shorter arms. Within the Compsognathidae, however, arm length is shorter in *Sinosauropteryx* (61–65%) than it is in *Compsognathus* (90–99%).

Both specimens of *Sinosauropteryx* have 10 cervical and 13 dorsal vertebrae. The posterior cervical vertebrae have biconcave centra. We could not determine the number of sacrals. The tail is extremely long. In the smaller specimen it is almost double the snout–vent length, and there are 59 caudal vertebrae exposed with an estimated five more than have been lost from the middle of the tail of NIGP 127586 (but present in GMV 2123). Only the first 23 vertebrae are preserved in the larger specimen, but this section is longer than the summed lengths of the cervical, dorsal and sacral vertebrae. Neither of the European specimens has a complete tail, but in both cases the tail was clearly longer than the body. When vertebral lengths are normalized (divided by the average lengths of caudal vertebrae 2–5), there are no significant differences between vertebral lengths in any of the four tails. As in *Compsognathus*, the dorsal neural spines are peculiar in that they are anteroposteriorly long but low, and often are fan-shaped.

The caudal centra increase in length over the first six segments, but posteriorly decrease progressively in length and all other dimensions. The first 10 tail vertebrae have neural spines, most of which slope posterodorsally. There are at least four pairs of caudal ribs in NIGP 127586, and more distal caudals have low bumps in this region that could also be interpreted as transverse processes. This could be another way to distinguish the Asian and European compsognathids, because the German specimen of *Compsognathus* apparently lacks caudal ribs and transverse processes<sup>11</sup>. Haemal spines are found on at least the first 47 caudals of NIGP 127586, and the anterior ones are simple spatulate structures that curve gently posteroventrally. The haemal spines are oriented more posteriorly than ventrally, and are more strongly curved.

Both specimens have 13 pairs of dorsal ribs. The ribs indicate a high but narrow body. The distal ends of the first two pairs of ribs are expanded and end in cup-like depressions that suggest the presence of a cartilaginous sternum. The gastralia are well preserved with two gastralia on each side of a segment. The median gastralia cross to form the interconnected ‘zig-zag’ pattern characteristic of

all theropods<sup>14</sup> and primitive birds like *Archaeopteryx* and *Confuciusornis*.

The front limb is relatively short and stout. Both NIGP 127586 and NIGP 127587 have articulated hands, something that is lacking in the two European specimens. What has been interpreted by some as the first metacarpal<sup>11</sup> in *Compsognathus* is the first phalanx of digit I, as was originally proposed by von Huene<sup>15</sup>. The first metacarpal is short (4.2 mm long in NIGP 127586, and double that length in 127587), and is probably the element identified as a carpal in the French specimen<sup>12</sup>. As is typical of all theropods, the collateral ligament pits of the first phalanx are much closer to the extensor surface of the bone than they are to the flexor surface. Both phalanx I–1 and the ungual that it supports are relatively large, each being as long as the radius, and thicker than the shafts and the distal ends of either the radius or the ulna. This unusual character seems to have been partially developed in at least phalanx I–1 of *Compsognathus*. Relative to the length of the radius, both these elements are longer in *Sinosauropteryx* than in any other known theropod except for *Mononykus*<sup>16</sup>. As indicated by the proposed phylogenetic placement<sup>16</sup> of *Mononykus*, there are too many anatomical differences between compsognathids and *Mononykus* to suggest a close relationship, and the similarities probably represent convergence.

The long (39 mm in NIGP 127586, 67.5 mm in NIGP 127587), low (22.2 mm high at both pubic and ischial peduncles in NIGP 127587) ilium is shallowly convex on the dorsal side in lateral aspect. The pubis, which is 82.8 mm long in NIGP 127587, is oriented anteroventrally, but is closer to vertical than it is in most non-avian theropods. The distal end expands into a pubic boot as in most tetanuran theropods. In the larger specimen, this expansion is 17.7 mm. As in *Archaeopteryx*<sup>17</sup>, *Compsognathus*<sup>11</sup> and dromaeosaurs<sup>18</sup>, the boot expands posteriorly from the shaft of the pubis, and the anterior expansion is moderate. The lack of the significant anterior expansion of the pubic boot may be correlated with the inclination of the shaft. The ischium is only two-thirds the length of the pubis in NIGP 127587. It tapers distally into a narrow shaft (3.2 mm in diameter), and like *Compsognathus*, there is a slight expansion at the end (6 mm in NIGP 127587). The prominent obturator process is also found in *Compsognathus*.

The shaft of the femur is gently curved. Both tibia and fibula are elongate. The astragalus and calcaneum are present in both specimens, although not clearly seen in either. There are five metatarsals, but as in other theropods and early birds, the first is reduced to a distal articular condyle, and the fifth is reduced to a proximal splint (Fig. 2b). Metatarsals II, III and IV are closely appressed and elongate, but are not co-ossified. The second and fourth metatarsals do not contact each other. Pedal phalanges are conservative in number (2–3–4–5–0) and morphology.

### Inclusions within the body cavity

Like the German *Compsognathus*, the larger Chinese specimen has stomach contents preserved within the rib cage. This consists of a semi-articulated skeleton of a lizard, complete with skull (Fig. 4a,b). Numerous lizard skeletons have been recovered from these beds, but have yet to be described. Low in the abdomen of NIGP 127587, anterior to and slightly above the pubic boot, lies a pair of small eggs (37 × 26 mm) (Fig. 4a,c), one in front of the other. Additional eggs may lie underneath. Gastralia lie over the exposed surfaces of the eggs, and the left femur protrudes from beneath them, so there can be no doubt that they were within the body cavity. It is possible that the eggs were eaten by the dinosaur. However, given their position in the abdomen behind and below the stomach contents, and the fact that they are in the wrong part of the body cavity for the egg shell to be intact, it is more likely that these were unlaidd eggs of the compsognathid. Eggs have also been reported in the holotype of *Compsognathus*<sup>19</sup>, but they are more numerous and are only 10 mm in diameter. As they were also found outside the body cavity, their



**Figure 3** *Sinosauropteryx prima* Ji and Ji, NIGP 127587, an adult individual from the same locality as holotype.



identification as *Compsognathus* eggs has not been widely accepted. The presence of fewer but larger eggs in *Sinosauropteryx* casts additional doubt on this identification.

Although more than two eggs may have been present in the larger specimen of *Sinosauropteryx*, it does not seem as though many could have been held within the abdomen. It may well be that these dinosaurs laid fewer eggs than most (some species are known to have produced in excess of 40)<sup>20</sup>. However, it is more likely that their presence demonstrates paired ovulation, as has been suggested for *Oviraptor*<sup>21</sup>, *Troodon*<sup>22</sup> and other theropods. *Sinosauropteryx* therefore probably laid eggs in pairs, with a delay for ovulation between each pair.

### Integumentary structures

One of the most remarkable features of both Chinese specimens is the preservation of integumentary structures. In the larger speci-



**Figure 4** Body of NIGP 127587. **a**, Stomach contents are preserved within the rib cage, and include a small lizard and a pair of eggs. **b**, A close-up of the lizard skull. **c**, A close-up of a pair of the eggs.

men, these structures can be seen along the dorsal surface of the neck and back, and along the upper and lower margins of the tail, but in the smaller specimen the integumentary structures are clearer (Fig. 5). They cover the top of the back half of the skull, the neck, the back, the hips and the tail. They also extend along the entire ventral margin of the tail. Small patches can be seen on the side of the skull (behind the quadrate and over the articular), behind the right humerus, and in front of the right ulna. With the exception of a small patch outside the left ribs of NIGP 127587 and several areas on the left side of the tail (lateral to the vertebrae), integumentary structures cannot be seen along the sides of the body. The structures were probably present in the living animals, as indicated by the density of the covering dorsal to the body, and by the few random patches of integumentary structures that can be seen elsewhere.

In the two theropods, the distances separating the integumentary structures from the underlying bones are directly proportional to the amount of skin and muscle that would have been present. As in modern animals, the integument closely adheres to the tops of the skull and hips, and becomes progressively closer to the caudal vertebrae towards the tip of the tail. In the posterior part of the neck, over the shoulders, and at the base of the tail, the integumentary structures are more distant from the underlying skeletal elements, and in life would have been separated by greater thicknesses of muscle and other soft tissues.

The orientation and frequently sinuous lines of the integumentary structures suggest they were soft and pliable, and semi-independent of each other. They frequently cross each other, and are tangled in some areas. There is an apparent tendency for the integumentary structures to clump along the tail of the smaller specimen, but this is an artefact of the splitting plane between NIGP 127586 (Fig. 2a) and GMV 2123. As both individuals were lying in the water of a lake when they were buried, it is clear that we are not looking at the normal orientation of the integumentary structures in the fossils. Under magnification, the margins of the larger structures are darker



along the edges, but lighter medially, which indicates that they might have been hollow. Overall, the integumentary structures are rather coarse for such a small animal, and the thickest strands are much thicker than the hairs of the vast majority of small mammals<sup>23</sup>. In NIGP 127586, integumentary structures are first seen on the dorsal surface of the skull in front of the orbit. The skull is semidisarticulated, and sediment still covers the snout region, so it is possible that the integumentary structures extended more anteriorly. The most rostral integumentary structures are 5.5 mm long, and extend about 4 mm above the skull. They quickly lengthen to at least 21 mm above the distal ends of the scapulae. This axial length seems to stay constant along most of the back, but decreases sharply to 16 mm dorsal to the ilium. The longest integumentary structures seem to have been above the base of the tail, although it is impossible to measure any single structure. More distally along the tail, integumentary structures decrease more rapidly on the lower side of the tail than on the upper. By caudal 47, the ventral structures are 4.2 mm long, about half the length of the dorsal structures in that region.

The size distribution of the integumentary structures of NIGP 127587 follow the same general pattern as in the smaller specimen. Although the integument tends to look thinner on this specimen, it is simply because the integumentary structures are lying closer to the body. Individual measurements are consistently larger than those of NIGP 127586. The integumentary structures are 13 mm long above the skull, 23.5 mm above the fourth cervical, at least 35 mm over the scapulae, at least 40 mm over caudal 27 (Fig. 6), and at least 35 mm below caudal 25. Integumentary structures on the left side of the body are largely covered by ribs, gastralia, stomach contents and matrix, so it is only possible to say that each is more than 5 mm long. Those associated with the right ulna are 14 mm long.

Integumentary structures have also been reported in the theropod *Pelecanimimus*<sup>24</sup> from the Lower Cretaceous of Spain. These consist of subparallel fibres arranged perpendicular to the bones, with a less conspicuous secondary system parallel to them. As described, they seem to be similar to the integumentary structures of *Sinosauropteryx*.

Skin impressions have been found on most main types of dinosaurs, including sauropods, ankylosaurs, ornithopods, stego-

saurs, ceratopsians, and several genera of large theropods. In all of these animals, there is no evidence of integumentary structures, and the skin usually has a ‘pebbly’ surface texture. Integumentary structures have been claimed for both specimens of *Compsognathus*<sup>11,25</sup> though the interpretations have been questioned in both cases<sup>11</sup>. In the German specimen, there was supposedly a patch of skin over the abdominal region. The French specimen included some strange markings in the region of the forearm, that were originally identified as a swimming appendage formed either of dermal bone or of thick skin<sup>12</sup>, but it is clearly not well enough preserved to be positively identified. The identification of these structures as integumentary is questionable<sup>11</sup>, and there is nothing on the Chinese specimens to support the presence of such structures in compsognathids. Evidence of feathers in *Compsognathus* was sought<sup>11</sup> without success, but this lack of evidence on the German specimen of *Compsognathus* does not eliminate the possibility that they might have existed.

### Discussion

The integumentary structures of *Sinosauropteryx* are extremely interesting regardless of whether they are referred to as feathers, protofeathers, or some other structure. Unfortunately, they are piled so thick that we have been unable to isolate a single one for examination. Comparison with birds from the same locality shows that the same problem exists with identifying individual feathers (other than the flight feathers) and components of feathers in avian specimens. The morphological characteristics that we describe suggest that the integumentary structures seem to resemble most closely the plumules of modern birds, having relatively short quills and long, filamentous barbs. The absence of barbules and hooklets is uncommon in modern birds, but has been noted in Cretaceous specimens<sup>26</sup>.

It has been proposed that the feathers of another recently discovered animal from the same locality in Liaoning are structurally intermediate between the integumentary structures of *Sinosauropteryx* and the feathers of *Archaeopteryx*<sup>27</sup>. The clearly preserved feathers of *Protarchaeopteryx robusta* are symmetrical, which indicates that the animal was not capable of flight. This is confirmed by the relatively short length of the forelimb. Both *Sinosauropteryx* and *Protarchaeopteryx* had been identified as



**Figure 5** (Far left) Integumentary structures in the neck and dorsal sides of NIGP 127586.

**Figure 6** (Left) Integumentary structures over caudal 27 of NIGP 127587.

birds because of the presence of feathers<sup>27</sup>, but much more work needs to be done to prove that the integumentary structures of *Sinosauropteryx* have any structural relationship to feathers, and phylogenetic analysis of the skeleton clearly places compsognathids far from the ancestry of birds. Despite arguments to the contrary<sup>28</sup>, cladistic analysis favours the notion that the bird lineage originated within theropod dinosaurs<sup>29,30</sup>. If this phylogenetic framework is accepted, the integumentary structures of *Sinosauropteryx* could shed light on some of the many hypotheses concerning feather origins. Three main functions have been suggested for the initial development of feathers—display, aerodynamics and insulation.

The integumentary structures of *Sinosauropteryx* have no apparent aerodynamic characteristics, but might be representative of what covered the ancestral stock of birds. It is highly unlikely that something as complex as a bird feather could evolve in one step, and many animals glide and fly with much simpler structures. Even birds secondarily simplify feathers when airborne flight ceases to be their main method of locomotion, and produce structures that are intermediate between reptilian scales and feathers<sup>31</sup>. The multi-branched integumentary structures of the Chinese compsognathids are relatively simple, but are suitable for modification into the more complex structures required for flight.

Feathers may have appeared first as display structures<sup>31</sup>, but the density, distribution, and relatively short lengths of the integumentary structures of *Sinosauropteryx* suggest that they were not used for display. It is conceivable that both specimens are female, and that the males had more elaborate integumentary structures for display. It is also possible that the integumentary structures were coloured to serve a display function. Therefore, the existing *Sinosauropteryx* specimens do not support the hypothesis that feathers evolved primarily for display, but do not disprove it either.

The dense, pliable integumentary structures of the Chinese compsognathids would not have been appropriate as heat shields to screen and shade the body from the Sun's rays<sup>32</sup>. Although they may have been effective in protecting the body from solar radiation in warm weather, they would also have been effective in preventing an ectothermic theropod from rapidly warming up by basking in the sunshine. If small theropods were endothermic, they would have needed insulation to maintain high body temperatures<sup>33–35</sup>. The presence of dense integumentary structures may suggest that *Sinosauropteryx* was endothermic, and that heat retention was the primary function for the evolution of integumentary structures<sup>36–38</sup>. Recently published histological studies suggest at least some early birds were not truly endothermic<sup>39</sup>, although they may have been physiologically intermediate between poikilothermic ectotherms and homeothermic endotherms<sup>40</sup>.

The Chinese compsognathids have integumentary structures consisting of vertical fibres running from the base of the head along the back and around the tail extending forwards almost to the legs. There are no structures showing the fundamental morphological features of modern bird feathers, but they could be previously unidentified protofeathers which are not as complex as either down feathers or even the hair-like feathers of secondarily flightless birds. Their simplicity would not have made them ineffective for insulation when wet any more than it negates the insulatory capabilities of mammalian hair. We cannot determine whether or not the integumentary structures were arranged in pterygiae, but they were long enough to cover apteria, if they existed, and could therefore still have been effective in thermoregulation. Continuous distribution is not essential to be effective in this function<sup>28</sup>, especially if the apteria are part of a mechanism for dispersing excess heat. Finally, the aerodynamic capabilities of bird feathers are not comprised by the previous evolution of less complex protofeathers that had some other function, such as insulation.

In addition to the integumentary structures, there is dark pigmentation over the eyes of both specimens. A second region of dark pigmentation in the abdominal region of the smaller specimen

might represent some soft tissues of viscera.

Multidisciplinary and multinational research is just beginning on these unique small theropods. Techniques developed to study fossil feathers<sup>38,41</sup> will be useful research tools as work progresses. In the meantime, the integumentary structures of *Sinosauropteryx* suggest that feathers evolved from simpler, branched structures that evolved in non-avian theropod dinosaurs, possibly for insulation. □

Received 14 January; accepted 18 September 1997.

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**Acknowledgements.** This study was supported by NSFC. We thank L.-s. Chen and P. J. Currie (Royal Tyrrell Museum of Paleontology) for helping to prepare the fossil materials and manuscript; M.-m. Zhang, X.-n. Mu, G. Sun, J. H. Ostram, A. Brush, L. Martin, P. Wellnhofer, N. J. Mateer, E. B. Koppelhus, D. B. Brinkman, D. A. Eberth, J. A. Ruben, L. Chiappe, S. Czerkas, R. O'Brien, D. Rimplinger, M. Vickaryous and D. Unwin for assistance and comments; and L. Mazzatenta and M. Skrepnick for help producing the photographs and drawings.

Correspondence and requests for materials should be addressed to P.-j.C. (e-mail: lpsnigp@nanjing.jspta.chinamail.sprint.com).