# Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China

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**Abstract**: A spectacular pair of *Sinosauropteryx* skeletons from Jurassic–Cretaceous strata of Liaoning in northeastern China attracted worldwide notoriety in 1996 as the first dinosaurs covered with feather-like structures. *Sinosauropteryx prima* is important not only because of its integument, but also because it is a basal coelurosaur and represents an important stage in theropod evolution that is poorly understood. Coelurosauria, which includes (but is not limited to) dromaeosaurids, ornithomimosaurs, oviraptorosaurs, troodontids, and tyrannosaurids, formed the most important radiation of Cretaceous carnivorous dinosaurs in the Northern Hemisphere. It also includes Aves. *Sinosauropteryx prima* has a number of characters that were poorly preserved in known specimens of the closely related *Compsognathus longipes* from Europe. These include the longest tail known for any theropod and a three-fingered hand dominated by the first digit, which is longer and thicker than either of the bones of the forearm. Both specimens have a thick coat of feather-like structures, which seem to be simple branching structures. The claim that one skeleton of *Sinosauropteryx* has preserved the shape of the liver is unsupportable, if only because the fossil had collapsed into a single plane, which would have distorted any soft, internal organs.

**Résumé** : Deux impressionnants squelettes de *Sinosauropteryx*, provenant des strates du Jurassique–Crétacé à Liaoning dans le nord-est de la Chine, attirèrent une notoriété mondiale en 1996 en tant que les premiers dinosaures recouverts de structures ressemblant à des plumes. *Sinosauropteryx prima* est significatif non seulement en raison de son tégument, mais aussi parce qu'il s'agit d'un cœlurosaure de base et qu'il représente une étape importante dans l'évolution mal comprise des Thérapodes. Cœlurosauria, qui comprend (sans s'y limiter) les dromæosauridés, les ornithomimosaures, les oviraptorosaures, les troodontidés et les tyrannosauridés, formait le plus important rayonnement de dinosaures carnivores du Crétacé dans l'hémisphère Nord. On y inclut aussi Aves. *Sinosauropteryx prima* présente certains caractères qui ont été mal préservés dans les spécimens connus de son proche parent européen *Compsognathus longipes*. Ces caractères comprennent la plus longue queue connue pour tout Théropode et une main à trois doigts dominée par le premier doigt, qui est plus long et plus épais que l'un ou l'autre des os de l'avant-bras. Les deux spécimens ont un épais manteau de structures de type plumes, lesquelles semblent être de simples structures de branchements. L'allégation qu'un squelette de *Sinosauropteryx* aurait préservé la forme du foie n'est pas justifiable, si ce n'est pour la simple raison que le fossile s'était effondré dans un seul plan, ce qui aurait déformé tout organe interne mou.

[Traduit par la Rédaction]

## Introduction

The well-known Jehol freshwater and terrestrial fossil fauna (Grabau 1928) was widely distributed in eastern Asia during latest Jurassic and early Cretaceous times. Macroplants (including the earliest known angiosperms; Sun et al. 1998; Wu 1999), palynomorphs (Li and Liu 1999), charophytes, conchostracans (Chen 1999), ostracods, shrimp, insects (Ren 1998), bivalves, gastropods, fish (Jin 1999), frogs (Ji and Ji 1998), turtles, lizards, champsosaurs (Gao et al. 2000), crocodiles, pterosaurs (Ji and Ji 1997c; Ji et al. 1999), psittacosaurs (Xu and Wang 1998), theropods with an integumentary covering (Ji et al. 1998; Xu et al. 1999a,

1999b, 2000; Zhou and Wang 2000), birds (Hou et al. 1995; Hou 1996, 1997, 1998; Chiappe et al. 1999; Hou and Chen 1999); and mammals (Hu et al. 1997) have been recovered. The Jehol Group can be subdivided into three stages (Chen 1988). The Early Jehol fauna from the Dabei-Gou Formation may be Kimmeridgian in age, based on the presence of *Nestoria*. The Middle Jehol fauna is recovered from the Yixian Formation of western Liaoning and coeval horizons in other parts of northern China. The revised Late Jehol fauna only contains fossils collected from the lacustrine deposits of the Jiufotang Formation in western Liaoning and northern Hebei. The early Cretaceous conchostracan *Yanjiestheria*, and a diverse assemblage of volant birds (*Cathayornis*,

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*Chaoyangia*, and *Sinornis*) from the Chaoyang district suggest that the Late Jehol beds are Neocomian in age (Hou et al. 1995).

*Sinosauropteryx prima* is a compsognathid theropod from the Middle Jehol fauna, based on specimens from Sihetun near Beipiao, Liaoning (Ji and Ji 1996, 1997*a*; Chen et al. 1998) discovered by farmers (Ackerman 1998). Here, the Yixian Formation is mainly composed of andesites, andesite breccia, agglomerates, and basalts, but has three fossil-bearing sedimentary intercalations that are rich in tuffaceous materials. The Jianshangou (Chen et al. 1980; Chen 1996) intercalated bed (28–95 m) 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 (Table 1) of mixed Jurassic–Cretaceous character. The primitive characters of the fossil birds of the Jianshangou fossil group have been used to suggest that the beds could be as early as Tithonian in age (Hou et al. 1995). However, even though *Confuciusornis* and the other birds (Hou et al. 1996) are more advanced than *Archaeopteryx* in a number of significant features, all that can really be said is that the beds they come from are probably younger than the Solnhofen Lithographic Limestones (lower Tithonian). The presence of *Psittacosaurus* (Dong 1993; Xu and Wang 1998) suggests an Early Cretaceous Age, as do radiometric dates of the formation (Smith et al. 1995; Swisher et al. 1999). However, other radiometric dates have produced older ages (Wang and Diao 1984; Lo et al. 1999), and much of the fauna, including a rhamphorhynchoid pterosaur (Ji et al. 1999), is more consistent with a Late Jurassic age. This suggests that the debate is not yet resolved and reinforces the importance of keeping separate lithostratigraphic and biostratigraphic evidence (Ji et al. 1999).

The holotype of *Sinosauropteryx prima* is complete, but is split into part (Ji and Ji 1996) and counterpart (Fig. 1*a*), and the sections reside in two different institutions. Two larger specimens lack only the distal ends of their tails, and are housed in the collections of the Nanjing Institute of Geology and Palaeontology (Chen et al. 1998), and the National Geological Museum of China (Ji and Ji 1997*b*).

*Sinosauropteryx* is comparable in size and morphology to known specimens of *Compsognathus* (Bidar et al. 1972; Ostrom 1978) from Europe. The smallest specimen (NIGP 127586) is 0.68 m long (snout to end of tail), and has a femur length of 53.2 mm. It is, therefore, smaller than the type specimen of *Compsognathus longipes* (femur length about 67 mm). NIGP 127587 (Fig. 1*b*) is larger than both (femur is 86.4 mm). Its preserved length is 0.69 m, but based on the length of the tail of the smaller specimen, the total length would have been 1.07 m. It is smaller than the third specimen of *Sinosauropteryx* (Ji and Ji 1997*a*) and the second specimen of *Compsognathus* (Bidar et al. 1972; Ostrom 1978) from Canjuers (France), which have femoral lengths of 108 and 110 mm, respectively. Assuming that *Compsognathus* has a tail comparable to that of *Sinosauropteryx*, these larger specimens had estimated lengths in excess of 1.2 m, more than double the length of NIGP 127586.

*Sinosauropteryx* and *Compsognathus* share a suite of characters that indicate close relationship. These include several characters of variable distribution within Theropoda,

**Table 1.** Fossils yielded from the Jianshangou intercalated bed of the Yixian Formation.

| | |
|---|---|
| Plants | *Tyrmia* sp., *Coniopteris* sp., *Baiera* sp., *Czekanowskia* sp., *Phoenicopsis* sp., *Potomogeton* sp., *Sdenites* sp. |
| Conchostracans | *Eosestheria lingyuanensis*, *E. ovata*, *Diestheria shangyuanensis* |
| Ostracods | *Cypridea lioningensis*, *Ulwellia* sp., *Darwinula contracta*, *Tiwiriasevia jianshangouensis* |
| Insects | *Ephemeropsis trisetalis*, *Chrysogomphus beipiaoensis*, *Alloraphidia obliquivenatica* |
| Bivalves | *Feganochoncha* sp., *Sphaerium jeholense* |
| Gastropods | *Omozaphychius angulatus*, *Probaicalia vitimensis*, *Galba* sp. |
| Fish | *Lycoptera davidi*, *Peipiaosteus panii* |
| Reptiles | *Caudipteryx zoui*, *Manchuochelys liaoxiensis*, *Yabenosaurus tenuis*, *Manchurosuchus splendens*, *Protarchaeopteryx robusta*, *Psittacosaurus* sp., *Liaoningosaurus paradoxus*, *Jeholosaurus shangyuanensis* |
| Birds | *Confuciusornis sanctus*, *Changchengornis hengdaoziensis*, *Protopteryx fengningensis* |

including the presence of a relatively large skull (40% length of presacral column in NIGP 127586 and 36% in NIGP 127587), unserrated premaxillary but serrated maxillary teeth, slender cervical ribs, short front limbs (lengths of humerus plus radius divided by the sum of femur and tibia lengths less than 45%), limited anterior expansion of the pubic boot, and a prominent obturator process of the ischium. Other characters that seem to be limited to compsognathids include fan-shaped neural spines on the dorsal vertebrae, an ulna with a large and powerful olecranon process, and a powerful manual phalanx I-1 (the shaft diameter of which is greater than that of the radius).

The known individuals of *Sinosauropteryx prima* were collected from the same horizon as the non-avian dinosaurs with integumentary structures: *Beipiaosaurus* (Xu et al. 1999*a*), *Caudipteryx* (Ji et al. 1998), *Protarchaeopteryx* (Ji and Ji 1997*a*) and *Sinornithosaurus* (Xu et al. 1999*b*), and the birds *Confuciusornis* (Chiappe et al. 1999), *Liaoxiornis* (Hou and Chen 1999) and *Protopteryx* (Zhang and Zhou 2000).

In spite of the widespread recovery of fossilized skin and feathers on non-avian dinosaurs and birds from the Yixian Formation, the identification of the integumentary structures has been controversial (Maderson and Homberger 2000; Xu et al. 2001) ever since the first paper (Ji and Ji 1996) was published. Even before researchers had an opportunity to see the specimens, comments on the validity of the feathers were being published (Morell 1997; Gibbons 1997).

In this paper, we describe the two specimens (Fig. 1) in the collections of the Nanjing Institute of Geology and Palaeontology.

**Fig. 1.** *Sinosauropteryx prima*. Specimen drawings of (*a*) NIGP 127586, counterpart of holotype, and (*b*) NIGP 127587. Right coracoid of the latter has been moved a centimetre closer to the body than it is in the specimen. Scale = 5 cm.
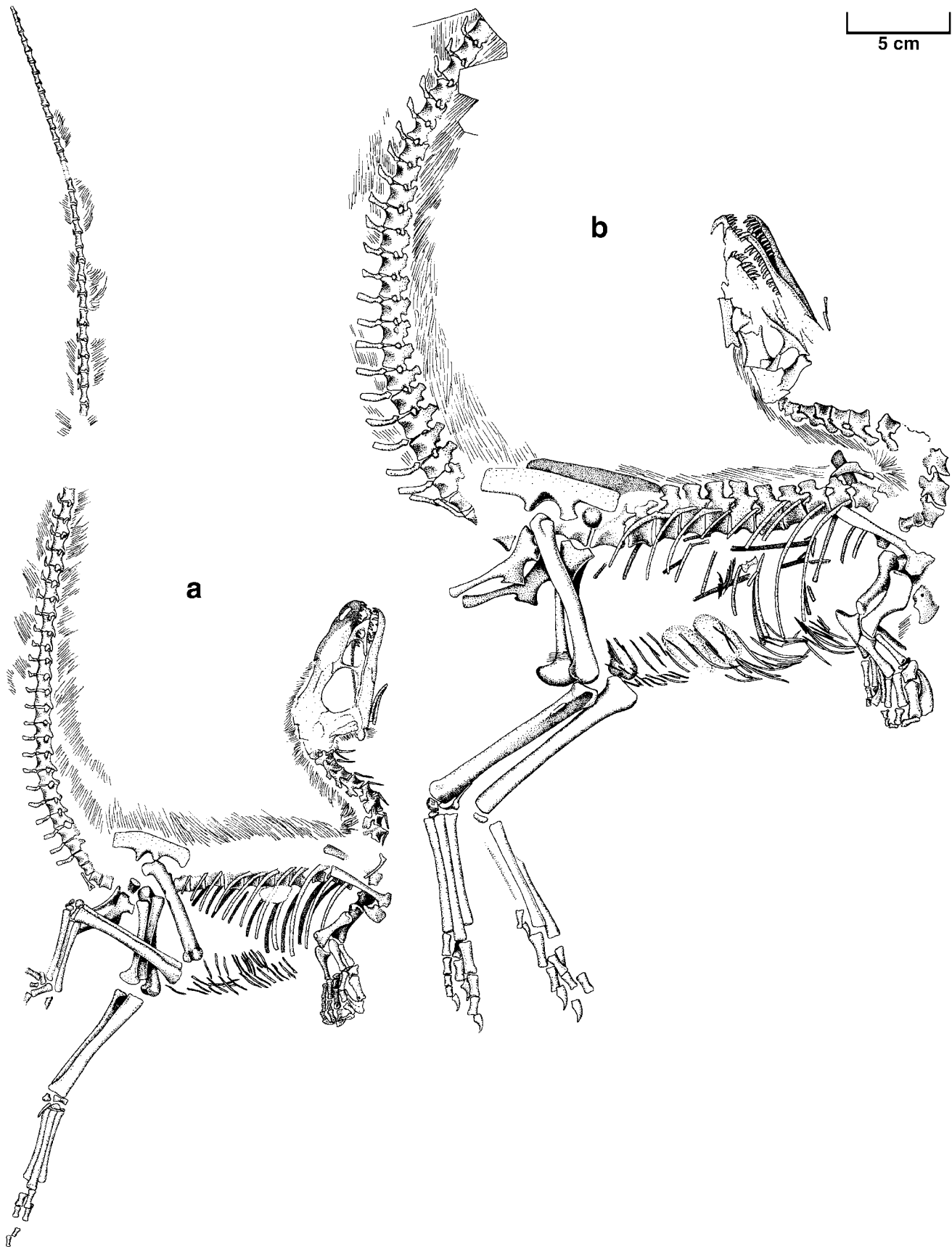
# Systematic palaeontology

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Coelurosauria von Huene, 1914
Compsognathidae Marsh, 1882
   *Sinosauropteryx prima* Ji and Ji, 1996

## Etymology

*Sinosauropteryx prima* should be translated as "first Chinese dragon feather."

## Holotype

A complete skeleton of a juvenile, split longitudinally into part and counterpart (NGMC 2123, NIGP 127586).

## Referred specimens

NIGP 127587, a nearly complete skeleton lacking only the distal half of the tail (Chen et al. 1998).

NGMC 2124, a nearly complete skeleton initially described by Ji and Ji (1997b). This specimen includes symmetrodont mammal jaws and skeletal elements in the stomach region.

## Locality and horizon

Sihetun-Jianshangou region, near Beipiao, Liaoning, People's Republic of China. Jianshangou intercalated bed in the lower part of the Yixian Formation (= Chaomidianzi Formation of Ji et al. 1998), Upper Jurassic or Lower Cretaceous.

## Diagnosis

Small theropod (the largest specimen is 1.2 m in length). Coelurosaur (defining characters after Holtz 2000 include amphiplatyan cervical centra, boat-shaped distal chevrons, boat-shaped pubic boot, fibula with proximal end that is 75% the width of the proximal end of the tibia, anteroposteriorly thin but tall ascending process) with short but powerful front limbs, in which the first digit is longer than the humerus or the radius. Powerful proximomedial flange on first metacarpal. *Sinosauropteryx* differs from *Compsognathus* in that the front limb is relatively smaller in comparison with the hind limb (lengths of the humerus plus radius divided by the sum of the femur and tibia lengths is about 30% in *Sinosauropteryx*, compared with 43% in *Compsognathus longipes*).

## Institutional abbreviations

BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHN, Museum National d'Histoire Naturelle, Paris, France; NGMC, National Geological Museum of China, Beijing, China; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

## Description

### Apertures

The narial opening is elongate and slopes upwards and backwards. In NIGP 127586, it is 7 mm long, and the width perpendicular to the longitudinal axis is 2.5 mm. Both specimens have a small maxillary fenestra and a large antorbital fenestra (13 mm long and 10 mm high in NIGP 127586). The orbit is large, occupying most of the height of the skull. It was almost certainly circular in outline, but suffered post-mortem dorsoventral crushing in both specimens. The orbit is at least 18 mm long in NIGP 127587, but because it is 19.5 mm in the smaller specimen, the orbital diameter was more likely about 20 mm. Little can be determined from the temporal fenestra. The lateral one is shorter anteroposteriorly than it is tall and appears to have been constricted at midheight by the squamosal and quadratojugal.

### Premaxilla

Both specimens include a pair of premaxillae, although only one of each specimen is well preserved (Fig. 2). Because of the preservation, it is difficult to determine exactly how many premaxillary teeth there were. Ji and Ji (1997b) expressed some uncertainty with NGMC 2124, as to whether there were four or five premaxillary teeth. In NIGP 127587, there are four teeth in the left premaxilla (Fig. 2b). The left premaxilla of NIGP 127586 (Fig. 2a) seems to have five teeth, but it is difficult to determine exactly where the suture with the maxilla is. The undetermined tooth consists of only the root and the base of the crown, and in cross-section is wider than it is anteroposteriorly long. This would suggest that it is a premaxillary tooth, although the first maxillary teeth of theropods are often difficult to distinguish from premaxillary teeth (Currie et al. 1990). Because few theropods have more than four teeth in the premaxilla, it is most parsimonious to interpret the fifth tooth as a maxillary one. Ostrom (1978) reported three premaxillary teeth plus an empty alveolus in *Compsognathus*, again suggesting that four premaxillary teeth is the most likely condition for *Sinosauropteryx*.

As in dromaeosaurids, ornithomimids, and several other types of coelurosaurs, a long, slender maxillary–nasal (subnarial) process extends posterodorsally along the floor of the external naris to contact the nasal bone (Fig. 2). The main body of the premaxilla is almost vertical anteriorly, but curves gradually posterodorsally into the internarial bar.
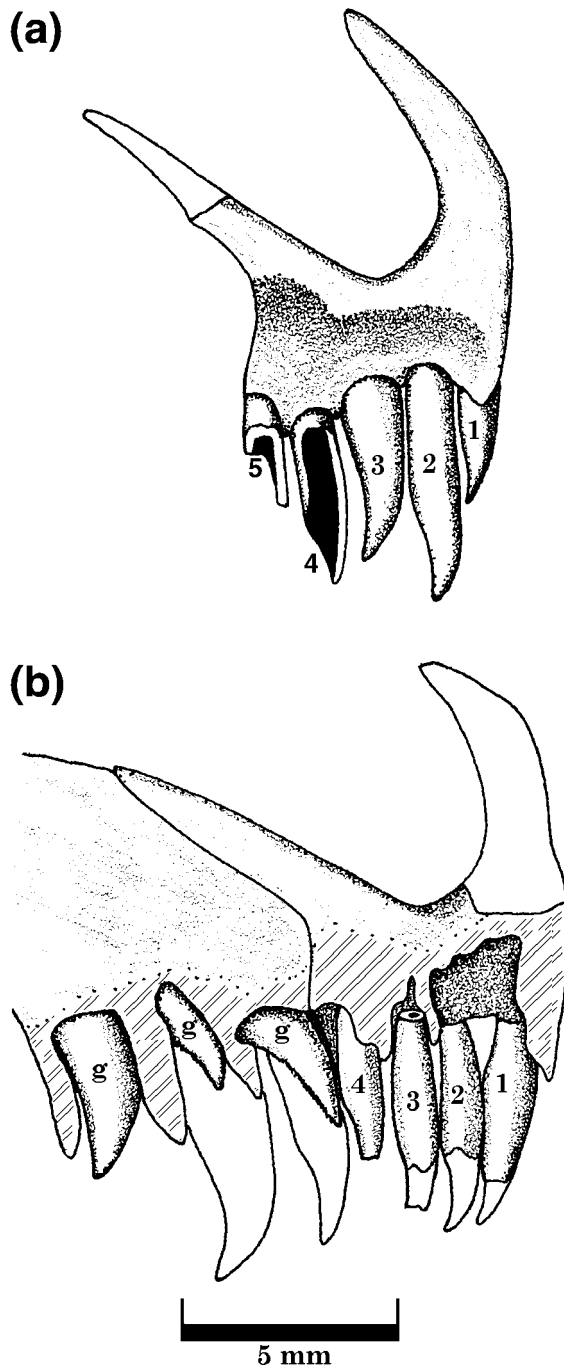
### Maxilla

The maxilla (Fig. 3a) is a complex, triangular bone that tapers posteriorly to end below the midpoint of the orbit. The posterodorsal nasal ramus is well developed, forming the roof of the maxillary fenestra and the anterodorsal margin of the antorbital fenestra. The maxilla is excluded from the margin of the external naris by the nasal and premaxilla. The lateral surface is smooth, and is pierced by numerous nutritive foramina above the dentigerous margin. A relatively large maxillary fenestra opens into the nasal cavity medially, although this may be because the medial wall collapsed.

### Nasal

The nasals on all specimens are badly fractured (Fig. 3d). The right nasal of NIGP 127587 as exposed is 25 mm long and 4.4 mm wide. The complete length of the left nasal seems to be preserved in NIGP 127586, where it is 28.5 mm long. It is a relatively flat bone, pierced anterolaterally by a series of foramina where it forms a ridge above the antorbital fenestra. Posteriorly the dorsal surface of NIGP

The subtemporal branch is relatively short and 3.6 mm high. The postorbital ramus is a thin tapering process that extends at least halfway up the orbit.

### Lacrimal–prefrontal

The prefrontal seems to be separate from the lacrimal in NIGP 127586 (Fig. 3*d*). It is relatively large compared with those of most other theropods, and is exposed mostly on the skull roof medial to the dorsal portion of the lacrimal. Together with the lacrimal, it forms the region of the skull roof lateral to the posterior portion of the nasal and tapers anteriorly. There is no lacrimal horn in NIGP 127587, and there does not appear to be a pneumatopore in the anterodorsal corner of the antorbital fossa.

### Frontal

The ventral surfaces of both frontals can be seen in NIGP 127587 (Fig. 3*c*), exposing the ridges that separate the braincase from the orbits. The bones were not fused and may have been telescoped slightly, but the interorbital distance would have been at least 10.5 mm in NIGP 127587 and about the same in NIGP 127586.

### Squamosal

The squamosal is best seen on the right side of the skull of NIGP 127586 (Fig. 3*b*). It is a complex, multipronged bone that wraps around the head of the quadrate, sends a tapering process anteroventrally to contact the quadratojugal, sits on top of the lateral portion of the paroccipital process, contacts the parietal posteromedially, and forms the posterior part of the intertemporal bar. Unlike in dromaeosaurs, it does not extend significantly lateral to the quadrate articulation.

### Quadrate

The quadrate (Fig. 3*f*) is a tall, relatively stout element that is inclined anteroventrally, as preserved. It is about 17 mm tall in NIGP 127586. In NIGP 127587, it is at least 20.6 mm tall, and the ventral condyles for the jaw articulation are 7 mm wide. The posterolateral surface is pierced by a pneumatopore at midheight (Fig. 3*f*). Only the base of the pterygoid wing is exposed, so it is not possible to see how far it extended anteriorly.

### Scleral plates

Rings of thin scleral plates are found within the orbits of NIGP 127586 and NIGP 127587. In both specimens, a heavy black substance in the orbit seems to represent a by-product of the eye. The black film is not unique to these specimens, but is also found in the orbits of fishes and other vertebrates that have been collected at the same site. In NIGP 127586, the outline of the pigmented area is coincident with the outer margin of the scleral ring. The scleral plates of both *Sinosauropteryx* specimens are covered externally by the black substance, suggesting that it may represent the retina or iris of the eye. Because the substance did not flow outside of the orbit before it became set and fossilized, it probably did not originate from the liquid inside the eyeball. At this stage, it is not clear whether the pigmentation represents a chemical by-product of something within the eyeball, whether it is a compression fossil representing either the eye

127587 (Fig. 3*d*) is longitudinally striated and has a series of low ridges on the sutural contact for the frontal. The dorsal surface of the nasal of NIGP 127586 is also flat posteriorly between the prefrontal–lacrimal, but becomes gently convex in section anteriorly.

### Jugal

The suborbital ramus of the jugal is long and low in NIGP 127587 (Fig. 3*c*), with a height of only 4.2 mm at midlength.

**Fig. 3.** *Sinosauropteryx prima*, cranial bones. (*a*) lateral view of right side of front part of the skull of NIGP 127586; (*b*) right squamosal of NIGP 127586; (*c*) orbital region of NIGP 127587 showing ventral surfaces of the frontals; (*d*) dorsal surface of right nasal of NIGP 127587; (*e*) scale bar for *c*, *d* and *f*; (*f*) right quadrate of NIGP 127587, showing prominent pneumatopore. d, dentary; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pm, premaxilla; pn, pneumatopore; po, postorbital; po-p, postorbital process; pop, paroccipital process; prf, prefrontal; pt-p, pterygoid process; q, quadrate; q cot, quadrate cotylus; qj-p, quadratojugal process; sq, squamosal; stf, supratemporal fenestra. Cross-hatching represents broken bone; dots represent impressions of lost bone.
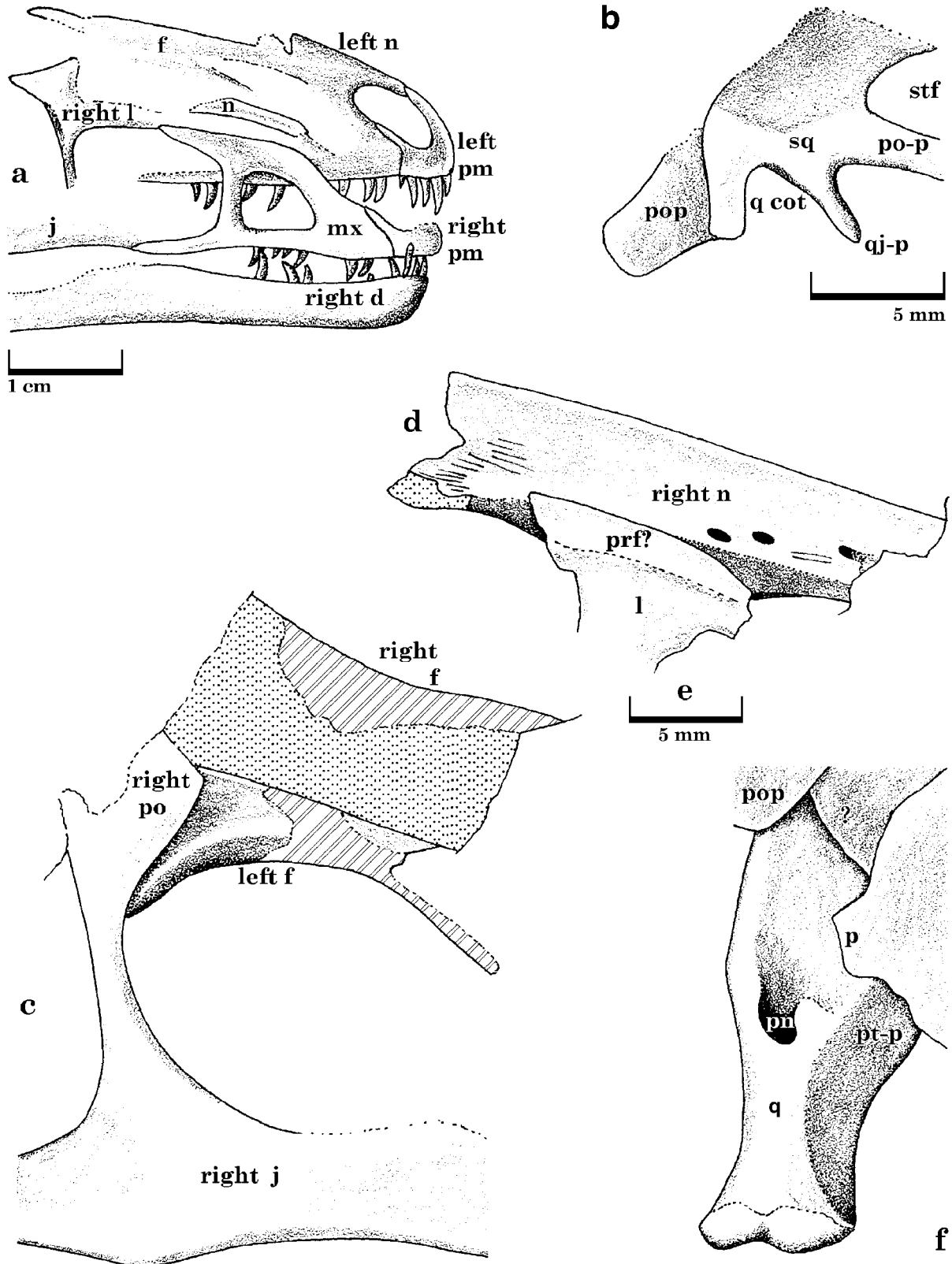
or the eyelids, or whether its presence is diagenetic and coincidental.

*Lower jaw*

The lower jaws of both specimens (Fig. 1) are difficult to interpret because the layering of crushed bone obscures sutural connections. However, as in *Compsognathus* (Ostrom 1978), the external mandibular fenestra appears to have been closed or at least very small.
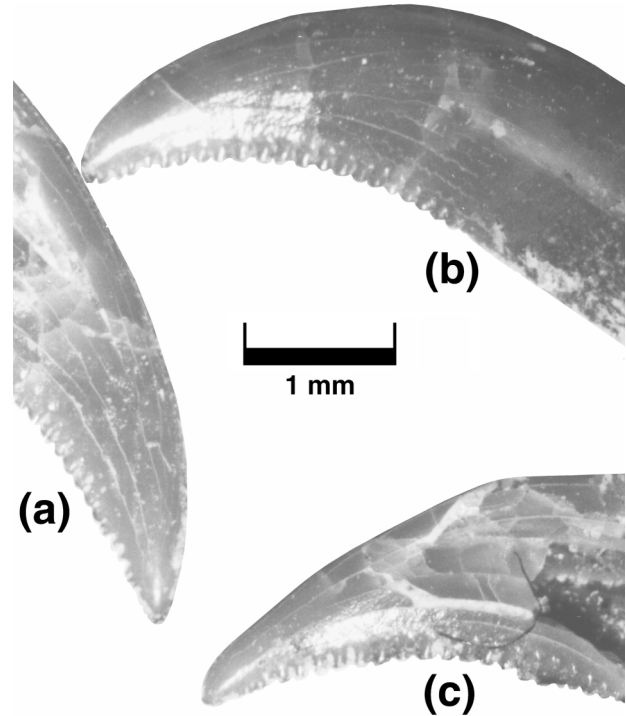
*Teeth*

There are four (NIGP 127587) or possibly five (NIGP 127586) premaxillary teeth (Fig. 2), 12 maxillary teeth (NIGP 127587; Ji and Ji 1997*b*) and 12 (Ji and Ji 1997) to 15 (NIGP 127587) dentary teeth. All teeth were closely set, and there is no evidence of a diastema between the premaxilla and maxilla, or between individual tooth positions.

The slender premaxillary teeth (Fig. 2) are almost as broad mediolaterally as the FABL (fore–aft base length, Farlow et al. 1991). Each is relatively straight at the base, but curves posteriorly in the distal third of the tooth. There is no evidence of either anterior or posterior carina or denticles in any of the specimens. This is similar to many other coelurosaurs, including *Compsognathus* (Ostrom 1978), *Caudipteryx* (Ji et al. 1998), *Sinornithosaurus* (Xu et al. 1999*b*), and *Microraptor* (Xu et al. 2000). In NIGP 127586, the longest premaxillary tooth preserved is the second, which is 3.8 mm long and has a FABL of 0.9 mm. The fourth premaxillary tooth of NIGP 127586 is only partially preserved as an impression, but appears to have been about the same size. The second premaxillary tooth of NIGP 127587 is also the longest one preserved (Fig. 3*b*), although the impression of the distal end of the third suggests that it was the same length. Ostrom (1978) reported only three teeth in the premaxilla of *Compsognathus*, but also referred to an empty alveolus that gives a total premaxillary tooth count of four.

All maxillary teeth of *Sinosauropteryx* seem to bear denticles on their posterior carina (Fig. 4). However, as in *Microraptor* (Xu et al. 2000), the anterior carina lacks serrations. The first maxillary tooth of NIGP 127587 (Fig. 2) has 11 posterior denticles per mm. The second or third maxillary tooth of NIGP 127587 has a length of 2.5 mm and a FABL of 1.0 mm. There are 12 denticles per mm on the posterior carina. None of the large maxillary teeth of NIGP 127586 are exposed, but a fragment of an anterior maxillary tooth has 13 denticles per mm, and posterior maxillary teeth have about 14 denticles per mm. One well-preserved posterior maxillary tooth has a crown height of 1.1 mm and a FABL of 0.6. The maxillary teeth are all relatively closely packed, and there is no sign of the diastema reported by Ostrom (1978) for *Compsognathus*.

The first two dentary teeth lack denticles in NIGP 127586 and look much like the premaxillary teeth. The second dentary tooth is 2.0 mm long and has a FABL of 0.6 mm. The third dentary tooth of NIGP 127587 has serrations on the posterior carina. Posterior dentary teeth look more like maxillary teeth (Fig. 4). They are laterally compressed, curve throughout their length, and bear denticles on the posterior carina. A well-preserved posterior dentary tooth in NIGP 127586 is

**Fig. 4.** *Sinosauropteryx prima*, NIGP 127587. Fourth maxillary tooth (*a*), fourth dentary tooth (*b*), and fifth dentary tooth (*c*).



1.8 mm long, has a FABL of 0.9 mm, and has 10 denticles per mm. Unlike *Compsognathus* (Ostrom 1978), in which the rear edge of the tooth in lateral aspect is almost straight and perpendicular to the jaw, the posterior dentary teeth of NIGP 127587 are curved posteriorly.

Because the bone broke away from the bases of the teeth in several places, germ teeth can be seen in a number of alveoli of NIGP 127587 (Fig. 2). The first two erupted teeth of the left maxilla are preserved only as impressions (Fig. 2*b*), but the germ teeth are intact. Whereas the longitudinal axes of the erupted teeth were almost vertical, those of the germ teeth are inclined forward. As the new tooth grew larger and the roots of the old were resorbed, differential growth would have straightened out the lower part of the shaft so that the curved tip would have rotated backwards as it erupted. The base of a germ tooth can be seen between the roots of the sixth and seventh dentary teeth. Like those in the maxilla, its longitudinal axis is inclined strongly forward. This tooth would have erupted out of the sixth alveolus at maturity.

*Hyoids*

There is a pair of rodlike hyoids in both NIGP 127586 and NIGP 127587 (Fig. 1). Also found in *Compsognathus*, where they are 30 mm long (Ostrom 1978), hyoids are known in most theropods, including abelisaurids (Bonaparte et al. 1990), coelophysids (Rowe 1989), dromaeosaurids (Colbert and Russell 1969), sinraptorids (Currie and Zhao 1993), tyrannosaurids (TMP 91.36.500), and troodontids (Russell and Dong 1993).

*Vertebrae*

Both specimens have 10 cervical and 13 dorsal vertebrae.

The number of sacrals cannot be seen. The tail is extremely long. In the smaller specimen, it is almost double the snout–vent length. There are 59 caudal vertebrae exposed, but five more have been lost from the middle of the tail of NIGP 127586 (but are present in NGMC 2123). Only the first 24 vertebrae are preserved with the larger specimen, but this section is longer than the summed lengths of the cervical, dorsal, and sacral vertebrae. Neither of the *Compsognathus* specimens has a complete tail, but in both cases the tails were clearly longer than the bodies. When vertebral lengths are normalized (divided by the average lengths of caudal vertebrae 2, 3, 4, and 5), there are no significant differences between vertebral lengths in any of the four tails. This suggests that the tails of *Compsognathus* and *Sinosauropteryx* were very similar, and that overall tail length was probably the same in both genera.

The centra and neural arches are not fused in NIGP 127586, showing that this specimen is immature. The cervical vertebrae of both specimens have biconcave centra (Figs. 5a, 5b), in contrast with the opisthocoelous cervicals reported for the German specimen (Ostrom 1978). True opisthocoelous vertebrae are not known in any other coelurosaur, although a moderate form of this condition has been reported in two coelurosaurs (Makovicky 1997). Neither published figures nor casts of *Compsognathus* convincingly show opisthocoelous vertebrae. It is therefore highly likely that *Compsognathus*, like *Sinosauropteryx*, has biconcave cervical centra.

The sixth to eighth cervicals (Fig. 5b) are longer than the anterior cervicals, and are only 10% shorter than the longest dorsals. The intervertebral central articulations are higher in position on the anterior surfaces of the centra than on the posterior sides. This is true for cervicals 4, 5, 6, and 7 and gives the neck its curvature.

The parapophyses of the anterior cervicals (Fig. 5a) are low on the anteroventral corners of the centra. There is a single pleurocoel posterodorsal to the parapophysis of the fifth cervical of NIGP 127586, and in the third (diameter 1 mm) and fourth cervicals of NIGP 127587. There were probably pleurocoels in all of the cervicals.

As in *Compsognathus* and other coelurosaurs, cervical neural spines are anteroposteriorly short and low (Figs. 5a, 5b), extending only 4.6 mm above the zygopophyses in the third cervical of NIGP 127587. The epiphyses are represented in only the first few cervicals of NIGP 127586 by low bumps. Prezygopophyses are elongate at the front of the neck, whereas postzygapophyses tend to be longer at the back. The zygapophyses extend far beyond the ends of their centra as in most coelurosaurs. For example, the length of the third centrum in NIGP 127587 is 9.6 mm, but the total anteroposterior length (between the tips of the zygapophyses) is 13.6 mm. Prezygapophyses incline anteroventrally, as in other coelurosaurs (Makovicky 1997).

Posterior dorsal centra (Fig. 5f) have high, deeply concave sides. Pleurocoels cannot be seen in any of the dorsal centra, but this may be a problem with preservation. Dorsal neural spines are peculiar in that they are anteroposteriorly long but low (Fig. 5f), but are expanded distally as in *Compsognathus*. In the 19th presacral, the neural spine rises 7.5 mm above the zygapophyses, which is only 30% of the total height of the vertebra and less than the height of the centrum. Above

**Fig. 5.** *Sinosauropteryx prima*, vertebrae of NIGP 127587 (*a*, *d*, *e*, *f*, *g*, *h*) and NIGP 127586 (*b*, *c*). ans, accessory neural spine; atp, accessory transverse process; cr, cervical rib; ep, epipophysis; ipz, intrapostzygapophyseal fossa; ns, neural spine; pn, pneumatopore; pp, parapophysis; pr, prezygapophysis; r, rib; su, suture on centrum for neural arch; tp, transverse process; 3–9, cervical vertebrae.
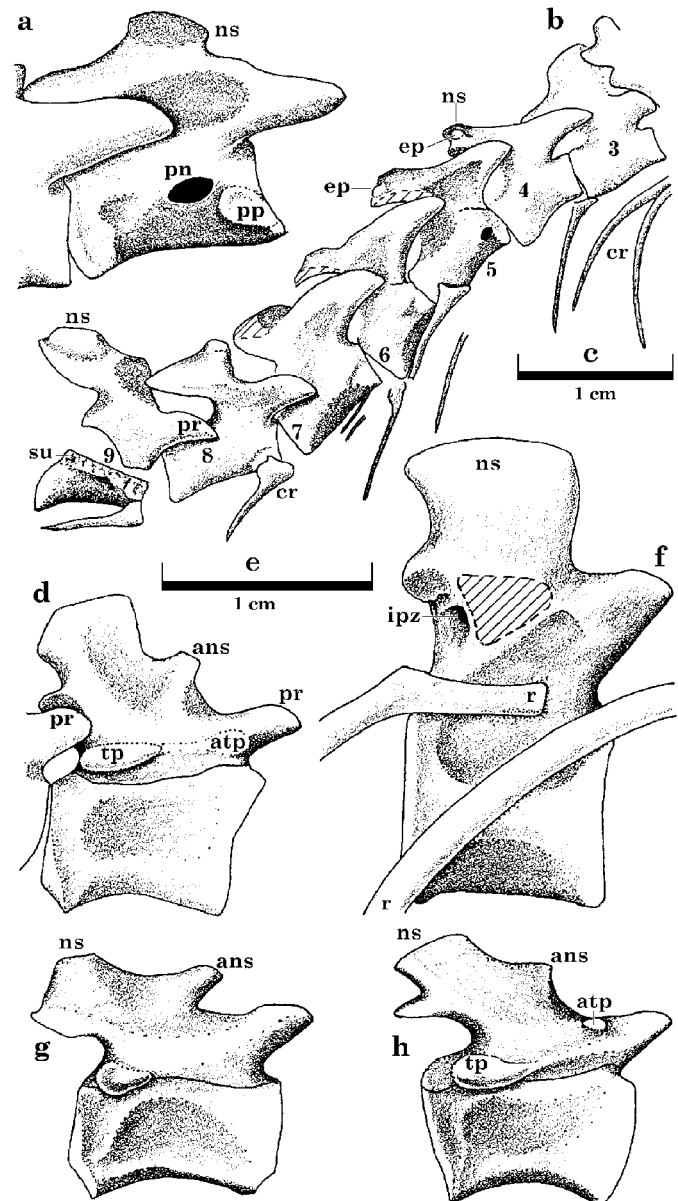


the zygapophyses, the anteroposterior length of the neural spine is 7.9 mm, but it expands distally to 9.9 mm. Although the dorsal centra are not pneumatized, the 19th presacral is well enough preserved to show an infrapostzygapophyseal pneumatopore (Fig. 5f).

Sacral vertebrae are present in both specimens but are largely covered by other elements and matrix. The lengths of the dorsal and caudal centra, and of the ilia, suggest that there were five sacrals. Ostrom (1978) suggested that there were only four sacrals in *Compsognathus*, although von

Huene (1926) felt there were five. The last two sacrals are exposed in NIGP 127587, where they appear to have been coossified but retained a distinct suture. A large attachment scar is present between the centra for a sacral rib, which was apparently not fused to the sacral vertebrae by the time of death. This feature was reported in a juvenile dromaeosaurid (Norell and Makovicky 1997).

The neural arches still show a line of fusion with the caudal centra of NIGP 127587, suggesting that this specimen was probably approaching mature size but was still young when it died. Caudal centra increase in length within the first half dozen segments, but behind that decrease progressively in length and all other dimensions. The first 10 tail vertebrae have prominent neural spines (Figs. 5d, 5g, 5h), most of which slope posterodorsally as in *Compsognathus* (Ostrom 1978). Short neural spines persist, however, until the 18th or 19th caudal of NIGP 127587. The neural spines are centred in the last half of the vertebra, but each caudal also has a smaller, anterior midline branch of the neural spine (Figs. 5d, 5g, 5h) similar to *Acrocanthosaurus* (Currie and Carpenter 2000) and many other theropods. As evident in the figures of Ostrom (1978), the bifurcated neural spine must have been present in *Compsognathus* as well. There are at least four pairs of well-developed transverse processes in NIGP 127586, which are replaced in more distal caudals by low bumps. In NIGP 127587, the small transverse processes persist until the 17th caudal. The transverse process is positioned at the posterior end of a ridge (Figs. 5d, 5h) that extends from the base of the prezygopophysis to the posterior end of the suture between the neural arch and the centrum. There is often a low bump on the anterior end of this ridge, which Harris (1998) referred to as an accessory transverse process. Between the ridge and the suture for the centrum is a shallow, longitudinal trough. 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 (Ostrom 1978).

Chevrons (Fig. 6) are found on at least the first 47 caudals of NIGP 127586. The second haemal arch of NIGP 127586 has a bridge of bone that spans the distance between the forks to close the haemal canal above (Fig. 6). Generally, the bridge is only found in anterior haemal arches and is not present in distal ones. The most proximal chevrons are spatulate structures that curve gently posteroventrally. Mid-caudal haemal spines are more strongly curved, so that the distal ends are oriented more posteriorly than ventrally. They also develop anterior and posterior processes proximally that extend beneath the ventral surfaces of the adjacent caudal centra. These processes make the mid-caudal haemal arches anteroposteriorly longer than those in more anterior caudals. Haemal spines disappear somewhere between the 28th and 33rd segment in NIGP 127586, but the haemal arches persist until at least the 42nd caudal. Posterior haemal arches have long anterior and posterior processes. The preserved anteroposterior length of the 40th haemal arch is 5.3 mm in NIGP 127586, which is almost as long as the vertebral centra that it articulates with. This suggests that the long tapering processes of adjacent haemal arches may have contacted each other to brace and support the distal end of the tail, as in other coelurosaurs.



**Fig. 6.** *Sinosauropteryx prima*. Haemal arches of NIGP 127587 (upper four rows) and NIGP 127586 (bottom level) in left lateral aspect (reversed from right lateral view of specimens). Numbers represent positions in the tail.
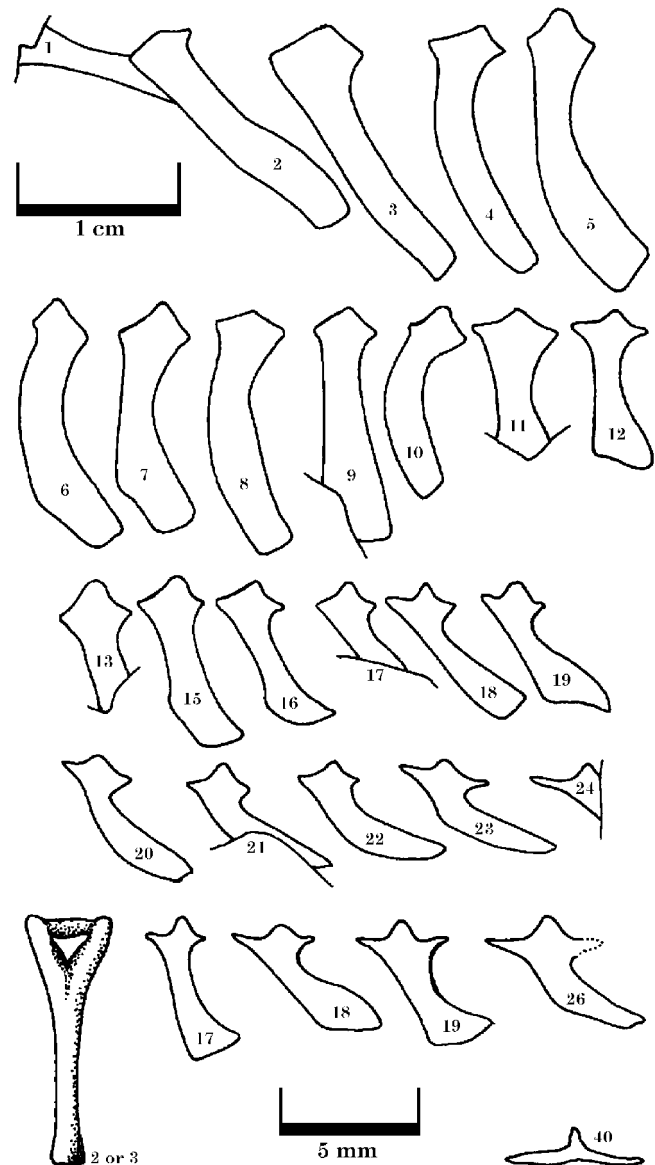
*Ribs*

The cervical ribs of NIGP 127586 are long and slender as in *Compsognathus* (Ostrom 1978). The long curved shaft of the third cervical is 12 mm long, when measured straight from one end to the other, and 13 mm when measured along the outside curve. The shaft is only 0.2 mm in diameter. The anterior cervical ribs are oriented down and back. The sixth cervical rib is straight, about 10 mm long, and has a narrow tapering shaft like the more anterior ribs. This rib has a diameter of only 0.1 mm halfway down the shaft in NIGP 127586. The eighth cervical rib is also thin and tapering, but is only 6 mm long. None of the cervical ribs are as long as those reported for *Compsognathus* (Ostrom 1978), where they can be more than double the length of the cervical

centra. The ninth and tenth cervical ribs lie parallel to the ventral margins of their corresponding centra and are only slightly longer than those centra. All cervical ribs seem to have had short processes anterior to the parapophyses, and none were fused to the vertebrae.

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 cuplike depressions that suggest the presence of sternal ribs and a cartilaginous sternum.

Gastralia (Fig. 1) are well preserved with two gastralia on each side of a segment. The median gastralia cross to form the interconnected zigzag pattern characteristic of all theropods (Claessens 1996; Norell and Makovicky 1997) and basal birds such as *Archaeopteryx* and *Confuciusornis*. The medial segments are longer than the lateral ones.

### Pectoral girdle and front limb

The scapula (Figs. 1, 7) is elongate and slender in *Sinosauropteryx*, the length being almost 10 times the width of the shaft. It is not particularly long, however, as it is only 54–60% the length of the femur and 40–60% longer than the humerus. In *Compsognathus* (BSP AS I 563), the scapula is also 54% the length of the femur. The acromial process is moderately developed and grades evenly into the anterior margin of the scapular blade. The distal end expands to about 70% of the proximal end. The glenoid fossa is directed posteriorly as in most non-avian theropods (Novas and Puerta 1997; Norell and Makovicky 1999).

The coracoid (Fig. 7) is almost as long as it is high in NIGP 127586, and it is well rounded in both specimens. Coracoids are not fused to the scapulae in either specimen, but this may relate to the immaturity of both individuals at the times of death. Unfortunately, all are either broken or covered by other bones. Consequently, the coracoid foramen cannot be seen. The glenoid articulation is a broad, convex surface in *Sinosauropteryx* and is oriented primarily dorsoposteriorly. The coracoid tubercle ("biceps" tubercle) is visible on the right coracoid of NIGP 127586 (Fig. 7) posteroventral to the glenoid.

The front limb (Fig. 8) is short and stout, is less than a third the length of the hind limb (summed lengths of the humerus and radius compared with the femur plus tibia), and is only 39% of the length of the presacral vertebral column in NIGP 127586. In contrast, *Compsognathus* has somewhat longer arms that are more than 40% the length of the hind limbs. The forearm is only 60% the length of the humerus.

The humerus is relatively short and massive (Fig. 8a). It is about 75% the length of the scapula, and is 20–26% longer than the ulna. The low but powerful deltopectoral crest, which extends for more than half the length of the bone, is oriented more laterally than anteriorly. The proximal and distal ends, which lie in almost the same plane, expand to about double the transverse shaft diameter. The distal condyles are low and rounded and are positioned on the flexor surface (NIGP 127587).

The ulna (Fig. 8) has a powerful olecranon process, similar to that on the ulna of *Compsognathus* (Ostrom 1978). The lateral surface of the olecranon has a shallow depression, presumably for a powerful insertion of the triceps tendon. The length of the olecranon is 3.3 mm (almost 20% the total length of the ulna) in NIGP 127586 and 6.9 (24%) in NIGP

**Fig. 7.** *Sinosauropteryx prima*. Right scapula and both coracoids of NIGP 127586. Co, coracoid.
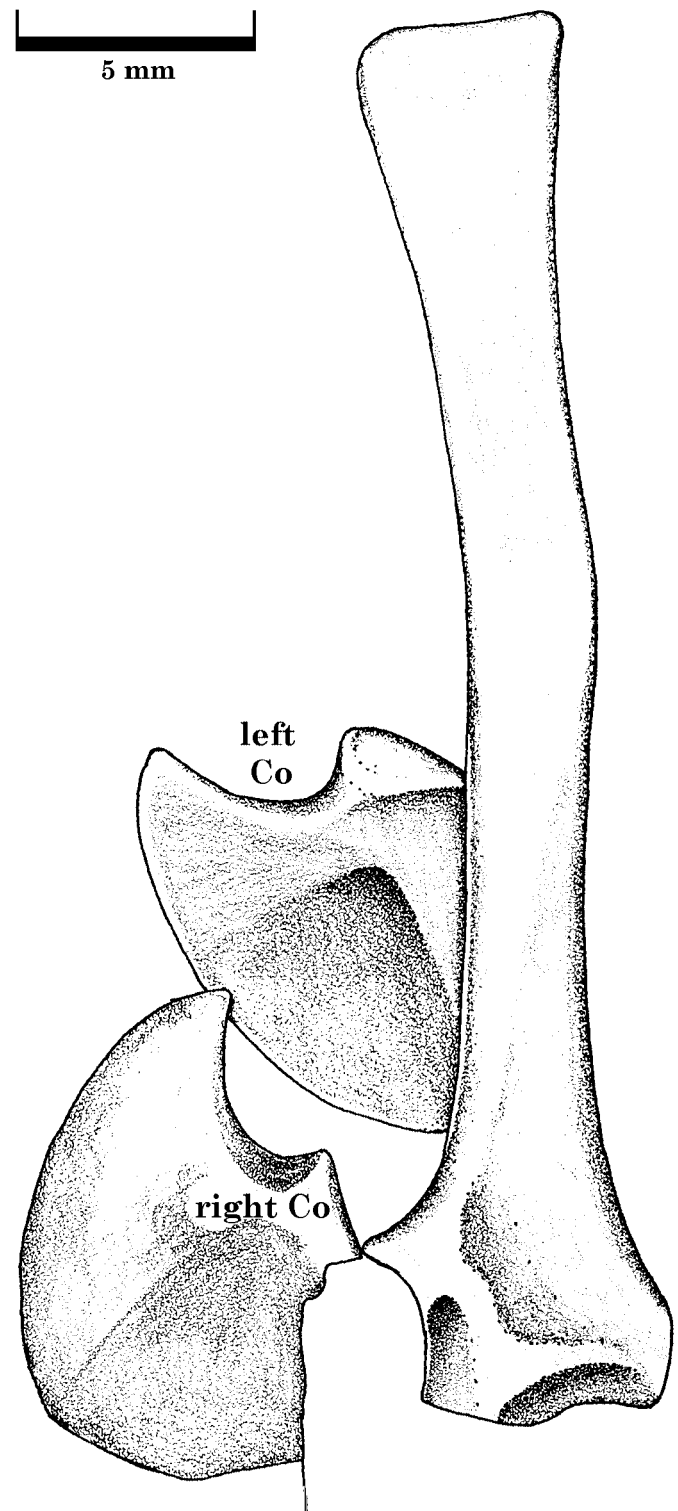


127587. The proximal width of the ulna is broad, with an anteroposterior width of 6.8 mm in NIGP 127586 and 10.3 in NIGP 127587 at the level of the lip beneath the humeral articulation. The shaft is relatively straight compared with most coelurosaurs, and is a flattened oval in cross-section. The transverse shaft diameter (2.7 in NIGP 127586 and 4.8

**Fig. 8.** *Sinosauropteryx prima*. (*a*) front limbs of NIGP 127587; (*b*) left phalanx III-1 in ventral view; (*c*) right phalanx III-1 in lateral aspect (image reversed). Co, coracoid; H, humerus; mc, metacarpal; R, radius; S, scapula; U, ulna. 1, phalanx III-4; 2, ulnare; 3, semilunate carpal; 4, radiale. Roman numerals represent digit numbers.
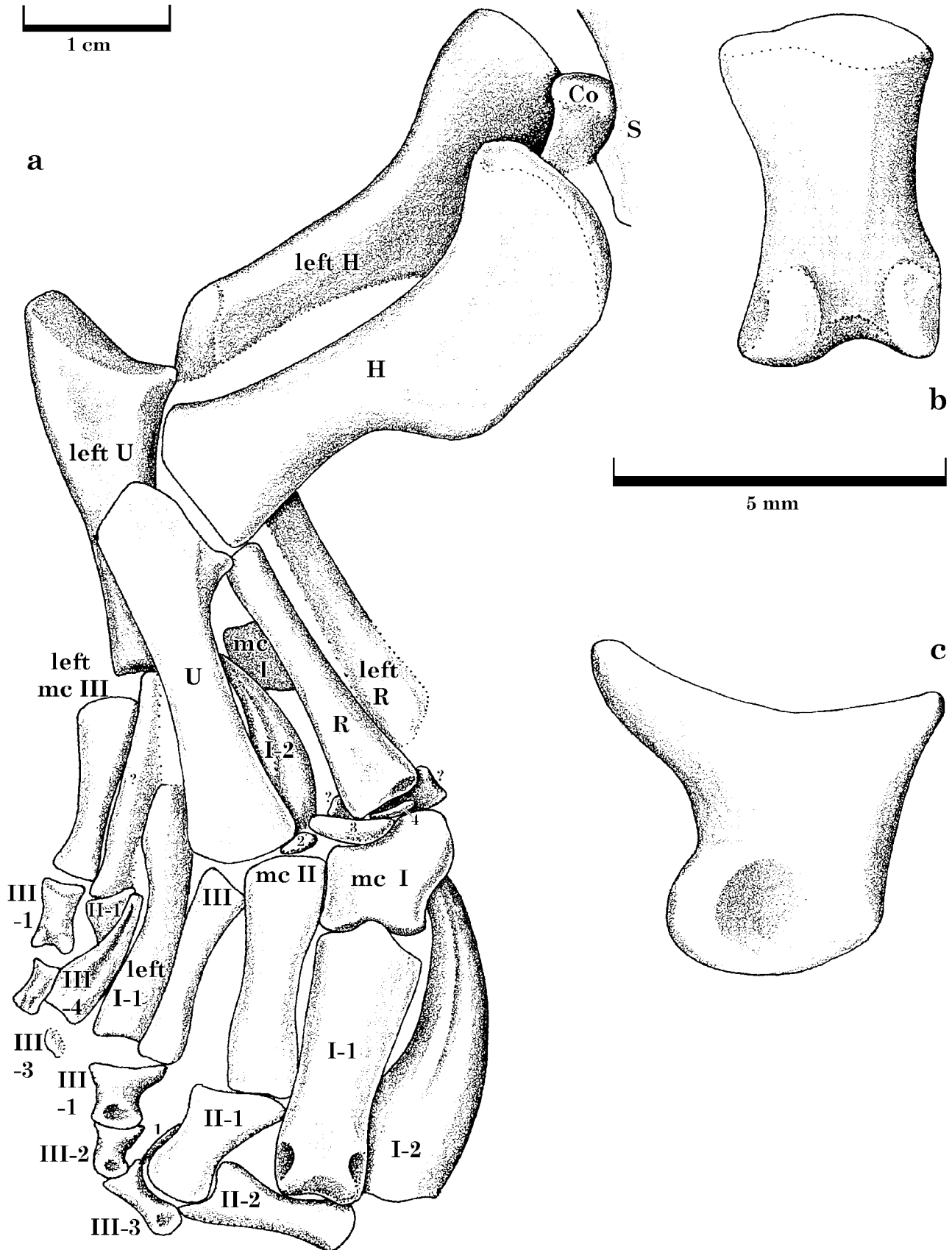
in NIGP 127587) is greater than that of the radius, although the difference is less pronounced than in advanced coelurosaurs. The distal end of the ulna is three times wider than long (NIGP 127586 is 1.1 mm in diameter anteroposteriorly, and 3.4 mm transversely).

The radius (Fig. 8) is a straight, slender element that is 57–61% of the length of the humerus. In comparison, the radius of *Compsognathus* is relatively longer at 63% of humerus length. The proximal articulation is partially obscured in both specimens. The transverse shaft diameter (2.1 in NIGP 127586 and 3.9 in NIGP 127587) is about 80% that of the ulna. The distal articular surface is a shallow, oval concavity that would have articulated with the radiale.

There are at least three carpals preserved in NIGP 127587 (Fig. 8). A small (3.0 mm wide, 0.8 mm deep) disk-like carpal is positioned below the middle of the distal end of the radius. Distally, it articulates with the first metacarpal medially and the distal carpal. This presumably represents the radiale. Another disk-like element (1.8 mm wide, 1.2 mm anteroposteriorly, and 0.7 mm deep) is found between the ulna and the second metacarpal and is best identified as an ulnare. There is also a broad, low carpal that caps the lateral half of the first metacarpal. This is preserved in both specimens. It is 5.6 mm wide in NIGP 127587 and has a proximodistal length of 1.4 mm. The same bone in NIGP 127586 is 2.9 mm across. The lateral region of this carpal extends beyond the first metacarpal and contacts Metacarpal II. The position of this distal carpal is the same as the semilunate carpal of more advanced coelurosaurs and early birds, although it does not extend as far laterally. It is comparable with the size of the same carpal in tyrannosaurids (such as TMP 91.36.500), but has more contact with the second metacarpal than is the situation in ornithomimids (Osmólska et al. 1972; Nicholls and Russell 1985; TMP 95.110.1). The proximal surface has a concave groove near the middle of the bone. Unfortunately, much of the surface is damaged, and it is not possible to determine how it articulated with more proximal limb elements. In addition to these three carpals, there are two other elements associated with the wrist of NIGP 127587. The largest one is positioned between the distomedial corner of the radius and the proximomedial extension of the first metacarpal. It is relatively large, the exposed parts measuring 3.2 mm high by 3.0 mm in width. It may represent a pisiforme that has shifted out of position, although there are other disarticulated phalanges and gastralia that have not been accounted for in that part of the specimen. On the lateral side of the radius, above the carpal that caps the first and part of the second metacarpal, there is another small bone (1.3 mm by 1.5 mm) that might be a disarticulated carpal.

Both NIGP 127586 and NIGP 127587 (Figs. 8, 9) have articulated hands, something that is lacking in the European compsognathids. What has previously been interpreted as the first metacarpal of *Compsognathus* (Ostrom 1978) is the first phalanx of digit I. The first metacarpal is short and broad (4.2 mm long in NIGP 127586 and 8.6 mm long by 8.8 mm across in 127587) and is probably the element identified as a carpal in the French specimen (Bidar et al. 1972). This bone extends proximomedially in an extensive flange, unlike any reported in other theropods. The entire lateral surface is closely appressed to the medial side of the second metacarpal.

**Fig. 9.** *Sinosauropteryx prima*. Reconstruction of hand (metacarpals (mc) and phalanges) in extensor view. Roman numerals represent digit numbers.
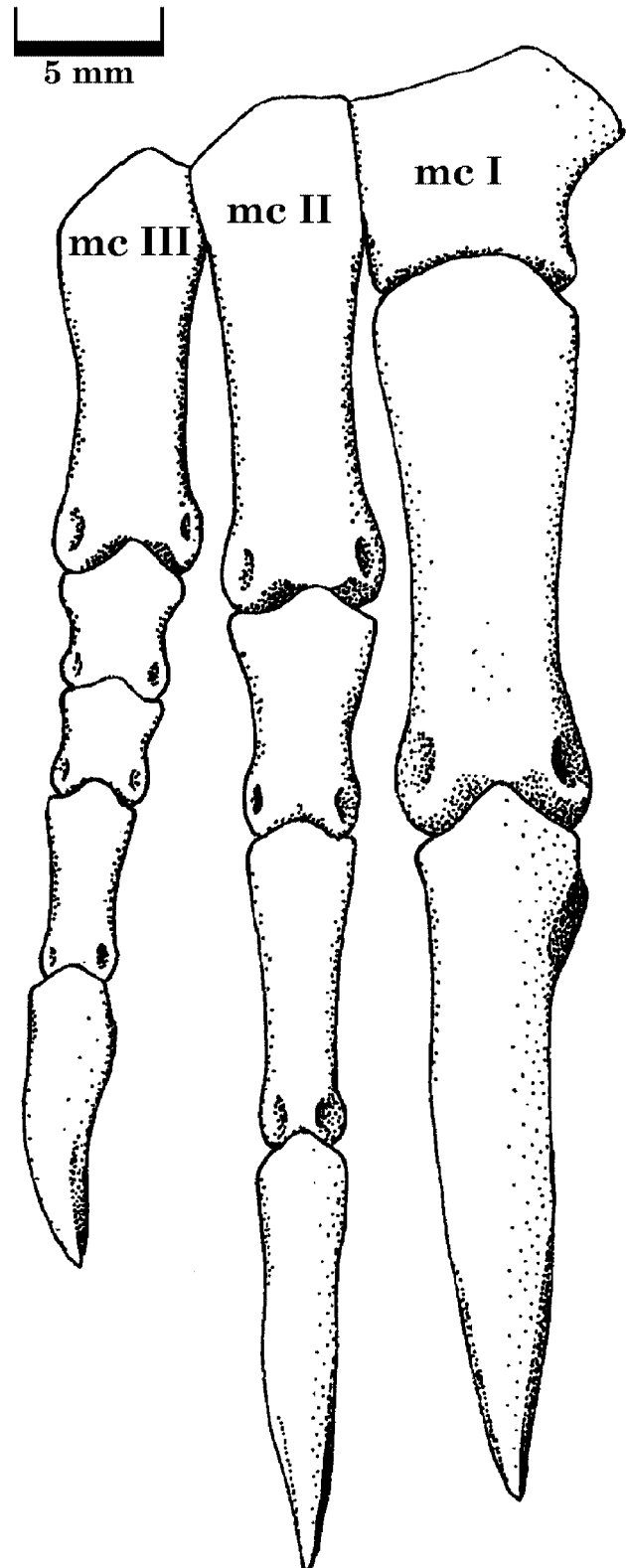
Even when the maximum length is taken from the medial side of the shaft, the first metacarpal is only 41% the length of Metacarpal II in NIGP 127586 and 49% in NIGP 127587. The second metacarpal is the longest element in the manus, but is just under half the length of the humerus. Its shaft (1.9 mm in NIGP 127586 and 4.3 mm in NIGP 127587) is much narrower than that of the first metacarpal. The third metacarpal is 81% the length of Metacarpal II in both specimens. It is the thinnest element in the metacarpus, with a shaft diameter almost half that of the second metacarpal. The medial surface of the proximal end of the third metacarpal is concave where it contacts the second metacarpal. In proximal view, the third is roughly triangular. The shaft of Metacarpal III is almost straight.

The first phalanx of digit one is large, but is easily identified because of its position. As is typical of all theropods, the colateral 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 massive, each being as long as the radius and thicker (shaft diameter of 3.5 mm in NIGP 127586 and 6.5 mm in NIGP 127587) than the shafts and the distal ends of either the radius or the ulna. The great size of the first phalanx of the first digit is a character that also seems to have been present in *Compsognathus*. The only other theropods with similar size relationships between the forearm and the first digit are alvarezsaurids like *Mononykus* (Perle et al. 1994). There are too many anatomical differences between compsognathids and alvarezsaurids to suggest close relationship, and the similarities probably represent convergences.

The first finger is longer than the other two, although it does not extend quite as far as digit II because of differences in metacarpal lengths. The third finger is the shortest (Fig. 9). Overall, the manus is 84–91% the combined lengths of the humerus and radius, and less than half the length of the foot.

All manual phalanges are narrow but deep. For example, III-1 of NIGP 127587 (Figs. 8*b*, 8*c*) is 3.4 mm wide at the proximal end, but expands proximoventrally to a depth of 5.4 mm. The penultimate phalanges are longer than the antepenultimate ones, which suggests that the hand was adapted for grasping. The shapes of the unguals, which are deep, moderately curved, and taper to sharp points, support this function. As in most theropods, ungual I-2 is the longest, and ungual III-4 is the shortest. The lengths of the unguals are 2–2.5 times their proximal depths.

The ilium (39 mm in NIGP 127586 and 67.5 mm in NIGP 127587) is conspicuously shorter than both the skull and femur, and is relatively low (22.2 mm high at both pubic and ischial peduncles in NIGP 127587), which gives the ilium its long, low appearance (Fig. 10). The ilium is long enough to cover five sacral vertebrae, as in most theropods. The height of the ilium at the level of the pubic peduncle is only a third of the total length, which compares well with most other coelurosaurs. The preacetabular and postacetabular regions of NIGP 127587 are both about 26 mm long, and the dorsal margin is shallowly convex in lateral aspect (Fig. 10). The ventral margin of the preacetabular ala curves gently anteroventrally, but does not have the distinct hooked process seen in many more advanced theropods. Preacetabular and postacetabular regions have almost the same depth. The

**Fig. 10.** *Sinosauropteryx prima*. Pelvic bones of NIGP 127586 (above) and NIGP 127587 (below) in right lateral view. Pubis (the shaft of which is covered by the right femur) and ischium diagramatically shifted into position in contact with ilium. I, ilium; Is, ischium; P, pubis.
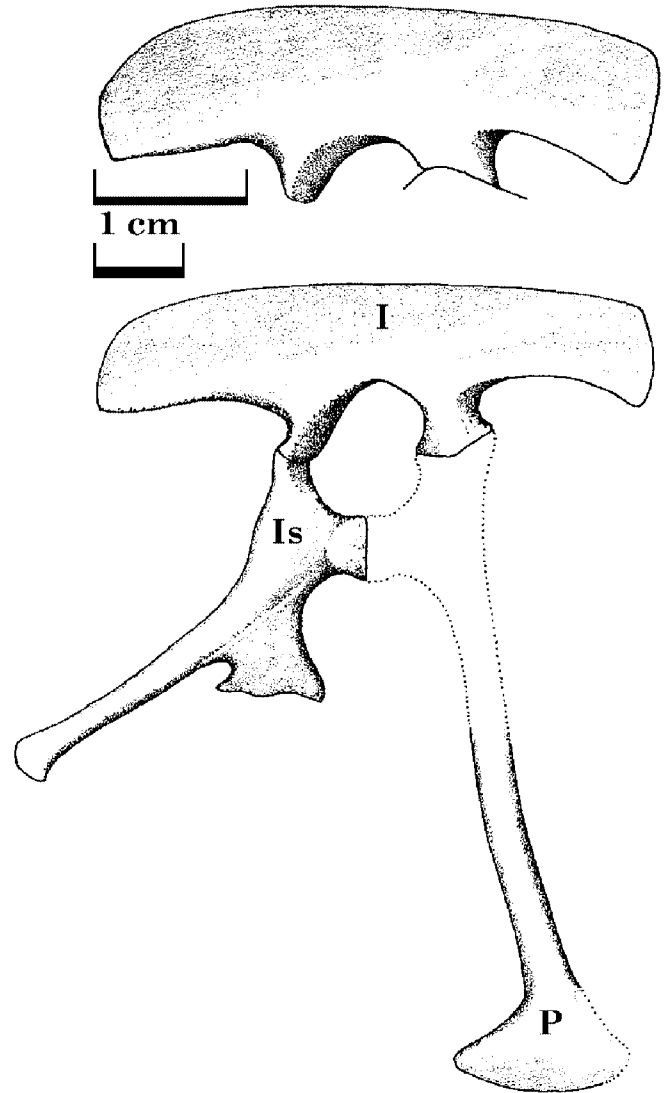


acetabulum of NIGP 127587 is 15.5 mm long anteroposteriorly, and its iliac portion is 9.5 mm high. There is no supraacetabular crest, and the pubic peduncle is only slightly taller than the ischial one.

The long but narrow pubis, which is 41.3 mm long in NIGP 127586 and 74 mm long in NIGP 127587, is oriented anteroventrally, but is closer to vertical (Fig. 10) 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* (Wellnhofer 1993), *Caudipteryx* (Ji et al. 1998), *Compsognathus* (Ostrom 1978), *Protarchaeopteryx* (Ji et al. 1998) and dromaeosaurs (Barsbold 1983), the boot expands posteriorly from the shaft of the pubis, and the anterior expansion is moderate. The lack of a significant anterior expansion of the pubic boot may be correlated with the nearly vertical inclination of the shaft.

As in *Compsognathus* and coelurosaurs, such as the

dromaeosaur *Achillobator* (Perle et al. 1999), the ischium (Figs. 1*b*, 10) is about 70% the length of the pubis. Distal to the obturator process, it tapers into a narrow shaft (3.2 mm in diameter). Similar to *Compsognathus*, there is a slight distal expansion (6 mm in NIGP 127587). The prominent, triangular obturator process in the proximal half of the pubis is characteristic of *Compsognathus* and other coelurosaurids and shows that the ischia contacted each other along the midline. The obturator process expands posteroventrally beyond a notch.

The femoral head is oriented perpendicular to the shaft (Fig. 1) and is separated from the low, ridge-like greater trochanter by a shallow depression. The lesser trochanter can be seen on the right femur of NIGP 127587 (Fig. 1*b*), where it is a tall, wing-like process separated from the shaft by a deep notch. The shaft curves gently ventroposteriorly. A 6.5 mm long ridge-like fourth trochanter can be seen a third of the way down the shaft of NIGP 127586. Although much of the surface is damaged in NIGP 127587, the distal end of the fourth trochanter is visible. The distal condyles are separated by a shallow depression, continuous with a shallow extensor groove on the anterior surface. The lateral condyle bears a prominent crista tibiofibularis that is positioned close to the distal end of the bone.

The tibia and fibula are elongate bones with a marked disparity in shaft diameters. The tibia is 15% longer than the femur in NIGP 127586 and 12% longer in NIGP 127587. There is a prominent cnemial crest on the tibia, and in NIGP 127587, the fibular condyle is well separated from it by a concavity. Although this part of the left tibia is not well preserved in this specimen, comparison with the proximal width of the head of the right tibia suggests that the fibular condyle was positioned midway between the anterior and posterior margins of the head. Not far from the proximal end of the tibia, the top of the fibular crest is preserved in NIGP 127587. Most of the crista fibularis has been lost, however. The distal end of the tibia expands to wrap around the back of the distal end of the fibula. The anterior surface of the distal end is shallowly concave rather than flat.

The broad proximal end of the fibula is only shallowly concave on the medial surface. The proximal end of the fibula of NIGP 127586 is 6.8 mm, which is about 80% of the anteroposterior length of the proximal end of the tibia. The fibular shaft tapers until it is only about a third of the transverse shaft width of the tibia. Distally, it expands moderately again where it overlaps the anterolateral expansion of the tibia and contacts astragalus and calcaneum. The region of the crista tibialis cannot be seen in either specimen.

The astragalus and calcaneum (Fig. 11) are present in both specimens, but are most clearly seen in NIGP 127587. Neither bone is fused to either the tibia or each other. In contrast with the situation reported in *Compsognathus* (Ostrom 1978), the astragalus of NIGP 127587 has a high ascending process. The total preserved height of the astragalus is 27.2 mm. Above the top of the ascending process, the tibia is damaged, suggesting that the ascending process may not be complete. The total height of the astragalus is, therefore, at least 25% of the length of the tibia. This is the height that is expected for a coelurosaur. Only the width of the astragalus can be seen in NIGP 127586, where both astragali are preserved only in section. As pointed out by



**Fig. 11.** *Sinosauropteryx prima*. Specimen drawing of right ankle of NIGP 127587 in anterolateral view. Cross-hatching represents broken bone. a, astragalus; ap, ascending process; c, calcaneum; dt, distal tarsal; mt, metatarsal; T, tibia. Roman numerals represent digit numbers.
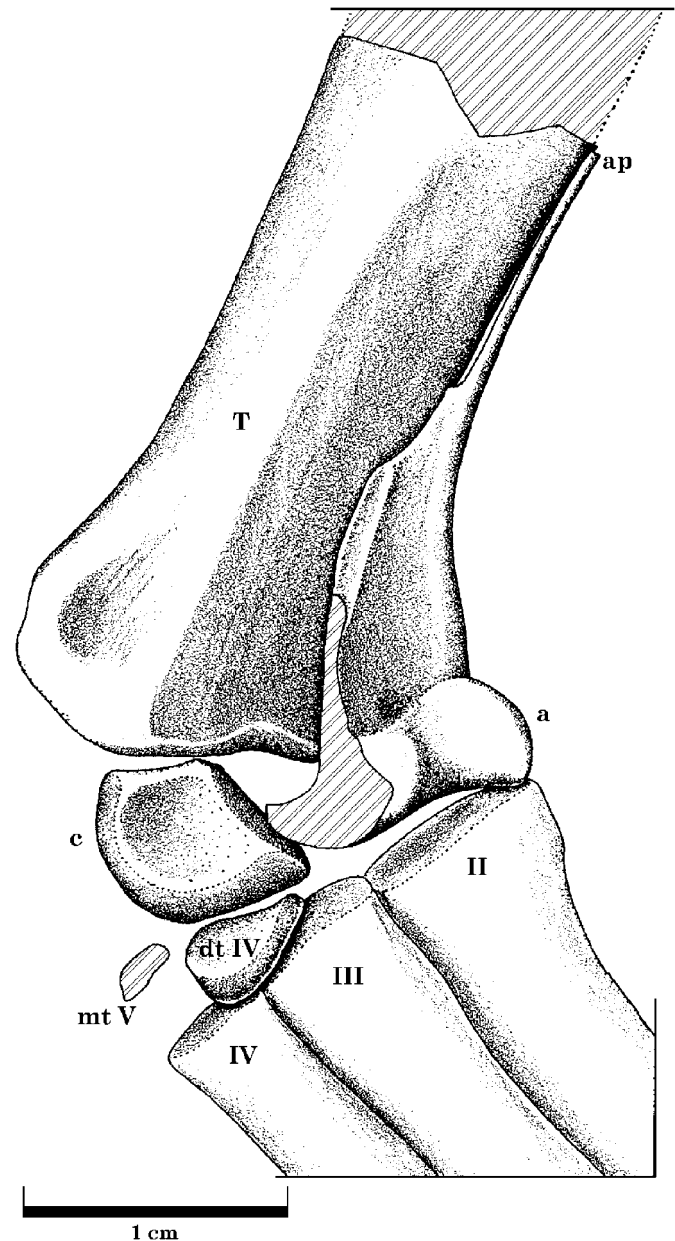
Ostrom (1978) for *Compsognathus*, this suggests that the astragalus only covered 70% of the distal width of the tibia. The distal condyles are well separated from each other and are positioned mostly on the flexor surface of the astragalus. There is no horizontal groove across the face of the condyles, such as found in allosauroids (Madsen 1976; Currie and Zhao 1993), and the depression in the ascending process above the condyles is shallow. Because the ascending process is preserved mostly in lateral view in NIGP 127587 (and is covered by the tibia in NIGP 127586), its shape and orientation are unknown. The lateral edge of the ascending process has a longitudinal facet, however, where it contacted the fibula.

Both specimens have calcanea, and it is clear that these were narrow, disk-like bones. The calcaneum is preserved in section in NIGP 127586 (Fig. 1) and in lateral aspect in NIGP 127587 (Fig. 11). It appears to have been relatively thin mediolaterally and is lower than it is anteroposteriorly long. The dorsal surface is divided into two concavities for articulation with the tibia behind and the fibula in front.

A left distal tarsal is preserved in section between the astragalus and third metatarsal of NIGP 127586 (Fig. 1). Both the third and fourth distal tarsals seem to be preserved in the somewhat disarticulated right ankle. Much of the relatively flat fourth distal tarsal is preserved between the calcaneum and the metatarsus of NIGP 127587 (Fig. 11). It is centred over the contact between the third and fourth metatarsals.

There are five metatarsals, but as in other theropods and early birds, the first is reduced to little more than a distal articular condyle, and the fifth is reduced to a proximal splint. Metatarsal I is positioned on the posteromedial corner of the second metatarsal, well above the distal end. Metatarsals II, III, and IV are closely appressed and elongate (Figs. 1a, 1b), but are not coossified. In relation to the lengths of the femur and tibia, the metatarsus is not particularly long considering the small size of *Sinosauropteryx*. The metatarsus to femur ratio is about 75% in the two Nanjing specimens, which is comparable with *Archaeopteryx* (77%), *Compsognathus* (76%), and other coelurosaurs in that size range. The cross-section of the third metatarsal is triangular, but is not constricted the way it is in an arctometatarsalian foot (Holtz 1994). The second and fourth metatarsals, which are almost the same length, do not contact each other. As in other theropods, the head of the fifth metatarsal extends above the head of the fourth metatarsal to the level of the proximal surface of the distal tarsals (Figs. 1, 11). Metatarsal V is 8.1 mm long in NIGP 127586, which is 22% the length of the fourth metatarsal.

Pedal phalanges are conservative in number and morphology. Digit I is relatively short, and the total length of the two phalanges is less than the length of the first phalanx of the third pedal digit. The second toe is 37.4 mm long in NIGP 127587, the third is 45.5 mm, and the fourth is 35.5 mm.

Like *Compsognathus* (Ostrom 1978), NIGP 127587 has stomach contents preserved within the rib cage. This consists of a semi-articulated skeleton of a lizard, complete with skull. Numerous lizard skeletons have been recovered from these beds, but have yet to be described. Another specimen of *Sinosauropteryx* (GMV 2124) has in its stomach (Ji and Ji 1997b) the remains of a mammal, which are also under study.

Low in the abdomen of NIGP 127587, anterior to and slightly above the pubic boot, lies a pair of what appear to be small eggs (Chen et al. 1998). 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. These oval structures (37 × 26 mm) are dark in colour and have a thin, shell-like covering. They are being described in a separate paper.

*"Feathers"*

All of the specimens of *Sinosauropteryx* (Ji and Ji 1996, 1997b; Chen et al. 1998) are covered with integumentary structures that have been variously referred to in the popular press (i.e., Morell 1997; Currie 2000) as "feathers" or "protofeathers." In NIGP 127586 (Fig. 1), the integumentary structures extend along the back half of the skull (Fig. 12b), the neck (Figs. 12d, 12e), the back, the hips and both sides of the tail. There are small patches on the side of the skull behind the quadrate and paroccipital process, anterior to the articular, and below the back of the mandible (Fig. 12a). Others can be seen behind the right humerus and in front of the right ulna. In NIGP 127587 (Figs. 1, 13), feather-like structures can be seen along the dorsal surface of the neck and back, and along both sides of the tail. There is a small patch lateral to the left ribs and several areas on the left side of the tail lateral to the vertebrae.

In *Sinosauropteryx*, 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 thickness of muscle and other soft tissues. Overlying integumentary structures would have been destroyed when the soft tissue decomposed. This separation is inconsistent with the interpretation by Ruben et al. (presented in Gibbons 1997) that the integumentary structures represent collagen fibres.

The integumentary structures were soft and pliable, and semi-independent of each other (Figs. 12, 13). The overwhelming majority of them are oriented both away from the body and posteriorly (Figs. 1, 12b, 12d, 12e, 12g, 13b, 13c). The integumentary structures appear to clump along the tail of the smaller specimen (Fig. 1), but this is an artefact of the uneven splitting plane between NIGP 127586 and NGMC 2123. Both NIGP 127586 and NIGP 127587 were lying in the water of a lake between death and burial, so the normal orientation of the integumentary structures would have been altered. The orientation in the fossils is consistent with the idea that the integumentary structures would have been smoothed down against the body in the living animals like feathers in birds and hair in mammals. In the cervical region of NIGP 127586 (Fig. 12e) and over the shoulder of NIGP 127587 (Fig. 13b), series of parallel structures overlap other series that lie at different angles.

Individual integumentary structures are easier to see in the tail, where the body was narrower and the number of structures piled on top of each other was fewer. The structures have variable thicknesses. Large ones commonly have a diameter of 0.2 mm, but smaller ones are considerably narrower than 0.1 mm. A few in the shoulder region have diameters that exceed 0.3 mm, but this may be an artefact of several larger ones lying against each other. Under magnification, the margins of the larger structures are darker along the edges but light medially, which suggests that they may have been hollow. This is consistent with the cross-sections of round hollow structures in the integument of the third specimen of *Sinosauropteryx* (Ji and Ji 1997b). Overall, the integumentary structures are rather coarse for such a small animal, and the

**Fig. 12.** *Sinosauropteryx prima*. Camera lucida drawings of integumentary structures in NIGP 127586 (right side exposed). Back of skull at jaw articulation (*a*), along the margin on top of the skull (*b*), over first six cervical vertebrae (*d*), at base of neck and front of thoracic region (*e*), above scapula (*f*), and over distal caudals (*g*). C) scale bar for *b*, *d*, *e*, and *f*. Cross-hatching represents broken bone. art, articular; pop, paroccipital process; q, quadrate; qj, quadratojugal; sur, surangular; v, vertebra; 2, region of fine integumentary structures.
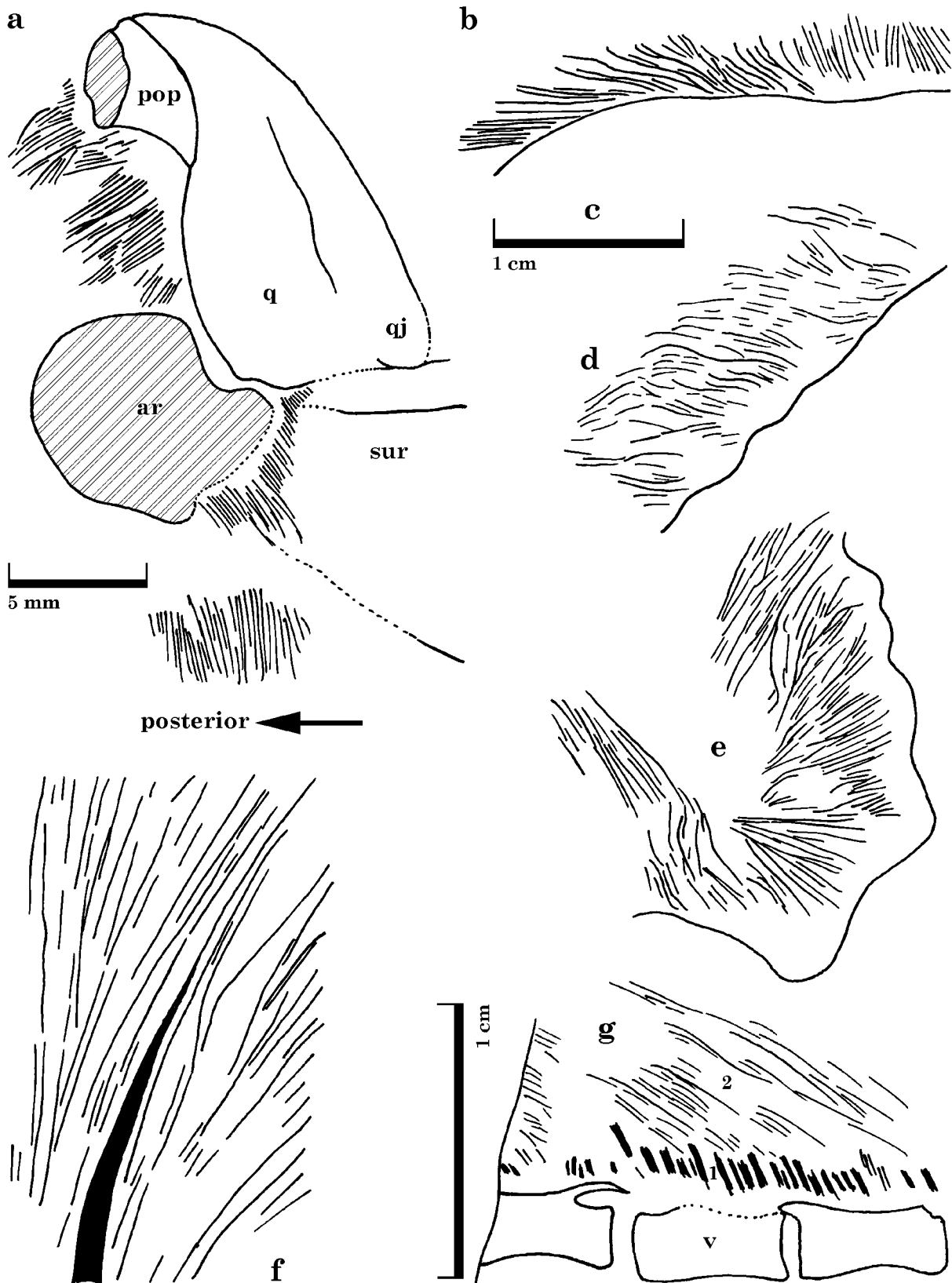
**Fig. 13.** *Sinosauropteryx prima*. Camera lucida drawings of integumentary structures in *Sinosauropteryx*. (*a*) integumentary structure above fifth cervical vertebra in NIGP 127586 (proximal end of structure to right, distal to left); (*b*) integumentary structures above dorsal vertebrae 15–17 in NIGP 127587, showing layering; (*c*) integumentary structures ventral to the 19th and 20th caudal vertebrae of NIGP 127587. cv, caudal vertebra; hs, haemal spine; ns, neural spine.

thickest strands are much thicker than the hairs of the vast majority of small mammals. The mixture of thick and thin strands close to the body, the increased presence of thinner strands distally, the fact that the thicker strands are positioned close to the body and are normally oriented at higher angles from the body than more distal strands (Fig. 12*g*), the presence of areas where many of the finer strands lie adjacent and parallel to each other (even kinking together in a few places), and the tendency of finer filaments to angle away on both sides from thicker structures (Fig. 13*a*) all suggest a feather-like structure with central shafts and plumulaceous barbs.

Unfortunately, the integumentary structures are piled so thick that it has not been possible to isolate a single one for examination. Comparison with birds from the same locality (see for example figures in Ackerman 1998; Chiappe et al. 1999) shows that the same problem exists with identifying individual feathers (other than the flight feathers) and components of feathers in avian specimens. We feel the evidence suggests that the integumentary structures consist of parts comparable with the rachis and barbs of a bird feather, but there is no evidence of barbules and hooklets. Structurally, the integumentary structures seem to most closely resemble plumules of modern birds with 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 (Ostrom 1978).

The integumentary structures are of different lengths in different parts of the body. Two measurements were taken for length, one along the axis of the structure and the other the height that the distal tip reaches above or below the closest skeletal element. In NIGP 127586, integumentary structures are first seen on the dorsal surface of the skull in front of the orbit. The skull is partially disarticulated, and sediment still covers the snout region, so it is possible the integumentary structures extended more anteriorly. The most rostral integumentary structures are 5.5 mm long and extend about 4 mm above the skull. At the back of the skull near the left side of the head, they have increased to 9.1 mm and extend 8.2 mm from the bone. There are several tufts of 2 mm-long integumentary structures preserved at the back of the skull, behind the distal end of the paroccipital process and the quadrate and anteroventral to the articular (Fig. 12*a*). The structures increase to a length of 13.4 mm above the fourth cervical vertebra, but decrease slightly to 12.7 mm over the eighth neck segment. At the base of the neck, the integumentary structures are difficult to measure because there is a sharp bend between the neck and the body (Fig. 12*e*), but 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
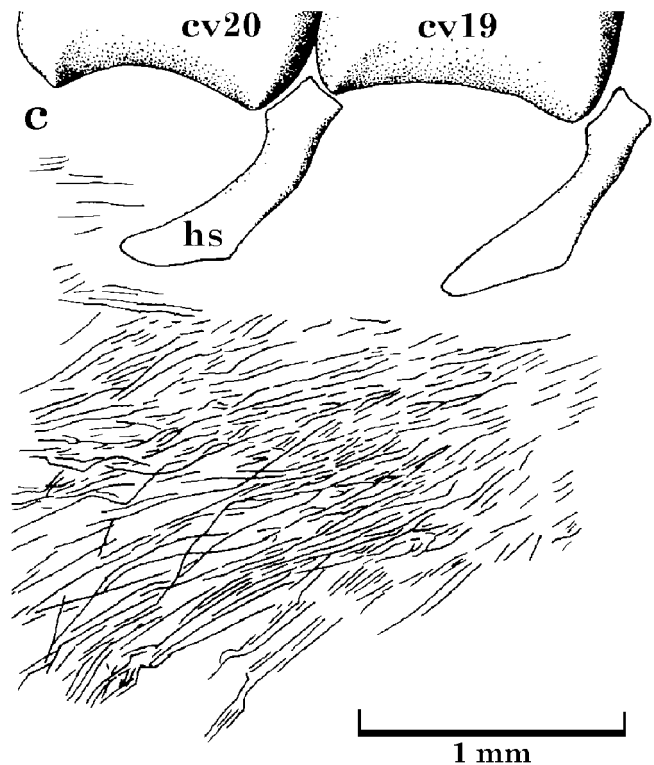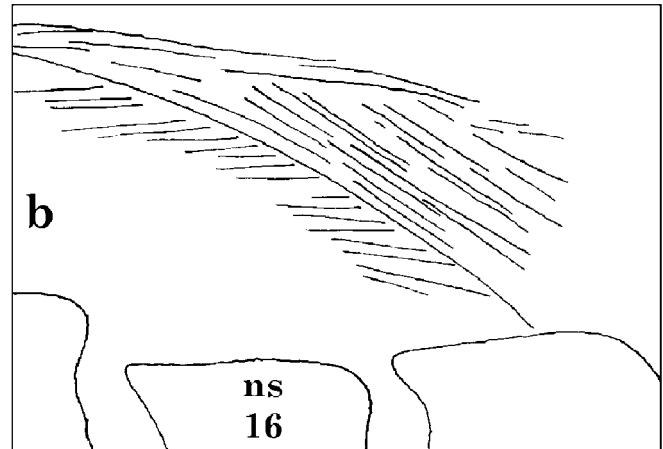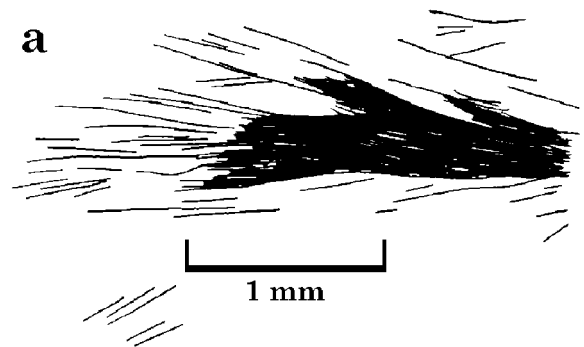
to 16 mm dorsal to the ilium. The longest integumentary structures seem to have been above the base of the tail. Close to the vertebrae, individual integumentary structures cannot be seen, either because they are too densely packed, or because other tissues are involved in the composition of the continuous black surface. The tips of the structures extend 23 mm above the neural spine of the seventh caudal vertebra, and the angles of their axial planes suggest they were more than 30 mm long. From this point backwards, they decrease steadily in size to the end of the tail (Fig. 12g), where they are 10 mm long above caudal 52, and the integument as preserved is 5.6 mm thick. Ventral to the tail, the integumentary structures are short near the pelvis, but increase to a length of 15 mm below caudal 25, where they extend 9 mm below the haemal spine. This is close to the lengths in the same region dorsal to the tail. But more distally along the tail, integumentary structures decrease more rapidly on the lower side of the tail than on the upper. By the 47th caudal the ventral structures are 4.2 mm long, which is about half the length of the dorsal ones in the same region. Behind the humerus, integumentary structures are 2.5 mm long. Those behind the left tibia and fibula are only visible through a small hole in the matrix, and all that can be said at present is that they would have been more than a millimetre long. 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 cervical 4, at least 35 mm over the scapulae, at least 40 mm over caudal 27, 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.

### Other soft body part preservation

A region of dark pigmentation in the abdominal region of the smaller specimen might represent stomach contents. However, this structure in NIGP 127586 has been interpreted in another way and merits careful description. Ruben et al. (1997) reported that the dark stain in the abdominal region of this specimen (and its counterpart NGMC 2123) represents the supposed liver. In the photographs of the part and counterpart of the specimen, the stain has a well-defined, rounded anterior margin. The dark, carbonized matter does seem to have substance and consistency different from those of the surrounding matrix. In NIGP 127586, the ribs of the left side are beneath the ribs of the right side. The carbonized layer clearly covers the medial surfaces of the left ribs. Most of the right ribs ended up in the counterpart block (NGMC 2123), but their positions are preserved as impressions in NIGP 127586. The exposed parts of the right ribs that remain are not covered by the carbon film. However, the black substance lines the inside of the rib impressions, showing that it covered the medial walls of the right ribs. There can be no doubt, therefore, that the carbonized layer

was something inside the body cavity and that it remained inside the rib cage as the carcass decomposed and the body walls collapsed. The overall shape of the stained area is rather amorphous. It is bounded above by the vertebrae and rib heads and disappears into the matrix. Ventrally and posteriorly, the black layer thins out, gradually turns brown and fades away. There are no precise edges. Anterodorsally, the stain is interrupted by a break in the specimen. When the specimen split into right and left sections, it did not break on the same plane everywhere. A small section in this region broke on a different plane, leaving a raised chip of rock in NIGP 127586 and a depressed area (where the chip came from) in NGMC 2123. The black carbonized stain presumably continues forward inside the chip in NIGP 127586. The anterior margin of the stain must also end somewhere inside the rock chip, because there is no heavy carbon film in front of it. There is also a vertical crack running through this region in both specimens. This has been filled in with plaster or cement in both NIGP 127586 and NGMC 2123, and the damaged area has been coloured to match the carbonized stain. Although it appears in the photographs as if the stain has a well-defined rounded margin, examination of the specimen (both part and counterpart) clearly shows that this is an artefact that was produced anterodorsally by the chipped surface and anteroventrally by a crack filled with coloured cement.

## Discussion

The two *Sinosauropteryx* specimens in the Nanjing Institute of Geology and Palaeontology are both relatively young animals. They are smaller than the third known specimen (Ji and Ji 1997b), and both show the bone texture expected of immature animals. Another sign of immaturity is the fact that the neural arches are not fused to the centra in NIGP 127586. Even though the sutures are still visible between the neural arches and centra in NIGP 127587, they were fused. The carpals are well ossified in NIGP 127587, and the specimen was of reproductive age (as evidenced by the eggs), which suggests that the specimen was a young adult.

*Sinosauropteryx* is different from *Compsognathus* primarily because it has shorter cervical ribs and a shorter but more robust arm. It is also supposedly different in lacking opisthocoelic cervical centra and caudal transverse processes, and in having integumentary structures. It is possible that differences in preservation account for the apparent differences between the two taxa. Coelurosaurs do not normally have opisthocoelic cervical vertebrae, and do have caudal transverse processes, suggesting that better preserved specimens of *Compsognathus* may show amphiplatyan cervical centra and caudal transverse processes. The absence of integumentary structures in the European specimens is negative evidence and should not be taken too seriously.

Compsognathids are readily identified by their short, distally expanded dorsal neural spines, hair-like cervical ribs, and huge olecranon processes. Amongst theropods, the length of the olecranon compared with the overall length of the ulna is only greater in alvarezsaurids, such as *Mononykus* (Perle et al. 1994). Compsognathids are considered basal coelurosaurian theropods by most workers (Hutchinson and Padian 1997).

Coelurosaurian synapomorphies include reduction or loss of the ischial boot, the presence of a triangular obturator process on the ischium, and the development of an ascending process of the astragalus that is more than a quarter the length of the tibia. Other characters used to diagnose Coelurosauria have included the reduction of the ischium to 70% or less of the length of the pubis and the presence of an expanded circular orbit, but these are at least partially size-related. Many large coelurosaurs, including ornithomimids, oviraptorids, and tyrannosaurids, have ischia that are more than 70% the length of the pubis, and smaller, more primitive theropods such as *Coelophysis* (AMNH 7224) and *Syntarsus* (Raath 1969) have ischia that are less than two-thirds the length of the pubis. There is even one dromaeosaurid, *Achillobator*, which has an ischium that is slightly more than two-thirds the length of the pubis (Perle et al. 1999). Another consideration is that smaller, more basal theropods like *Eoraptor* and *Coelophysis* have large round orbits, whereas large coelurosaurs, including all adult tyrannosaurids, have keyhole-shaped orbits. Orbit shape is highly variable (Chure 2000), but round orbits are generally found only in the smaller animals, both juveniles of large species and taxa of small adult size. *Sinosauropteryx* and *Compsognathus* both have weak expansions at the distal ends of their ischia, so loss of the ischial boot must now be considered a synapomorphy of the Maniraptoriformes. *Sinosauropteryx* also has more than 15 caudal vertebrae with transverse processes, so this is another character that must be transferred to the Maniraptoriformes rather than the more inclusive Coelurosauria.

Integumentary structures probably covered most of the body of living *Sinosauropteryx*, as evidenced by the density of the covering dorsal to the body and by the few random patches of integumentary structures that can be seen in other regions of the existing fossils. In the birds found at the same site (and all *Archaeopteryx* specimens), feathers are only preserved as a corona around the body. To be preserved, it is important for the keratinous feathers to be surrounded by and in direct contact with the encasing sediments. Feathers lying against the skin and other tissues were generally destroyed as the flesh decomposed. The exceptions on the flanks of the body and tail of NIGP 127587 may have been separated from the body by thin layers of sediment.

Integumentary structures have been reported with both specimens of the *Compsognathus* (Bidar et al. 1972; von Huene 1901), although the interpretations have been questioned in both cases (Ostrom 1978). In the German specimen, there was supposedly a patch of skin over the abdominal region. The French specimen included in the region of the forearm some strange markings that were originally identified as a swimming appendage formed of either dermal bone or thick skin (Bidar et al. 1972). Even if it is present, the swimming appendage is not well enough preserved to be positively identified. The identification of these structures as integumentary is questionable (Ostrom 1978), and there is nothing on the Chinese specimens to support the presence of such structures in compsognathids. Although the evidence for feathers in *Compsognathus* was avidly sought (Ostrom 1978) without success, the conclusion that there were no feathers on the German specimen of *Compsognathus* is based on negative evidence and cannot eliminate the possibility that they existed.

The integumentary structures of these dinosaurs are extremely interesting regardless of whether they are considered as feathers or something else. Cladistic analysis, notwithstanding arguments to the contrary (Feduccia 1996), at present overwhelming favours theropod dinosaurs as the direct ancestral stock for birds (Gauthier 1986; Chiappe 1995; Fastovsky and Weishampel 1996; Padian and Chiappe 1997; Forster et al. 1998; Gee 1999; Sumida and Brochu 2000). Assuming this is true, the integumentary structures of *Sinosauropteryx* can be used to test the many hypotheses that have been proposed concerning feather origins. Three main functions have been hypothesized for the initial development of feathers — display, aerodynamics, and insulation.

Feathers may have appeared first as display structures (Mayr 1960; Prum 1999). However, the density, distribution, and relatively short lengths of the integumentary structures of *Sinosauropteryx* suggest that they were not used for display. It is conceivable, however, that both specimens in Nanjing represent females, 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. It is suspected that other dinosaurs from the Jehol fauna may have used feathers for display, however (Ji et al. 1998).

Some authors have assumed that feathers arose directly for aerodynamic reasons (Parkes 1966; Feduccia 1996) and were subsequently adapted as insulators when birds became warm-blooded. Chinsamy et al. (1994) undertook histological studies that suggested to them that at least some early birds were ectothermic, but their arguments were countered by de Ricqlés et al. (1999). However, the integumentary structures of *Sinosauropteryx* and other "feathered" theropods have no apparent aerodynamic characteristics, and if they are representative of what covered the ancestral stock of birds, then feathers must have developed for some reason other than flight. The argument that feathers are too complex to have evolved for any function other than an aerodynamic one (Feduccia 1996) is circular reasoning in that feathers would have been preceded evolutionarily by less complex structures. It is unlikely that something as complex as a feather could evolve in one step (Padian 2001), and many animals glide and even fly with much simpler structures. Even birds secondarily simplify feathers when airborne flight ceases to be their prime function and produce structures that are intermediate between reptilian scales and feathers (McGowan 1989). The multibranched integumentary structures of the Chinese compsognathids are relatively simple, but are suitable for modification into the more complex structures required for flight.

The evolution of feathers for insulation follows two distinct lines of reasoning. One possibility is that feathers evolved as heat shields to screen and shade the body from the sun's rays (Regal 1975). This hypothesis assumes that the protofeathers were wide, pennate structures that could be raised and lowered to shade the skin from insolation, while permitting air circulation underneath. The Chinese compsognathids, on the other hand, suggest that protofeathers may have formed a dense, pliable covering over much of the body. Although this may have

been effective in protecting the body from solar radiation in warm weather, it would also have been effective in preventing an ectothermic theropod from rapidly warming up by basking in the sunshine.

The most prevalent theory in recent years assumes that small theropods were endothermic and used feathers to maintain high body temperatures (Ostrom 1974; Bakker 1975; Paul 1988). The presence of dense integumentary structures may suggest that *Sinosauropteryx* was endothermic, and that heat retention was the primary function for the evolution of feathers (Ewart 1921; van Tyne and Berger 1976; Young 1950). Recent arguments (Feduccia 1996) against the concept of dinosaurs having feathers specifically target a proposal that these animals had "down feathers." The Chinese compsognathids, therizinosaurids, and dromaeosaurids seem to have had integumentary structures that were more complex than mammalian hair, in having at least two components (rachis and barb). Nevertheless, they are clearly 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 mammalian hair is. It cannot be determined whether or not the integumentary structures were arranged in pterylae, 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 (Feduccia 1996), especially if the apteria are part of a mechanism for dispersing excess heat. Finally, the aerodynamic capabilities of bird feathers are not compromised by the previous evolution of less complex protofeathers that had some other function, such as insulation.

In this context, Prum (1999) proposed a model for the origin and evolutionary diversification of feathers. The integumentary structures of *Sinosauropteryx* match his model's predictions of the form for early feathers (Xu et al. 2001).

Techniques worked out to study fossil feathers (Brush 1993; Davis and Briggs 1995) 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 developed in ancestral theropod dinosaurs, possibly for insulation.

Ruben et al. (1997) reported the preservation of liver tissue in NIGP 127586 and NGMC 2123, the smaller specimen of *Sinosauropteryx*. Their paper was published before they had an opportunity to see either of the specimens, and the only evidence they had for the presence of a liver was the position and shape of the dark stain that could be seen in photographs. As shown in the descriptive section, the front margin of the stain is an artefact. Even if it had been a real edge, it is unreasonable to think that the liver would have maintained its position and shape as the specimen decomposed and collapsed into two dimensions. It is conceivable that such a thing might happen, but it is impossible to show that no distortion occurred in the *Sinosauropteryx* specimen. The claim for preserved liver tissue was repeated in a second paper (Ruben et al. 1999) on *Scipionyx*. In this case, the shape of the "liver" could not be seen without the aid of ultraviolet light, and even then, the shape is vague. As in the case of *Sinosauropteryx*, the skeleton of *Scipionyx* had collapsed into two dimensions after decomposition, making

it unlikely that any soft structures inside would have maintained their original shapes. *Scipionyx* does show evidence of some soft anatomy, including traces of the trachea and the large intestine (Dal Sasso and Signore 1998). Tracheal rings are often supported by cartilage, however, and are more amenable for preservation. The walls of the intestine are not preserved, although their inner surfaces left impressions on the "steinkern" (personal observations, 1999). The "muscle fibres" reported (Dal Sasso and Signore 1998) from the base of the tail look similar to the integumentary structures of *Sinosauropteryx* and occupy a more external position than would be expected for muscle tissue. The claim that "diaphragmatic muscles" are also preserved in *Scipionyx* (Ruben et al. 1999) is based on a series of faint scratches in the specimen that could be explained in many other ways.

In summary, the *Sinosauropteryx* specimens provide valuable new information on the anatomy of basal coelurosaurs. This animal corrects a number of misconceptions concerning the closely related *Compsognathus*. Integumentary structures are preserved in both the specimens from Nanjing. Although most are preserved in a "corona" around the fossilized skeleton, enough are preserved on other parts of the body to show that these structures clothed most of *Sinosauropteryx*. Preserved mostly as multi-layered carbonized traces, it is difficult to see the detailed structure. However, the evidence does favour the interpretation that each has a simple branching structure similar to that reported in *Microraptor* (Xu et al. 2000). Feathers and feather-like structures are widely distributed amongst non-avian theropods, and have now been reported in oviraptorosaurs (Ji et al. 1998; Barsbold et al. 2000), therizinosaurs (Xu et al. 1999*a*), and dromaeosaurids (Xu et al. 1999*b*, 2000, 2001; Ji et al. 2001). Given the overwhelming evidence supporting the hypothesis that birds are the direct descendents of coelurosaurs, further investigation of the integumentary structures of *Sinosauropteryx* will likely provide some insight into the evolution of feathers.

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