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A New Giant Compsognathid Dinosaur with Long Filamentous Integuments from Lower Cretaceous of Northeastern China

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Abstract: A new compsognathid dinosaur, *Sinocalliopteryx gigas* gen. et sp. nov., is erected based on a complete skeleton from the Early Cretaceous Yixian Formation of western Liaoning, northeastern China. It shares the features with *Huaxiagnathus orientalis* in having a manus as long as the humerus plus radius, very large and subequally long manual claws I and II, and reduced olecranon process on the ulna. But it differs from *Huaxiagnathus orientalis* in having the much large size, a very long maxillary process of premaxilla not extending the vertical level of the maxillary antorbital fossa, and the proportionally longer ulna and so on. *Sinocalliopteryx gigas* gen. et sp. nov. represents the largest species among the known compsognathid dinosaurs, suggesting the tendency of the body enlargement in compsognathids to some extent. The long filamentous integuments are attached to the whole body of this compsognathid, confirming that such integuments evolved firstly in the basal coelurosaurs. This new giant compsognathid was a fierce carnivorous theropod, as shown further by an incomplete dromaeosaurid leg inside its abdominal cavity.

Key words: Compsognathidae, *Sinocalliopteryx* gen. nov., giant skeleton, filamentous integuments, Yixian Formation, Early Cretaceous, western Liaoning

1 Introduction

Compsognathids are a small group of theropods commonly placed at the basal position within Coelurosauria (Sereno, 1999; Rauhut, 2003; Holtz and Osmólska, 2004; Norell and Xu, 2005). Recently new findings make the number of valid compsognathid genera increase rapidly. This group contains the relatively complete *Compsoganthus* (Ostrom, 1978; Bidar et al., 1972) and *Juravenator* (Göhlich and Chiappe, 2006) from the Upper Jurassic of West Europe, and *Sinosauropteryx* (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001) and *Huaxiagnathus* (Hwang et al., 2004) from the Early Cretaceous Jehol Biota of northeastern China. Two more incomplete Early Cretaceous *Aristosuchus* (England) (Naish, 2002) and *Mirischia* (Brazil) (Martill et al., 2000; Naish et al., 2004) have also been included within this group. The filamentous integuments in *Sinosauropteryx* (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001) indicate that such integuments evolved firstly in the basal coelurosaurians (i.e., compsognathids), and the presence of protofeathers or pennaceous feathers may be suggested as one of the synapomorphies of Coelurosauria. But the integuments of the newly reported *Juravenator* lacks the feather-like structures along its tail, suggesting that the evolution of the filamentous integuments might be more complex than previously thought (Göhlich and Chiappe, 2006). Here we report a giant compsognathid, *Sinocalliopteryx gigas* gen. et sp. nov., with exceptionally complete skeleton and well-developed filamentous integuments, from the Early Cretaceous Yixian Formation of western Liaoning, northeastern China. This new finding provides us not only much information on the anatomical features of compsognathids, but also more evidence for the presence of the filamentous integuments within compsognathids.

The Early Cretaceous Jehol Biota of northeastern China yields several different non-avialan coelurosaurian theropods, some of which possess filamentous integuments or feathers of modern aspect (Norell and Xu, 2005). Except the therizinosauroid *Beipiaosaurus* (2.2 m long) (Xu et al., 1999) and the tyrannosauroid *Dilong* (2 m long) (Xu et al., 2004), almost all other known theropods in the Jehol Biota

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are less than or roughly 1 m in length. But this new compsognathid from western Liaoning is about 2.37 m long from snout to tail tip. Obviously, it represents the longest coelurosaur among the known Jehol theropods. On the other hand, the new fossil is also the largest, in comparison with other compsognathids. It is more than twice as long as *Compsognathus* (Ostrom, 1978; Bidar et al., 1972), *Juravenator* (Göhlich and Chiappe, 2006) and *Sinosauropteryx* (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001), and much larger than *Huaxiagnathus* that is estimated 1.6 m long (Hwang et al., 2004). It shows that the tendency of the body enlargement is also present in compsognathids to some extent.

2 Systematic Description

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Coelurosauria von Huene, 1914
Compsognathidae Marsh, 1882
Sinocalliopteryx gigas gen. et sp. nov.

Etymology: *Sino*, an ancient name for China; *callio* (Greek), beautiful; *pteryx* (Greek), feather; and *gigas* (Greek), giant.

Holotype: JMP-V-05-8-01 (Jinzhou Museum of Paleontology, Jinzhou, Liaoning Province), a very complete and excellently-preserved skeleton with long filamentous integuments only on one slab (Fig. 1).

Type locality and horizon: Hengdaozi at the Sihetun area of Beipiao, western Liaoning Province, northeastern China; Yixian Formation, Lower Cretaceous (Swisher et al., 1999, 2002).

Diagnosis: A very large compsognathid (2.37 m long) with 49 caudal vertebrae. Differing from other compsognathids (but sharing the similar features with *Huaxiagnathus*) in having a manus as long as the humerus plus radius, very large and subequally long manual unguals I and II, smaller proximal transverse width of the first metacarpal, and reduced olecranon process on the ulna. Distinguishable from *Huaxiagnathus* in having the much larger size, a long maxillary process of premaxilla not extending the vertical level of the maxillary antorbital fossa, the proportionally longer ulna (length ratio of humerus to ulna is 114%, compared with 160% in *Huaxiagnathus*), the preacetabular wing of ilium bending downwards at its anteroventral margin, and the distally unfused ischia.

Description: *Sinocalliopteryx* gen. nov. is the known longest compsognathid (2.37 m), with a proportionally large skull (29 cm long), long tail, relatively short arm, robust and long leg, and relatively small body (Fig. 1). The skull is almost complete, with some bones weakly disarticulated (Figs. 2a, b). Despite being long and slender, the maxillary process of premaxilla does not reach the level of the maxillary antorbital fossa, differing from that of *Huaxiagnathus* (Hwang et al., 2004). The premaxilla bears four somewhat conical teeth with small serrations on the lingual sides of distal portions of the first and second ones (Fig. 2c), and on the posterior carina of the fourth one. The external naris is elongate, only enclosed by premaxilla and nasal. The paired nasal is long with the dorsal surface of its posterior half relatively flat with the lateral margin slightly upwards. The maxilla is basically triangular with its posterior edge strongly concave, and the antorbital fossa is separated from other part of maxilla by a distinct ridge. Six compressed, distally backwards curved teeth are widely spaced on the left maxilla, serrated on posterior carina in anterior teeth and on both carinae in posterior teeth. The lacrimal is basically L-shaped in lateral view with long anterior process. There seems to be a distinct prefrontal just preserved behind the lacrimal. The jugal is a quite large bone with a long and dorsoposteriorly projected postorbital process. Each of the frontals is exposed by its ventral side. There is a distinct ventral ridge that subdivided the brain and eyeball. The postorbital is roughly T-shaped, with the three long rami. The squamosal bears a long descending ramus. The palatine appears long with two prominent anterior processes. The ectopterygoid consists of a wide medial portion and a caudally curved and pointed jugal process. The supraoccipital shows a pair of shallow lateral recesses on the posterior side of this bone. The exoccipital bears developed paroccipital process that projects laterocaudally. The basioccipital-basisphenoid evidently has a width larger than length, with a small but prominent occipital condyle, but the basisphenoid recess is absent.

The dentary is long anteroposteriorly, with the ventral margin curving upwards to meet the dorsal margin at the rostral end. Eight right dentary teeth are at their original position, showing similar shape and serration to the maxillary teeth. The surangular is long and has sub-parallel dorsal and ventral margins. The splenial has a very widely V-shaped posterior margin, and bears a small round mylohyal foramen completely enclosed in this bone anteroventrally. The mandibular foramen seems absent as in other compsognathids (Ostrom, 1978; Currie and Chen, 2001; Hwang et al., 2004; Göhlich and Chiappe, 2006), but the surangular fossa is visible. The articular has a large concave facet for articulated with the quadrate.

The vertebral column is composed of 11 cervical, 12 dorsal, unknown number of sacral, and 49 caudal vertebrae. The cervicals bear short and low neural spines, and the anterior cervical centra have one deep pneumatic concavity of each lateral side. The cervical ribs are extremely long,

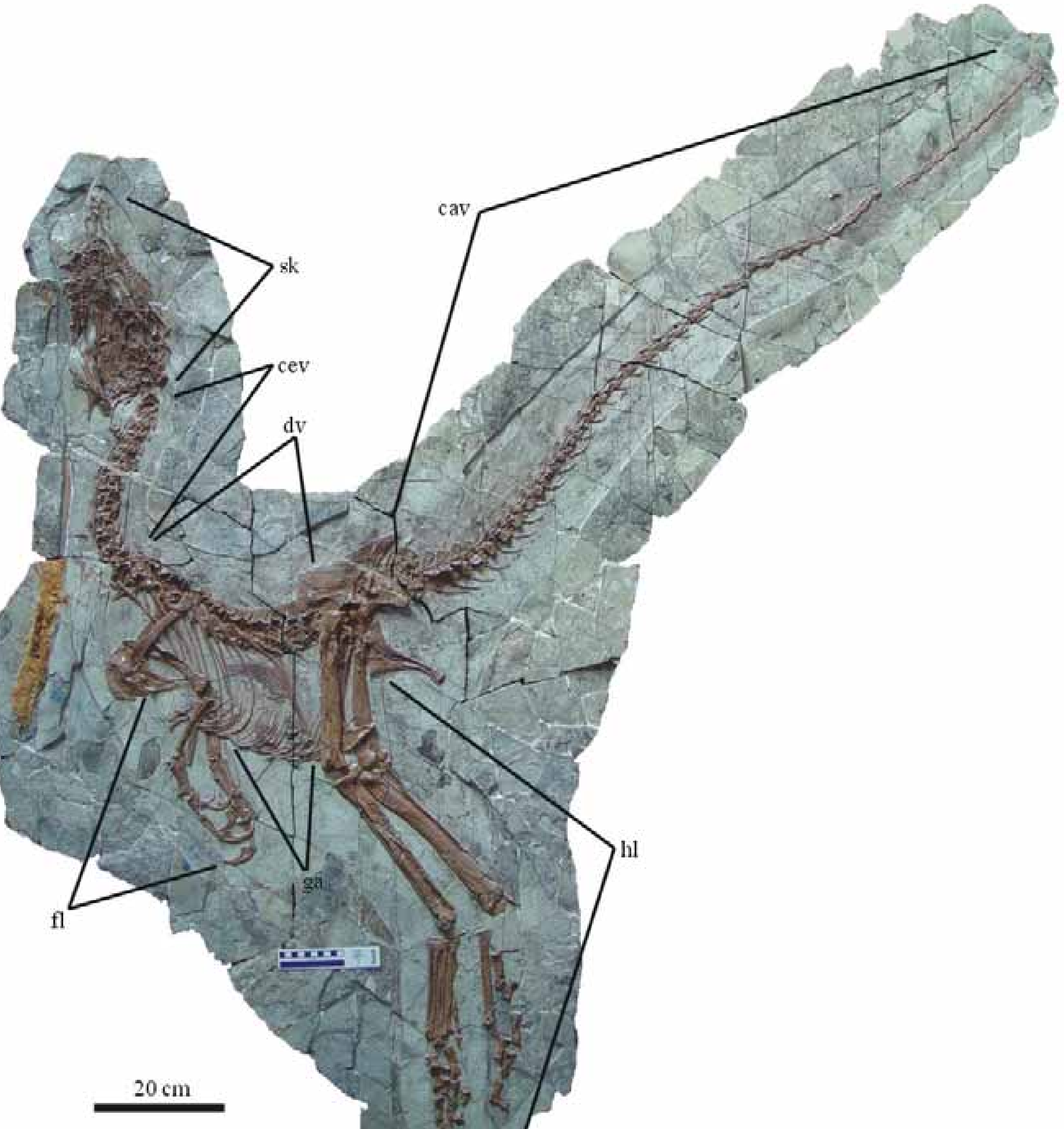

Fig. 1. Holotype of *Sinocalliopteryx gigas* gen. et sp. nov. (JMP-V-05-8-01).
Abbreviations: cav – caudal vertebrae; cev – cervical vertebrae; dv – dorsal vertebrae; fl – forelimb; ga – gastralia; hl – hindlimb; sk – skull.

thread-like with widening proximal ends, as in other compsognathids (Ostrom, 1978; Currie and Chen, 2001; Hwang et al., 2004; Göhlich and Chiappe, 2006). The dorsal margins of neural spines of dorsal vertebrae are anteroposteriorly expanded and look fan-shaped, one of the synapomorphies of compsognathids (Currie and Chen, 2001; Rauhut, 2003; Hwang et al., 2004; Naish et al., 2004; Göhlich and Chiappe, 2006). The completely preserved tail consists of 49 caudal vertebrae and occupies about 40% longer than the snout-vent length, compared with 64 caudals in *Sinosauropteryx* that is nearly twice the snout-vent length (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001). The anterior 16 caudals bear transverse processes and neural spines that decrease progressively posteriorly. The longest centra lie between 20th and 23rd caudals. The distal caudals are slender and short, and the

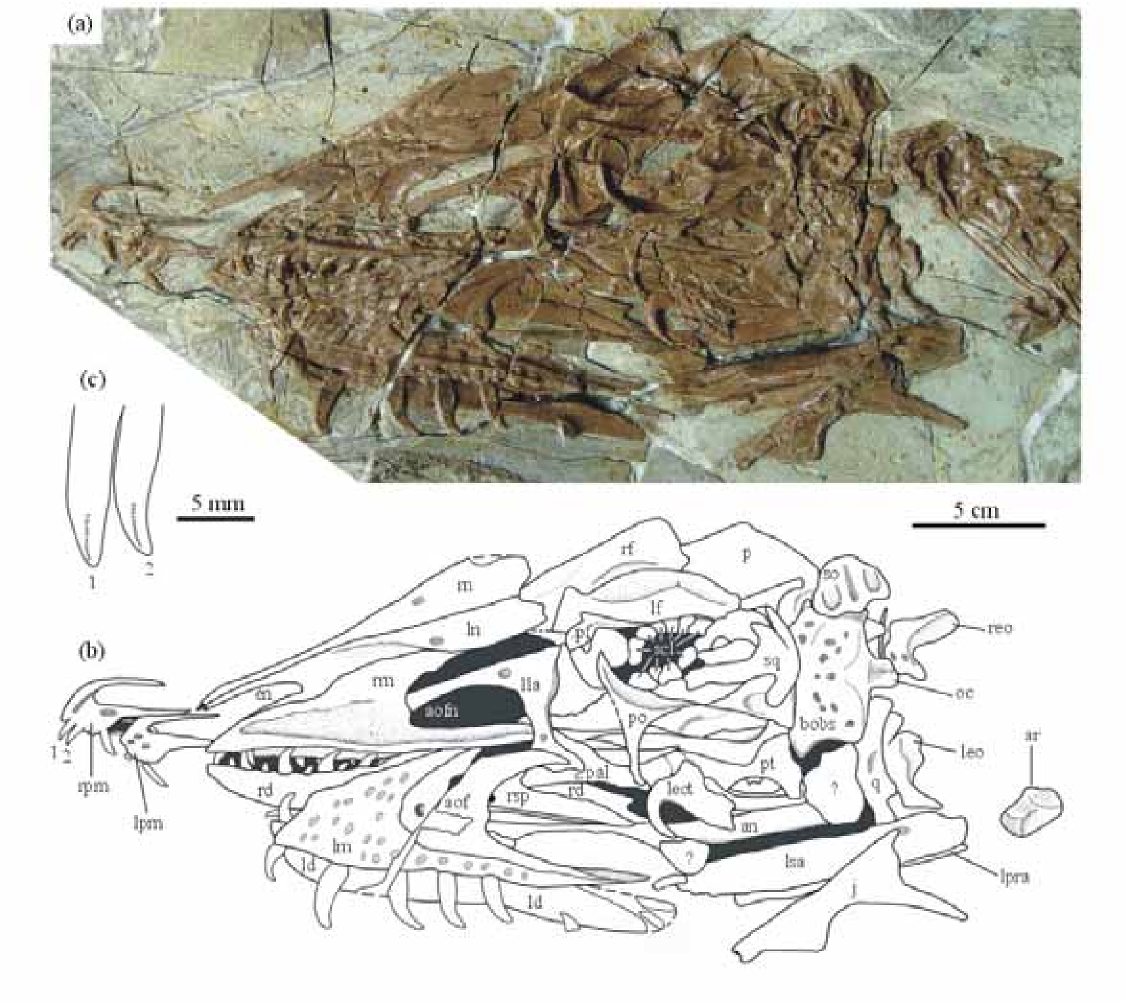

Fig. 2. Skull and lower jaw of *Sinocalliopteryx gigas* gen. et sp. nov. (JMP-V-05-8-01).

(a) Photo of specimen; (b) Line-drawing; (c) The first and second right premaxillary teeth in medial view. Abbreviations: an – angular; aof – antorbital fossa; aofn – antorbital fenestra; ar – articular; bobs – basioccipital-basisphenoid; en – external naris; j – jugal; ld – left dentary; lect – left ectopterygoid; leo – left exoccipital; lf – left frontal; lla – left lacrimal; lm – left maxilla; ln – left nasal; lpm – left premaxilla; lpra – left prearticular; lsa – left surangular; oc – occipital condyle; p – parietal; pal – palatine; pf – prefrontal; po – postorbital; pt – pterygoid; q – quadrate; rd – right dentary; reo – right exoccipital; rf – right frontal; rm – right maxilla; rn – right nasal; rpm – right premaxilla; rsp – right splenial; scl – scleral; so – supraoccipital; sq – squamosal; 1 – 1st right premaxillary tooth; 2 – 2nd right premaxillary tooth.

last one rod-like. The chevrons are very similar to those of *Sinosauropteryx* (Currie and Chen, 2001).

Twelve rows of gastralia constitute a complete gastral basket. With the exception of the first row that is composed of just two straight medial elements, each of the following rows has four segments, the paired medial ones being thicker and longer than the lateral ones.

The scapula is almost straight and slender, about 130% and 60% the length of the humerus and femur respectively. The large, triangular acromion process merges smoothly with the anterior margin of the scapular blade, as in *Huaxiagnathus* (Hwang et al., 2004). The coracoid is subcircular, presenting a small coracoid foramen and relatively large coracoid tubercle. The glenoid is semi-circular in lateral view, and caudally directed (Fig. 3a). A clear furcula is boomerang-shaped and slender with no hypocleideum, providing the second example of this bone within compsognathids following *Huaxiagnathus* (Hwang et al., 2004). The forelimb is short but stout, about half of the hindlimb length, similar to that of *Juravenator* (Göhlich and Chiappe, 2006) and *Huaxiagnathus* (Hwang et al., 2004). This ratio is 36% in *Sinosauropteryx* (Chen et al., 1998; Currie and Chen, 2001) and 39% in *Compsognathus* (Bidar et al., 1972) respectively. The humerus bears a developed deltopectoral crest that is dorsoventrally twice the humeral midshaft diameter. This bone is 114% length of the ulna, distinctly different from 160% in *Huaxiagnathus* (Hwang et al., 2004). The ulna and radius are slender and subequal in length, the former bearing a weak olecranon. There are four carpals including a relatively large semilunate carpal in the wrist (Fig. 3b). Metacarpal I is stout with a transversely narrow proximal end, and it is

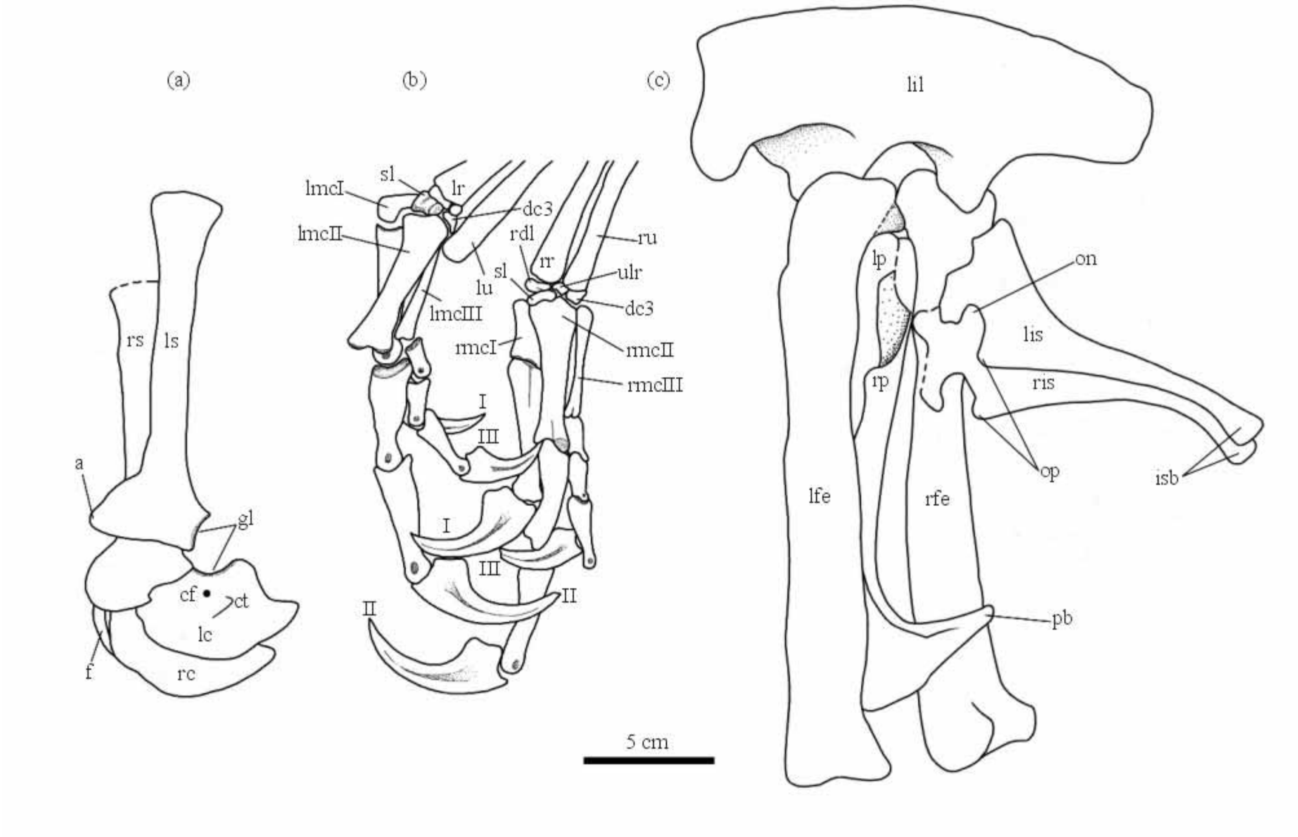

Fig. 3. Some appendicular bones of *Sinocalliopteryx gigas* gen. et sp. nov. (JMP-V-05-8-01).
(a) Pectoral girdle; (b) Manus; (c) Pelvic girdle. Abbreviations: a – acromion process; cf – coracoid foramen; ct – coracoid tubercle; dc3 – distal carpal 3; f – furcula; gl – glenoid; isb – ischial boot; lc – left coracoid; lfe – left femur; lil – left ilium; lis – left ischium; lmcI~III – left metacarpal I~III; lp – left pubis; lr – left radius; ls – left scapula; lu – left ulna; on – obturator notch; op – obturator process; pb – pubic boot; rc – right coracoid; rdl – radiale; rfe – right femur; ris – right ischium; rmcI–III – right metacarpal I–III; rp – right pubis; rr – right radius; rs – right scapula; ru – right ulna; sl – semilunate carpal; ulr – ulnare; I–III – manual digit I–III.

about 45% the length of metacarpal II. Metacarpal III is very thin with its midshaft diameter just 1/3 of that of metacarpal II and 64% of its length. The manual phalangeal formula is 2-3-4. Digit II is the longest, and digit III shortest. Among all phalanges except unguals, phalanx I-1 is the longest, as in *Sinosauropteryx* (Currie and Chen, 2001) and *Huaxiagnathus* (Hwang et al., 2004). The robust digit I and II bear a massive ungual, comparable with the evidently thin digit III and its much smaller claw, a feature seen only in this fossil and *Huaxiagnathus* (Hwang et al., 2004).

The pelvic girdle is similar to those in other compsognathids, such as the rounded caudal extremity of the postacetabular wing of ilium, nearly vertical pubis, and the developed and proximally-positioned obturator process of ischium (Fig. 3c). In lateral view, the anterior rim of ilium is slightly concave dorsally, and there is a pronounced ventral "hook" on the anterior expansion of ilium. The ischium has an evident obturator notch in front of the obturator process. Both ischia are slightly expanded distally but not fused. Although its anterior margin is covered by the left femur, it reasonably concludes that the well-developed pubic boot lacks an anterior expansion, another synapomorphy of compsognathids (Ostrom, 1978; Martill et al., 2000; Currie and Chen, 2001; Naish, 2002; Rauhut, 2003; Naish et al., 2004). The hindlimb is long and strong. The femur is robust and slightly bowed anteriorly, about 90% the length of tibia. The straight tibia is the longest bone of this animal, and the fibula reaches the ankle distally. There are separate calcaneum and astragalus, and at least two flat distal tarsals in the ankle. Among the three main metatarsals, the III is the longest and 60% the length of tibia. The first metatarsal is short and highly positioned, and the fifth is slender, laterally bowed and distally tapering. The pedal phalangeal formula is 2-3-4-5-x. Digit III is the longest, followed by the subequal II and IV, then I. In each digit, the penultimate phalanx is the shortest.

There are clear filamentous integuments on the back half of the skull, the neck, the back, the hip, both sides of the tail, and some portions of limbs (Fig. 4). These integuments are very simple and semi-independent of each other, showing the same structures as in *Sinosauropteryx* (Ji and

Ji, 1996; Chen et al., 1998; Currie and Chen, 2001), therizinosauroid *Beipiaosaurus* (Xu et al., 1999), and tyrannosauroid *Dilong* (Xu et al., 2004). They are of different lengths in different parts of the body. The longest ones are at the hip, the base of tail, and the back portions of the femur, where they are averagely more than 10 cm long. It has to be emphasized that such integumentary structures appear to be present at the area of metatarsus (Fig. 4d). If this observation is correct, the protofeathers on metatarsus occurred firstly at much more basal clade in coelurosaurs than the late bird-like maniraptorans such as the dromaeosaurid *Microraptor gui*, which bears the long asymmetrical feathers on metatarsus (Xu et al., 2003).

Contents inside the abdominal cavity: Compared with the large skull, long tail and robust hindlimb, the abdominal cavity of *Sinocalliopteryx* gen. nov. looks small (Fig. 1). It is interesting that there is an incomplete dromaeosaurid leg, and four small stones in the abdominal cavity (Fig. 5). The dromaeosaurid leg contains the complete tibia, fibula, metatarsals and phalanges that are nearly naturally articulated. It is obvious that this dromaeosaruid tibia is very long (15.5 cm) in comparison with the height of abdominal cavity of *Sinocalliopteryx*. The proximal ends of tibia-fibula are situated between the posterior gastralia of both sides, while their distal ends are covered by the left ribs near the posterior dorsal vertebrae. This situation of preservation suggests the possibility that this dromaeosaurid leg was indeed inside the abdominal cavity of *Sinocalliopteryx*. Thus, it most probably was the prize of *Sinocalliopteryx*.

Four irregularly-shaped stones, about 15 to 20 mm in the long dimension, were preserved within the posterior gastral cavity. These stones are found neither at other portion of the skeleton, nor in the sediment surrounding the specimen (Fig. 5). They are most likely to be interpreted as the gastroliths, as in the basal coelurosaur *Nqwebasaurus* (de Klerk et al., 2000).

3 Discussion

Sinocalliopteryx gen. nov. is conspicuously characterized by its giant size among compsognathids and perfectly well-preserved condition. It is the largest compsognathid species, about two to three times the lengths of *Compsognathus* (Ostrom, 1978; Bidar et al., 1972), *Juravenator* (Göhlich and Chiappe, 2006), and *Sinosauropteryx* (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001). It is also strikingly larger than *Huaxiagnathus* (Hwang et al., 2004). This shows the phenomenon of body enlargement in compsognathids is also present to some extent, as in some other clades of theropods. Exceptionally good preservation of *Sinocalliopteryx* provides us many important anatomical features for compsognathids. For example, more and more new material strengthens the fact that compsognathids had three functional manual digits (Currie and Chen, 2001; Peyer, 2003; Hwang et al., 2004; Göhlich and Chiappe, 2006), rather than the hypothesis of two fingers (Ostrom, 1978).

As in *Sinosauropteryx* (Ji and Ji, 1996; Chen et al., 1998; Currie and Chen, 2001), *Sinocalliopteryx* also bears the distinct filamentous integuments. This new fossil strengthens the presence of protofeathers occurred early at the base of Coelurosauria (Norell and Xu, 2005). It is noteworthy that such integuments were also present in the areas of metatarsus (Fig. 4d). As we know, the small dromaeosaurid *Microraptor gui* possesses the long and asymmetric vaned feathers on its metatarsus (Xu et al., 2003), suggesting the four-wing stage of the course from maniraptorans to birds. The protofeathers on metatarsus of *Sinocalliopteryx* could show this pattern appeared also as early as the basal coelurosaurs.

The gastroliths of *Sinocalliopteryx* are relatively big in size and less in number, showing some similarities to the basal coelurosaur *Nqwebasaurus* from the Lower Cretaceous of South Africa (de Klerk et al., 2000). The stomach stones have been known in more theropod taxa such as *Caudipteryx* (Ji et al., 1998; Zhou and Wang, 2000) and a Mongolian ornithomimid (Kobayashi et al., 1999). *Caudipteryx* and the Mongolian ornithomimid have many small gastroliths, related to their herbivorous diet. A long-snouted theropod *Baryonyx* from Lower Cretaceous of Wealden was reported to have gastraliths (Charig and Milner, 1986), but their sizes and number were not described. *Sinocalliopteryx* has relatively large but less gastroliths. It might come to the conclusion that the less but large gastroliths are related to the carnivorous theropods, and the many but small gastroliths to the herbivorous diet.

The large skull, serrated teeth, stout forelimb with massive manual claws indicates *Sinocalliopteryx* was a fierce preyer. Compsognathids were active raptors in the Late Jurassic and Early Cretaceous, as shown by the undigested bones of lizards within the stomach cavities in both *Compsognathus* (Ostrom, 1978) and *Sinosauropteryx* (Chen et al., 1998; Dong and Chen, 2000). An incomplete dromaeosaurid leg within the abdominal cavity of *Sinocalliopteryx* gives more proofs for that compsognathids were active carnivorous dinosaurs.

4 Conclusions

On the basis of the above description and discussion, we come to the following conclusions:

(1) The giant compsognathid described in this paper

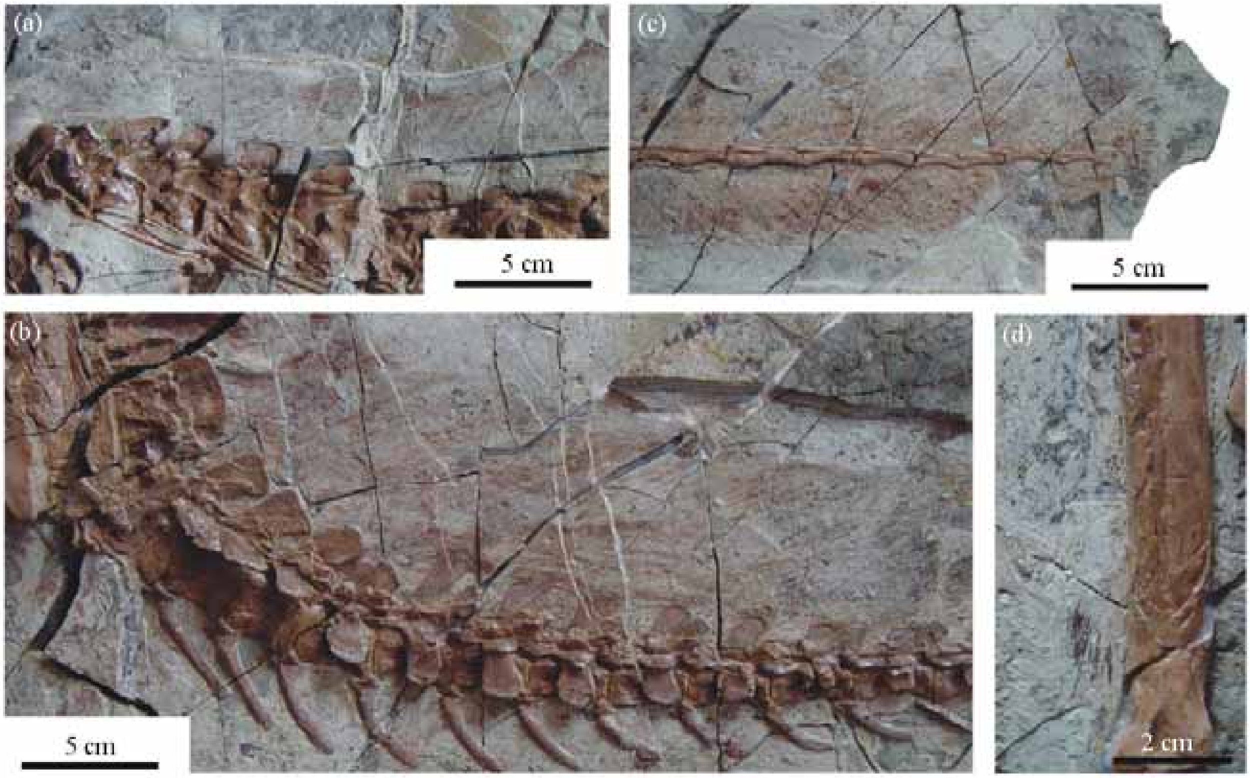

Fig. 4. Filamentous integuments of *Sinocalliopteryx gigas* gen. et sp. nov. (JMP-V-05-8-01).
(a) Integuments above the cervicals; (b) Integuments at the dorsal side of the proximal caudals; (c) Integuments at the distal portion of tail; (d) Integuments at the area of metatarsus.

represents a new genus and new species, *Sinocalliopteryx gigas*, which possesses the long and developed filamentous integuments covering its whole body. It is the third compsognathid taxon (after *Sinosauropteryx* and *Huaxiagnathus*) from the Early Cretaceous Yixian Formation of western Liaoning Province, northeastern China.

(2) *Sinocalliopteryx gigas* gen. et sp. nov. is the largest species (2.37 m in total length) among the known compsognathids, showing that the tendency of the body enlargement is also present in compsognathids to some extent.

(3) There is an incomplete dromaeosaurid hindlimb inside the abdominal cavity of *Sinocalliopteryx gigas* gen. et sp. nov., further supporting that compsognathids were fierce carnivorous dinosaurs. The only four and slightly big gastroliths in this new compsognathid may indicates that the less but large gastroliths are related to the carnivorous diet.

Fig. 5. Stomach contents of *Sinocalliopteryx gigas* gen. et sp. nov. (JMP-V-05-8-01).
Abbreviations: dro – dromaeosaurid tibia and pes; g – gastroliths.

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