

DESCRIPTION AND ONTOGENETIC ASSESSMENT OF A
NEW JEHOL MICRORAPTORINE

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Earth Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May, 2014

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ACKNOWLEDGEMENTS

Thanks to my committee members:

Dr. David J. Varricchio, Dr. Frankie Jackson, Dr. John R. Horner

Thanks to the Dalian Natural History Museum, PRC and in particular, Gao Chunling. Thanks to Zhang Fengjiao, Thérèse Lamm, Jim Schmitt, Gail Weidenaar and Melanie Baldwin.

Thanks to fellow cube-farmers at MSU: J. Stiegler, B. Boessenecker, L. Hall, S. Oser, J. Simon, M. Knell, T. Evans, D. Lawver, B. Scherzer, D. Fowler, C. Lash, E. Fowler (nee Freedman), A. Bailleul, J. Scannella, J. Fearon, H. Woodward, B. Helmke, B. Baziak, M. and D. Bechberger, D. Strosnider, D. Barta, B. Turner, and N. Carroll.

At Berkeley, Thanks to: K. Padian, S. Werning, VPL attendees, D. Strauss, E. Ferrer, P. Skipwith, P. Holroyd, and L. Chang.

For professional help thanks to: Alan Turner, Luis Chiappe, Jesus-Marugan-Lobon, Robert Kambic, Nathan Smith, Carl Mehling, and Matt Lamanna.

Finally: My family and especially my parents, Sally and Brad Bridges and David Poust, Thanks to these and many more people who helped me along the way, to whom all credit is due and who will have little trouble believing that any faults or omissions are entirely my own.

A generous grant from the Jurassic Foundation was integral in the completion of this study. Support was also provided by a start-up grant to David J. Varricchio.

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ABSTRACT

Fossils from the Jehol Group (Early Cretaceous, Liaoning Province, China) have greatly contributed to our understanding of the morphology and diversity of Paraves, the group of dinosaurs including sickle-clawed dromaeosaurs, large-brained troodontids, and avialians, the ancestors of modern birds. However, many taxa are represented by only a few specimens of unclear ontogenetic age. Without a thorough understanding of ontogeny, the evolutionary relationships and significance of character states may be obscured within paravian dinosaurs. A complete specimen of a new taxon of microraptorine dromaeosaur, *Wulong bohaisensis* gen. et sp. nov., from the Jiufotang Formation (upper Jehol Group) exhibits clearly juvenile morphology. The dinosaur is small and preserved in articulation on a single slab. It has microraptorine features such as a subarctometatarsalian foot, a short first manual digit, and a prominent tubercle on the pubis. Phylogenetic analysis substantiates this assignment. It also possesses more than 29 tail vertebrae, inclined pneumatic foramina on its dorsal vertebrae, and an unusually large coracoid fenestra, which with other features argue that it is a new taxon. This individual shows many osteological markers of immaturity identified in other archosaurs. Skull elements, all visible neurocentral sutures, pubes, and proximal tarsals remain unfused. Grainy surface texture of the cortical bone and poor ossification of long bone articular surfaces further supports an immature status. Histologic samples of the tibia, fibula, and humerus of this individual (the first microraptorine theropod to be sampled) confirm that it was around a single year in age and still growing at death, but that the growth had slowed. This slow down in growth is interesting in light of the presence of pennaceous feathers extending from the fore- and hind-limbs and, notably, two long plumes extending more than 12 cm from the tip of the caudal series. This indicates that presence of a variety of feather types, including filamentous feathers, pennaceous primaries, and long rectrices, likely used for ornamentation, preceded skeletal maturity and full adult size.

INTRODUCTION

Deinonychosauria, the clade consisting of Dromaeosauridae and Troodontidae, is consistently recovered with a close phyletic relationship to Aves (Sereno, 1999; Senter, 2007), a fact reflected in its position in Paraves sister to Avialae, which includes modern birds. Therefore, understanding the anatomy and behavior of members of this group represents an important step in evaluating the macroevolutionary history leading to the feathered dinosaurs of today.

The first dromaeosaur (*Dromaeosaurus*) was described in 1922 (Matthew and Brown, 1922). The description of the second (*Velociraptor*) followed in 1924 (Osborn, 1924). For decades following their discovery, the presumed ectothermic metabolism of dinosaurs appeared paradoxical to the gracile form and morphology of dromaeosaurids, but received little attention in the literature. Recognition of their truly unique character awaited the discovery and description of *Deinonychus* in the late 1960s (Ostrom, 1969a; Ostrom, 1969b), contemporaneous with the redescription of the original *Dromaeosaurus* (Colbert and Russel, 1969). Ostrom noted that the slim, gracile hunter *Deinonychus* would have been well suited to an energetic, active lifestyle (Ostrom, 1990). Later description of the dinosaurian features of *Archeopteryx* (e.g. Ostrom, 1976; Mayr et al. 2005) and purported evidence for pack hunting in *Deinonychus* (Ostrom, 1969b; Maxwell and Ostrom, 1995) added fuel to this renaissance. The recovery of feathered dinosaurs from the Yixian Formation since the mid-90s continues to change our understanding of the physiology and phylogenetic relations that characterize the theropod-bird transition (e.g Norell and Xu, 2005). Dromaeosaurs and the other members of Paraves are once

again the focus of this continuing conceptual revolution.

One of the groups most important to this growing body of research has been a small group of small dromaeosaurs, all but one from the Jehol Biota: the microraptorinae. First recognized by Senter et al., 2004, and defined by Sereno in 2005 as a stem-based monophyletic clade containing *Microraptor zhaoianus* Xu et al., 2000 and all coelurosaurs closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Velociraptor mongoliensis* Osborn, 1924, *Unenlagia comahuensis* Novas and Puerta, 1997, or *Passer domesticus* Linnaeus, 1758. This group includes in order of description: *Sinornithosaurus*, *Microraptor*, *Graciliraptor*, *Hesperonychus*, and *Tianyuraptor* (see table 1). This group is now consistently recovered as monophyletic (Xu and Wang, 2004; Makovicky et al., 2005; Senter, 2007; Turner et al., 2007; Longrich and Currie, 2009; Turner et al., 2012). To this group I here add a sixth member with the description of *Wulong bohaisensis* gen. et sp. nov., (to be thus named in a later publication) including a description of its feathers and an assessment of its ontogenetic status.

All but one member, *Hesperonychus* from North America, were discovered in the Jehol Group of North Eastern China. Composed of two recognized fossil bearing formations, the Jehol group is now confidently dated to the middle Early Cretaceous (Swisher et al., 1999). Early work on fishes established that the Jiufotang Formation was distinct from the older Yixian Formation, though the two are made of similar fluviolacustrine deposits (Fan, 1995). Not all of the beds within the formations preserve soft-tissues (Xu, 2002). Some beds are partially composed of sediment with clearly volcanic origin, including several ash beds (Zhou et al., 2003). In the last decade these

Table 1. Selected Comparisons of Microraptorines

Table 1 - <u>Selected Comparisons of Microraptorines</u>							
<u>Taxon (described holotype)</u>	<u>Formation</u>	<u>Feather Stages present</u>	<u>Tibia length (in mm)</u>	<u>Fusion of dorsal centra to arches</u>	<u>Fusion of pelvis</u>	<u>Cortical bone texture</u>	<u># of labels</u>
<i>Wulong</i> (D2933)	Jiufotang	II, III, IV, V?	117	Completely unfused	Entirely unfused	Unfinished	0
<i>Microraptor</i> (multiple specimens)	Jiufotang	II, III, IV, V?	71.2 (holotype)	Fused, sutures obliterated (CAGS 20-8-001), unknown (holotype)	Variable, most pubes fused	Variable	?
<i>Microraptor “gui”</i> (IVPP V)	Jiufotang	II, III, IV, V?	-	?	?	Mostly finished	?
<i>Sinornithosaurus millenii</i> (IVPP V12811)	Yixian	II, IIIa	>125	Fused, sutures obliterated	Sacrum fused, pubis fused	Mostly finished	?
<i>S. “haoiana”</i> (D2540)	Yixian	II, IIIa	143.4	Fused, sutures obliterated	Sacrum fused, pubis fused	Mostly finished	1-2
<i>“Dave”</i> (NGMC-91)	Yixian	II, IIIa+b, IV?	134.2 (may include astrag. & calc.)	?	?	Unfinished, but poorly preserved	?
<i>Graciliraptor</i> (IVPP V)	Lower Yixian	Unknown	>154	?	?	Unfinished	?
<i>Tianyuraptor</i> (IVPP V)	Yixian	Unknown	-	?	?	?	?
<i>Hesperonychus</i> (ULAVP 48778)	Dinosaur Park	Unknown	Unknown	?	Pubes fused, pubis fused to ilium	?	?

have allowed the more precise dating of the formations. The Yixian Formation has been bounded with $^{40}\text{Ar}/^{39}\text{Ar}$ dating to between 129.7 ± 0.5 Ma taken at the base of the Yixian

Formation itself and 122.1 ± 0.3 Ma taken at the base of the overlying Jiufotang Formation (Chang et al., 2009). The location where *Sinornithosaurus* was discovered, Sihetun, has been the focus of several radiometric dating studies, using various isotopes, including $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb, which have yielded a tighter range of dates (Smith et al. 1995, Swisher et al. 1999, Wang et al. 2001, Swisher et al. 2002). For the purposes of this description I accept the 125.0 Mya $^{40}\text{Ar}/^{39}\text{Ar}$ from Swisher et al (2002).

The younger Jiufotang Formation was dated at the same site from which *Wulong* was recovered; the Shanheshou locality. The locality dates to 120.3 ± 0.7 Ma (He et al., 2004).

These middle Early Cretaceous Liaoning deposits preserve flighted Avialans that co-existed with small, feathered dinosaurs. These, along with many other animals and plants present in the formations are known collectively as the Jehol Biota (Norell and Xu, 2005). Although birds as functional flyers date to at least the Tithonian of the Late Jurassic (Ostrom, 1976), the Liaoning beds preserve in great detail the myriad forms produced by the mosaic-style evolution that characterized the earlier development of birds. The exposures of the Jehol Group are currently the most important in the world for understanding the evolution of vertebrate flight, the origin of modern birds, and the phylogeny and behavior of two of the most derived groups of Cretaceous dinosaurs; the Troodontidae and the Dromaeosauridae. This can be seen both in the quality of preservation, leading to the recognition of the first feathers in dinosaurs (Chen, 1998) and in the myriad revelations that continue to come from Jehol material from fossil ovaries (Zheng et al., 2013) to piscivory in dromaeosaurids (Xing et al., 2013).

The smallest of the Jehol dromaeosaurs, *Microraptor zhaoianus*, was described from a partial skeleton. It was noteworthy at the time for its small size and the features that it shared with Aves, especially its feather-like integument preserved near the femur (Xu et al., 2000). Later specimens would expand the knowledge of its feathers greatly, especially the description of *Microraptor gui*, which preserved pennaceous feathers on its hindlimbs leading to suggestions of a four-winged gliding stage on the road to flight (Xu et al., 2003). It is worth adding that many authors have increasingly been treating the two described species of *Microraptor* as a single unit for analysis (Turner et al., 2012; Li et al., 2012).

Along with *Microraptor*, the most significant member of this clade is the larger *Sinornithosaurus*, a genus with two described species, *S. millenii* and *S. haoiana*. Of these, *S. millenii* is the better known, being the first described Yixian dromaeosaurid in 1999, the timing of which underlies the species epithet conferred by Xu et al. A comprehensive monograph on its cranial anatomy followed in 2001 (Xu and Wu, 2001). *S. haoiana* is similar in most ways to *S. millenii* and is of a similar size (Liu 2004). Notably, both specimens are covered with a downy pelage preserved across most of the body, but do not possess other feather types. This downy covering was redescribed by Xu et al. (2001) as possessing branched structures, which place the feathers of *Sinornithosaurus* at stage 2 or 3a of Prum's model of feather evolution (Prum, 1999). Turner (2012) later synonymized these two taxa. Ji et al (2001) described NGMC-91 from the Yixian formation, a putatively juvenile theropod with feathers colloquially known as "Dave". This taxon is not well preserved skeletally and so has not provided

strong evidence for the ontogenetic trajectories of dromaeosaurid, but several features led the authors to suggest similarities to *Sinornithosaurus* (Ji, 2001). Other authors have agreed that it may be a juvenile individual of *Sinornithosaurus* (Turner et al., 2012).

In 2004, Xu and Wang described a new genus, *Graciliraptor*, from a partial skeleton. The specimen in many ways is similar to other microraptorines, particularly *Microraptor* (Turner et al., 2012). The material was recovered from the lowest part of the Yixian, making it the oldest of the microraptorines.

The most recently described of the Jehol dromaeosaurs, *Tianyuraptor*, is notable for its larger size and differently proportioned forelimbs. It was described from the Yixian formation, making it contemporaneous with *Sinornithosaurus* and thus older than *Wulong* and *Microraptor*. It falls outside the microraptorinae in a majority of analyses (Zheng, 2009; although see the recent Turner et al., 2012 for a dissenting opinion).

The rest of the world has produced a very limited crop of potential members of this group, only one of which this analysis recovers as a microraptorine. Their rarity is likely attributable to size-related taphonomic and collecting bias (Longrich and Currie, 2009). In 2009, Longrich and Currie described *Hesperonychus elizabethae* from the Dinosaur Park Formation of Canada. This animal is similar in size and morphology to the Jehol forms, though the material is more limited, with the holotype comprising an articulated pelvic girdle without the ischia. Two other animals have been suggested to be members of the group: *Bambiraptor feinbergi* from Montana (Burnham et al, 2000) and *Shanag ashile* from Mongolia (Turner et al., 2007). But later analyses have placed these groups in a variety of positions outside microraptorinae (Longrich and Currie, 2009;

Turner et al., 2012). Thus, *Hesperonychus* is the only theropod outside of Asia confidently assigned to the microraptorinae.

The other basal-most group of dromaeosaurids, the Unenlaginae, is in flux with the recent hypothesis that this Gondwanan clade falls outside of the dromaeosauridae even while maintaining its monophyly (Agnolin and Novas, 2011). This basal instability suggests that it is more important than ever to correctly assign character states in ways that account as much as possible for ontogeny, as they will help to form the basis for understanding the placement of paraves as a whole, including the ancestral state of birds.

There are several reasons to be interested in ontogeny and life history strategy at the base of radiations: complex phylogenies, like those associated with divergence of major clades may be skewed by inappropriate character choice making ontogenetically variable characters problematic; one might be interested in how variation in development can become material for evolutionary transitions or, conversely, one might wish to factor out as much developmental variation as possible to better evaluate taxonomic differences; description of juvenile taxa as adults may skew our understanding of diversity dynamics; and lastly failure to consider fully ontogenetic implications may fatally color our interpretations of everything in an organism's life history. Thus, a paucity of ontogenetic information at the base of paraves (though there are a few excellent forays into this field, e.g. Erickson et al. 2009) limits our understanding of adult body size, growth patterns, and the distribution of feathers across the body and their implications for gliding or flight. An important part of any approach to assessing the ontogenetic status in fossil organisms is consilience of evidence including, but not limited to cortical texture, bone fusion,

proportional difference along with scaling and allometry, and of course when possible, histology.

Recent work on fossil feathers has been exciting. Not only has the discovery of feathered dinosaurs in the Jehol since 1995 revitalized our thinking about bird origins and dinosaurian behavior and relationships in general but subsequent advancements have brought us an ever-clearer picture of this story. The integumentary structures that led to feathers may have an ornithodiran origin as suggested by the “down” present in pterosaurs (Wang et al 2002). This hypothesis that feathers or at least the developmental pathways to make them preceded other bird-like features is supported by the discovery of possible integumentary structures in ornithiscians (Mayr et al 2002, Zheng et al 2009). While those structures remain somewhat enigmatic, previous claims that feathers in theropod dinosaurs were the result of taphonomic processes (Lingham-Soliar 2003a, 2003b, Lingham-Soliar et al 2011) have been largely debunked both on the basis of gross morphology and, strikingly, by the near-simultaneous discovery by two groups that the pigment organelles found in modern feathers were preserved in these fossil feathers and were observable under scanning electron microscope (Vinther et al., 2010; Zhang et al., 2010). Fossil pigment work in dinosaurs built directly on previous work by Vinther et al (2008) on feathers from the Messel and so is a method equally applicable to fossil birds. This was not only compelling evidence that the feathers were authentic and correctly identified, but it opened a world of investigation previously thought as closed as that of dinosaur sounds: color. Though the full range of dinosaur colors probably remains to be explored general color patterns for several non-avian dinosaurs and fossil birds has been

discovered and structural color, so vibrant in modern birds, has even been discovered in *Microraptor* (Li et al., 2012). It may take some time for the physiological and behavioral implications of all this recent work to be synthesized. Meanwhile, the taxonomic and morphological breadth of discovered feathers continues to broaden, with quill knobs discovered on the ulna of a *Velociraptor* (Turner, 2007b) and recently *Yutyrannus*, a 1,400 kg tyrannosauroid from China (Xu et al., 2012). This latter is interesting as it shows that earlier hypotheses about the function of filamentous feathers for thermoregulation may have been too simple, leaving out phylogenetic, climatic, or additional functional explanations. Most recently Zelenitsky et al. (2012) have filled in some of the phylogenetic gap between tyrannosaurids and maniraptorans by discovering feathers in ornithomimosaur in North America. Not only does this find expand the phylogenetic and geographic distribution of feathers in the fossil record, but the feathers were found in sandstone so it opens up a whole new sedimentary realm for exploration as well.

The discovery of a number of differing feather types has led to the proposal of different series of the acquisition of feather features from the assumed simplest ancestral conditions to the feathers found in modern flighted birds (Prum 1999, 2005, Yu et al 2002). Pathways in which this might occur have been suggested, going from simple filaments to an asymmetric flight feather. Some feathers beautifully preserved in amber and recently imaged in impressive detail by McKeller et al (2011) seem to lend credence to these pathways. Xu et al (2010) published on an oviraptorid dinosaur with very different feathers implying a different route or perhaps multiple routes to the evolution of

the modern structures. These feathers have more recently been cogently argued to be pinfeathers in the process of growing (Prum et al 2010). This work has suggested that scientists can learn something about the ontogeny of individual feathers, or at best entire moults, from the fossil record, but so far we know little about fledging or about how feathers fit into the life histories of extinct animals.

Here I describe a new microraptorine with feathers distributed across its entire body. Histological analysis allows us to better contextualize both these feathers and markers of age in the well preserved skeleton.

METHODS

For consistency, anatomical terminology has largely followed the nomenclature applied by Xu et al. 1999, Hwang et al. 2002, and Norell et al. 2002 in their various descriptions of other Yixian dromaeosaurids. Some terms without consistent names in this system have been taken from Brochu (2003).

X-ray radiography was performed using Computed Axial Tomography (CAT) at Dalian Medical University Hospital to check the veracity of the specimen. Images were captured at 90kV at an 82 percent scale.

In order to further test the veracity of the feathers, rock was prepared away from where it was overlying the edges of exposed feathers. This was performed in two places; along the dorsal edge of the feathers extending from the tail, and in the center of the patch of feathers exposed along the posterior dorsal vertebrae

In order to examine the skeleton histologically, samples were removed from the right tibia and fibula and the mid-shaft of the left humerus on D2933 and from the left tibia and fibula and left radius of D2140, the holotype of *Sinornithosaurus "haoiana"*. The tibiae were chosen for sampling under the constraint of the material; the femora were not available from the mid-shaft of *Sinornithosaurus*. But there are other reasons to use these bones. Not only does sampling the tibia/fibula increase our sample size to three bones on each animal, but there is good evidence that the fibula is one of the most useful bones for accurate aging, at least in reptiles (de Buffrenil and Castanet, 2000). Additionally, across dinosauria the tibia is one of the most sampled bones and thus easily comparable to related animals (e.g. *Troodon*: Varricchio, 1993). Likewise the fibula has

been used in many studies, especially of theropods (e.g. *Tyrannosaurus*: Erickson et al, 2004). The tibiae and fibulae were sampled in the midshaft on both animals to increase the equivalence of the samples and to avoid sampling within the metaphysis. Cross sections of the tibia and fibula from both D2140 and D2933 were removed from their slabs with a diamond blade on a Dremel rotary tool. A section of the anterior portion of the humerus was also removed as a comparison. The pieces were molded and cast and the casts painted and replaced in the specimen with their artificial status indicated by painted dots (as in Lamm, 2013). The samples were repainted with coats of B-72 and were carried to the United States where they were prepared in Silmar polyester resin and sectioned. Sections were attached to slides and ground to optical clarity. These methods conform to traditional methods of dry histological preparation (Chinsamy and Raath, 1992; Lamm, 1999)

As noted in the introduction, the current position of the two named species of *Microraptor* is in flux. A convenient review is provided in a recent paper by Li et al (2012, supplementary online material). Here I treat the clade as a single group, except for specific anatomical features. Note that what is currently referred to as *Microraptor zhaoianus* is better described and most comparisons should be assumed to refer to that taxon or to a concatenation of the characters present across all specimens of both purported taxa, *sensu* Turner 2012.

Similarly Turner (2012) synonymizes the two taxa of *Sinornithosaurus* and so the second taxon will here be called *S. "haoiana"* in quotations as way of referencing its type specimen, DNHM D2140.

The phylogenetic position of *Wulong bohaisensis* was analyzed with equally weighted parsimony using TNT v.1.0 (Goloboff et al., 2008). The tree search strategy follows that from Turner et al. (2012), from which our matrix is derived. I performed a heuristic tree search with 1000 replicates of Wagner trees followed by TBR branch swapping (holding ten trees per replicate). This was then followed by branch swapping on these best trees. After excluding problematic, underscored taxa this generated 3170 most parsimonious trees. These were subjected to a strict (Nelsen's) consensus and to a majority rules consensus.

SYSTEMATIC PALEONTOLOGY

(Note: This thesis is not intended to constitute publication of new names or nomenclatural acts and such names as are given are not here intended for public and permanent scientific record – this is a model of what will be published later)

Systematic Paleontology

Dinosauria

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Paraves Sereno, 1997

Dromaeosauridae Matthew & Brown, 1922

Microraptorinae Senter 2004 (*sensu* Sereno 2005)*Wulong bohaiensis* gen. et sp. nov

- etymology

Wulong, from the chinese 舞 (*wǔ*) meaning “dancing” and 龙 (*lóng*) meaning “dragon”, in reference to its delicately poised posture and presumed cursorial nature, and *bohaiensis*, from the Chinese 渤海 (*Bó Hǎi*) for the Bohai Sea combined with the suffix –ensis, Latin for “of or from a place”, in honor of its accession at the Dalian Natural History Museum (DNHM) situated on the shore of the Bohai strait.

- holotype

DNHM D2933, a complete, articulated skeleton on a single slab.

- Locality and horizon

Shangheshou, Chaoyang, Liaoning, China. Early Cretaceous Jiufotang Formation with a minimum age of 120.3 Ma (Zhou et al., 2003, and He et al., 2004).

- Diagnosis

A small, feathered theropod differing from other dromaeosaurids in the following derived features: long jugal process of quadratojugal, anteriorly inclined pneumatic foramina on the anterior half of dorsal centra, transverse processes of proximal caudals significantly longer than width of centrum, presence of more than 29 caudal vertebrae, large size of supracoracoid fenestra (>15% of total area).

- Description and comparison (in description section)

DESCRIPTION

Taphonomy

The skeleton of D2933 is preserved lying on its left side (Figs.1-4). The animal lies on a single bedding plane, though the laminae of fine siltstone are so thin (~1mm) that it took several of them to cover the small skeleton. The skeleton is preserved in dorsally hyperextended posture, with the head thrown fully over the back so that the dorsal surface of the skull is at least perpendicular with the dorsal surface of the thoracic spine. If this is true opisthotony (*sensu* Faux and Padian, 2007) then the preservation of this perimortem positioning is further evidence for low energy burial and little transport. The specimen is markedly complete; only some ribs are missing. However, the thin ventral ribs and gastralria are numerous, well preserved, and generally in life positions. The gastralria drape over the left femur but pass under the right, showing their appropriate track from sterna to pelvis and indicating that they have undergone minimal post-mortem dislocation. The articulation of the gastralria and sternal ribs suggests that decay-related gas expansion of the abdominal cavity may not appropriately explain the loss of ribs. X-ray analysis (fig. 5) failed to reveal further still-buried ribs. Some on the right side may have been removed with the counterpart, which was not kept with the slab and was likely discarded. Other than the ribs, only the tiny first phalanges of the third manual digits are missing.



Figure 1. Photograph of D2933. *Wulong bohaisensis*, specimen DNHM D2933, view of entire slab.

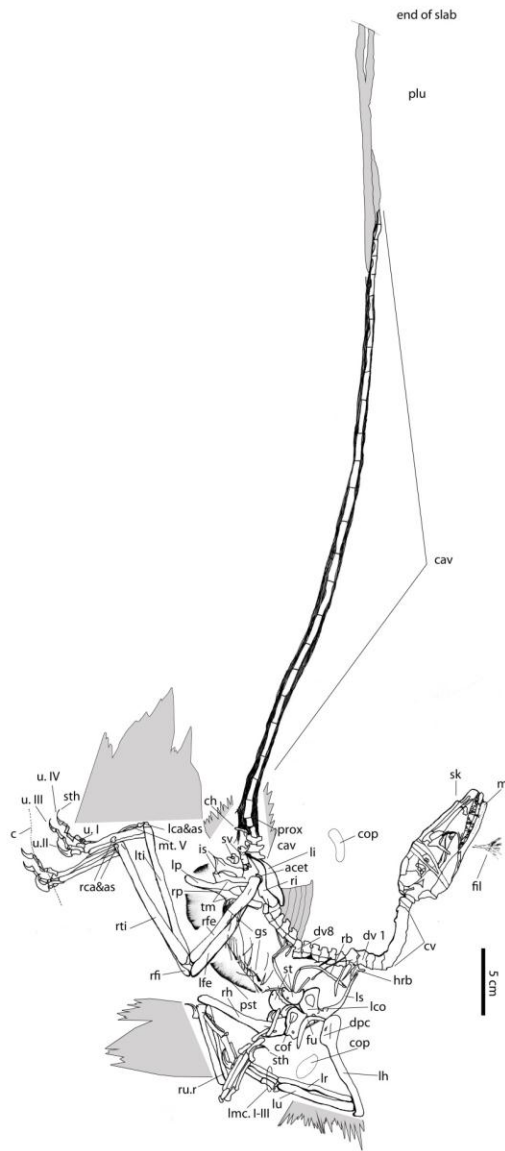


Figure 2. Drawing of specimen shown in Figure 1. *Wulong bohaiensis*, DNHM D2933
 Abbreviations: acet, acetabulum; c, crack; cav, caudal vertebrae; ch, chevrons; cof, supracoracoid fenestra; cop, coprolite; cv, cerviocal vertebrae; dpc, deltapectoral crest; dv, dorsal vertebrae; fil, filamentous feathers; fu, furcula; gs, gastralia; hrb, head of rib; is, ischia; lca&as, left calcaneum and astragalus; lco, left coracoid; lfe, left femur, lh, left humerus, li, left ilium; lmc.I-III, left metacarpals 1-3; lp, left pubis; lr, left radius; ls, left scapula; lu, left ulna; lu.r, left ulna and radius; m, mandible; mt.V, metatarsal 5; plu, plumes; proxcav, proximal caudal vertebrae; pst, possible soft tissue; rb, ribs; rca&as, right calcaneum and astragalus; rfe, right femur; rfi, right fibula; rh, right humerus; ri, right ischium; rp, right pubis; rti, right tibia; ru.r, right ulna and radius; sk, skull; st, sterna; sth, horny sheath; sv, sacral vertebrae; tm, tubercle; u.I-IV, terminal unguals of digits 1-5. Scale bar 5cm.

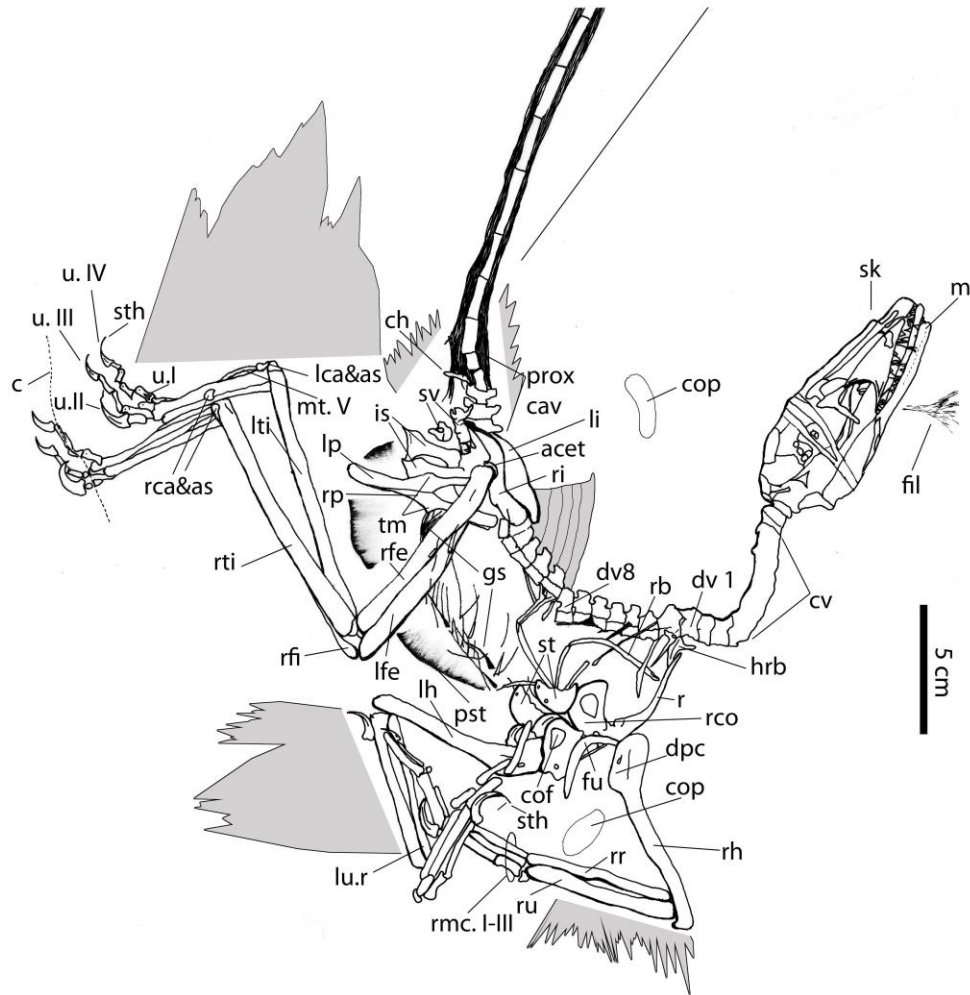


Figure 3. Detail of Figure 2 showing body of *Wulong*. Abbreviations as in fig. 2. Feathers shown in gray.

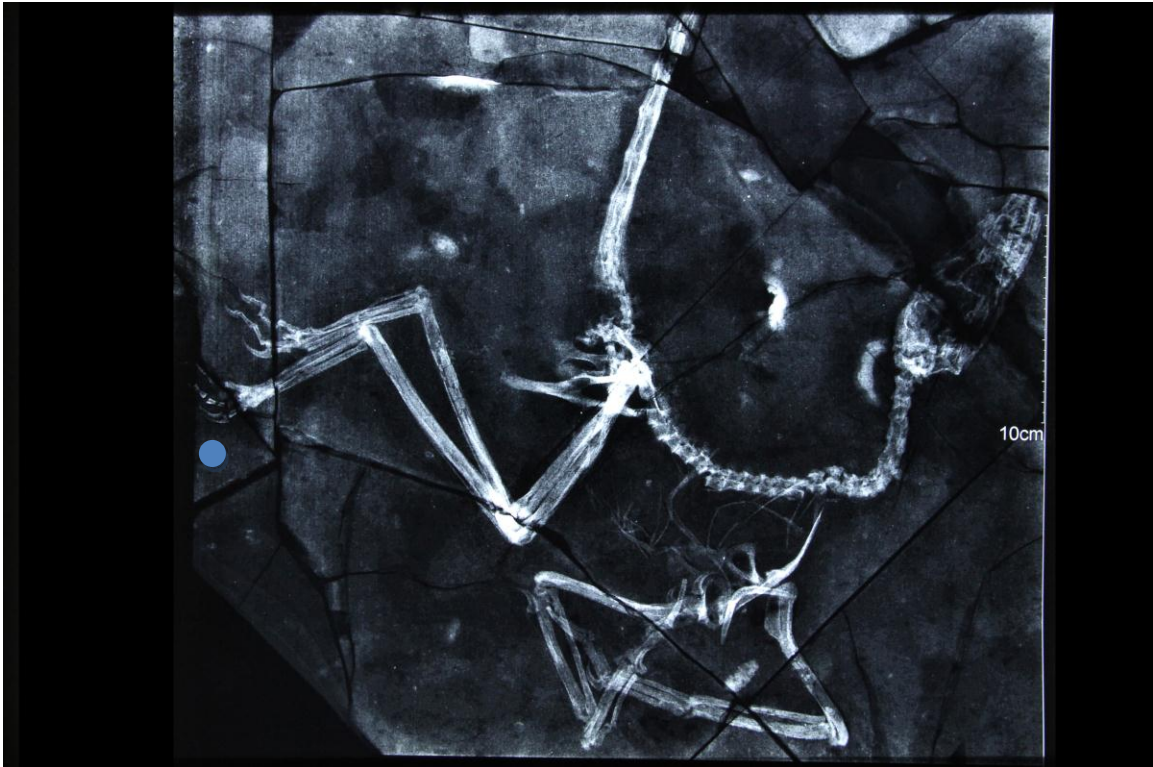


Figure 4. X-ray of D2933. Triangular block (marked by blue dot) by right foot is restored, though likely partially from original material. The dark lines running through the skull are the result of decreased density in those areas due to thinning for the slab from the other side. Cracks in the area of the skull were joined, but no creative restoration was attempted.

Unlike the rest of the elements, however the delicate bones of the skull have undergone not only lateral crushing, but also a degree of dorso-ventral smearing that has moved the right side of the skull ventral relative to the left elements. This shearing has largely moved entire elements, leaving the original shape of the bones intact. Crushing similar to that affecting the rest of the body has obscured some of the morphology.

The quality of preservation is generally high with the exception of the cervical vertebrae, which have been strongly affected by crushing. The ends of some bones have a roughened or pitted texture and appear more rounded off than might be expected. This texture might be reminiscent of abrasion, but since it is only present on some long bone

ends and the pubis rather than being broadly distributed across the skeleton and considering the high degree of articulation of small bones indicating a low energy environment of deposition I interpret this rough texture as an indicator of incomplete ossification (see discussion).

Radiography did not reveal any major inconsistencies as might be introduced by fossil alteration beyond those visible to the naked eye, but did help to establish the extent of fixative present in the skull (Fig. 4). This is primarily confined to two lines; one extending from the anterior edge of the frontal to the base of the articular, the second beginning less than one centimeter behind and converging with the first line as it passes through the jugal and enters the lower jaw. The material is not significantly denser than the bone and does not fluoresce under UV light; however it is identifiable under both x-ray and light microscopy, and generally visible in the specimen (Fig. 4). Restoration efforts by technically proficient but inexperienced preparators untrained in anatomy have resulted in one noticeable error. The distal pedal phalanges of the right digit II (2, 3, and the ungual) have been reconstructed incorrectly. Though this has been accomplished using what appears to be the original material, possibly from the opposing slab, measurements from these elements will not be used.

The D2933 slab contains several other fossils. There are three oblong masses found by the ankle, encircled by the arms, and above the central dorsals. These may also be easily seen as white ovals on the x-ray (Fig. 4). They are each uniform in color, lighter than the surrounding matrix, and are each about 3cm long. The material that composes them is finer grained than the surrounding matrix with no grains visible, even under a

handlens. This material is softer than the lamina surrounding them. The lamina also drapes over the edges of these objects, revealing that they were most likely buried and not formed in situ. They are not entirely uniform in shape and sediment obscures the entirety of their outlines, but they are generally fusiform. They also have three-dimensional relief, helping to further distinguish them from pedogenic spots. Based on these features and comparison with other specimens (such as University of California Museum of Paleontology specimen, UCMP150282) I interpret these to be coprolites. Interestingly, considering their burial in a lacustrine environment, they are straight, rather than coiled. At least one of them, located by the forearms, preserves small amounts of bone, suggesting that these may have been from a carnivore. Further study is underway to better characterize these interesting trace fossils.

There are two confusing masses of bone at separate points on the slab and there is a stringer of bones and bone fragments parallel to the tail (Fig. 5), as well as at least four other accumulations of bone. These are not embedded in sediment discernibly different from the matrix and have less confined shapes than the coprolites, so they may represent fecal masses, but the morphology is less distinct. These bones are not easily identifiable, though many are elongate, rib-like, and sub-millimeter in width. Among other features of the slab there is also a small object darker than the surrounding matrix, possibly a pebble or accumulation of plant matter and an enigmatic object which has two flat veined sections which resembles the wings of a small insect or a winged seed. A future paper will explore the microsite/coprolite aspects of this slab and others in the Jehol group.

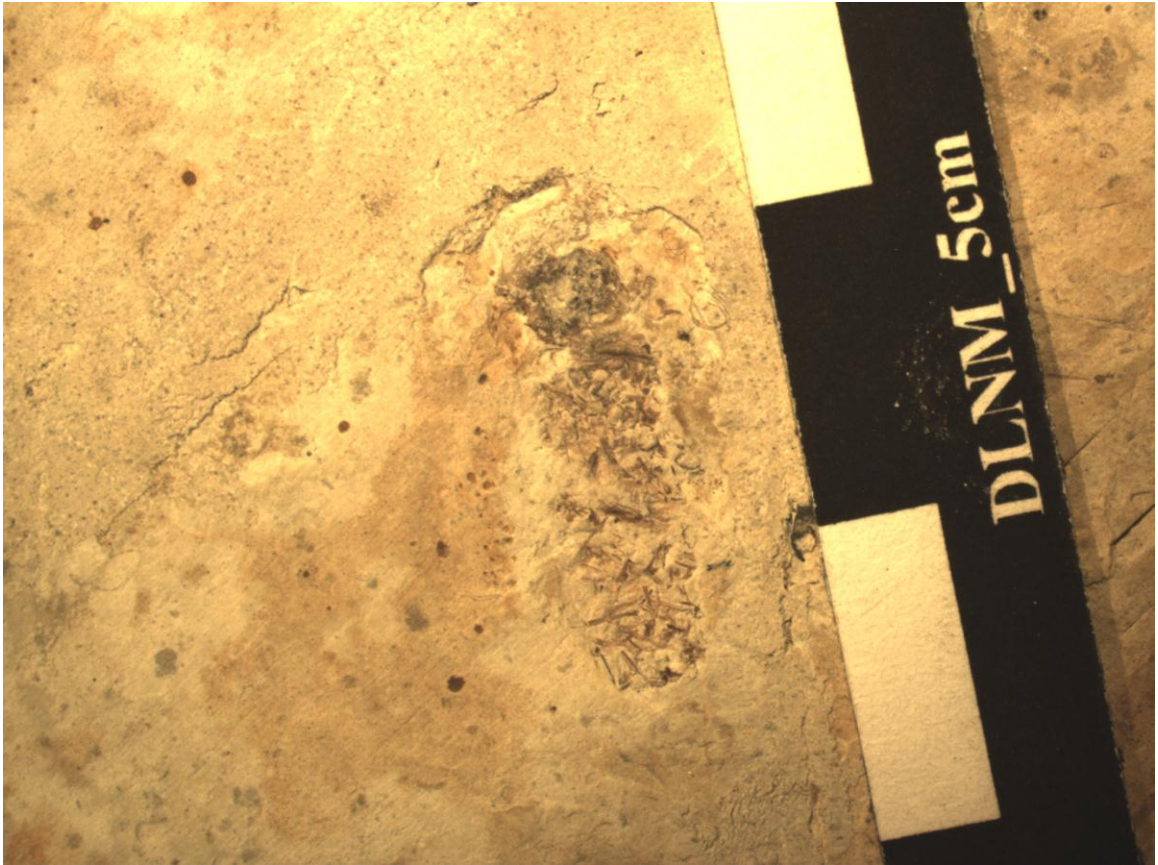


Fig. 5 Near-tail bone accumulation or coprolite.

Special preservation on the dinosaur includes the keratin sheaths on most of the unguals as well as the feathers. Darkened masses along the ventral surface are in the right position to be part of the body wall and may represent soft tissue remnants. The arrangement of the scleral ring and the gastralia is also noteworthy, in that they seem to approximate the original positions of these small, often displaced elements.

Osteology

Skull:

Skull The skull is lightly built as with other small dromaeosaurs (Figs. 6, 7). It is large in relation to the body as in NGMC-91, “Dave” (Ji et al., 2001); for example the skull is 1.15 times the length of the femur compared to NGMC-91 at only 1.05 times as long as its femur. The length of the skull of D2933 and other select measurements may be found in Table 2 below. The midline of the skull and parts of the braincase and posterior dentary are obscured by overlying bones and crushed. Bones such as the vomer, pterygoid, palatine, articular, and hyoid may be present they cannot be identified. Cranial elements not described below were obscured or could not be identified with confidence.

Premaxilla The premaxilla is lightly built and relatively short dorsoventrally for a dromaeosaurid. The long maxillary and nasal processes sit closely together creating a elongate, inclined, oval shape for the narial opening. The anterior angle of the premaxilla as measured along the ventral margin and up the anterior face forms an angle of about 60 degrees. This is intermediate to the very tight angle of *Sinornithosaurus* with 45 degrees (Xu and Wu, 2001) and that of *Velociraptor* (Kirkland et al., 1993). *Wulong* lacks the vertical posterior section ventral to the maxillary process present in some dromaeosaurs,



Figure 6. Skull with lower jaws, *Wulong bohaiensis*. Each block of scale bar 1cm.

and so the maxillary process is a direct continuation of the reduced body of the premaxilla. The diastema identified in *Sinornithosaurus* (Xu, 1999) does not appear on the premaxilla, though the anterior portion of maxilla is here devoid of teeth, producing a look more similar to *S. "haoiana"* than to *S. millenii*. Also noteworthy is that the sub-narial or maxillary process of the premaxilla is very long, isolating the naris from the maxilla.

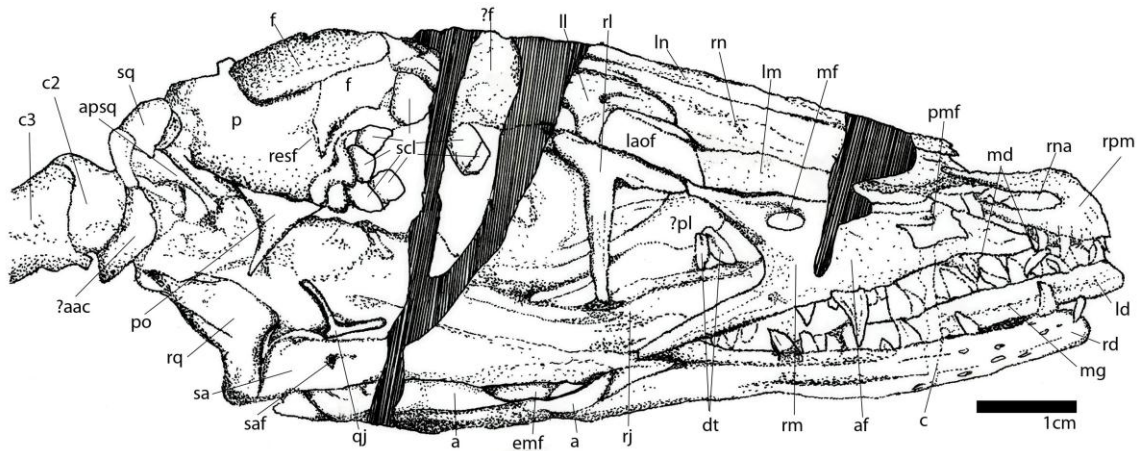


Figure 7. Sketch of skull shown in figure 3 with lower jaws and beginning of cervical series. Abbreviations: a, angular; ?aac, atlas axis complex; ?f, ?frontal; ?pl, ?palatine; a, angular; af, antorbital fossa; apsq, anterior process of squamosal; c, crack; c2, cervical vertebra 2; c3, cervical vertebra 3; dt, displaced teeth; emf, external mandibular fenestra; f, frontal; laof, left antorbital fenestra; ld, left dentary; ll, left lacrimal; lm, left maxilla; ln, left nasal; md, maxillary diastema; mf, maxillary fenestra; mg, Meckelian groove; p, parietal; pmf, promaxillary fenestra; po, postorbital; qj, quadratojugal; rd, right dentary; resf, rostral edge of supratemporal fossa; rj, right jugal; rl, right lacrimal; rm, right maxilla; rn, right nasal; rna, right naris; rq, right quadrate; sa, surangular; saf, surangular foramen; scl, sclerotic bones; sq, squamosal. Broken areas indicated by oblique hash marks. Scale bar 1cm.

Table 2. Selected Measurements for DMNH D2933

	<u>left</u>	<u>right</u>
<u>skull</u>		
anteroposterior length	-	98.6
rostral dorsoventral height	-	33.1
caudal dorsoventral height	-	39.2
tooth row length	-	43.2
dentary	-	53.1
<u>Forelimb</u>		
scapula	-	44.8
coracoid (thin bar length)	17	17.2
full coracoid	22.3	25.4
humerus length	75.4	76.6

Figure 2 Continued

delta-pectoral crest length	25.8	26
width of delta-pectoral crest	13.2	12.7
width (midshaft)	6.3	6.5
radius	>59.5	61.4
radius width	3.3	3.8
ulna	64.5	63.4
ulna width	5	5.7
Hand		
<i>digit 1</i>		
MC I	12.3	12.3
ph 1	15.8	15.9
ph 2 (ungual)	14.8	15.3
<i>digit 2</i>		
MC II	41.3	39.1
ph 1	19	20
ph 2	22.7	22.7
ph 3 (ungual)	15.3	15.1
<i>digit 3</i>		
MC III	18.7	17.1
ph 1	13.1	12.8
ph 2	7.5	8.3
ph 3	>13.2	14.2
Table 2 Continued		
ph 4 (ungual)	9.9	10.1
Pelvis		
ilium length	-	49.5
ilium height at front	-	12.3
Pubis	68.4	62.4
width at top	23.8	-
width at tubercle	16.9	-
length of symphysis	37.8	-
ischium height	27.5	26.9
ischium bottom	15.6	-
ischium top (proximal)	9.7	-
Foot		
<i>digit 1 (hallux)</i>		
MT I	>6.8	-
ph1	6.5	-

Table 2 Continued

ph2 (ungual)	5.2	-
<i>digit 2 (sickle)</i>		
MT II	54	53.5
ph 1	9	-
ph 2	9.2	-
ph 3 (ungual)	16.1	16.4
<i>digit 3</i>		
MT III	56.9	56.5
ph 1	14.3	-
ph 2	10	-
ph 3	9.3	-
ph 4 (ungual)	11.3	-
<i>digit 4</i>		
MT IV	53.5	56.7
ph 1	11.1	10.7
ph 2	8.5	7.6
ph 3	6.5	5.9
ph 4	6.7	6.1
ph 5 (ungual)	10.1	>8.9
<i>MT V</i>		
	>24.9	>25.8

The holotype of *Sinornithosaurus* does not show very long maxillary processes, but preservation is such that the actual state may be to exclude contact as well. *S. "haoiana"* possesses long processes, which even though disarticulated in the specimen, should be long enough to exclude the maxilla, so to the best of our knowledge this state is present in all microraptorines, except the holotype of *Microraptor* (Xu et al., 2000). This suggests that it may not be a useful diagnostic feature for *Sinornithosaurus "haoiana"* adding weight to the suggestion of Turner et al. (2012) that this taxon be synonymized with *S. millenii*. There are four premaxillary teeth. All are unserrated. The second premaxillary

tooth is not noticeably longer than the other three teeth. This could be the result of tooth replacement, but x-rays do not show the body of a larger tooth still emerging. Therefore, it is most likely that this tooth will not be replaced with a larger one like that of *Sinornithosaurs* until later in life or that this taxon has relatively uniform teeth in its premaxilla.

Maxilla The maxilla has the same roughly triangular shape as other dromaeosaurids, though the angle formed anteriorly is far more acute than most other dromaeosaurids. The right anorbital fenestra is fully visible and, due to taphonomic offset, the borders of the left are discernible when viewed through the right. In spite of this offset the fenestra maintains its shape; the lacrimals and maxillae on the right and left sides are preserved in articulation with the jugals, though the jugal is slightly detached from posterior ventral process of the maxilla. The acute anterior angle is very similar to the shape of the *Shanag* holotype (Turner, 2007).

The anterior 1 cm of the maxilla is devoid of teeth. Some teeth have been displaced from the maxilla as often happens in theropod fossils, but the anterior section shows no evidence of alveoli as in the narrow anterior of the maxilla in the dromaeosaurid *Shanag ashile* (Turner, 2007). Turner et al. (2012) reinterpreted the premaxillary diastema of *Sinornithosaurus "haoiana"* as spanning only that portion of the premaxilla which would articulate with the maxilla, leaving no gap in the tooth row. This would not explain the lack of teeth on the anterior maxillary of D2933. Though I am cautious about extrapolating too much from a single specimen, especially one preserved in two dimensions, this appears to be a true diastema. The ventral margin of the maxilla

angles ventrally across the first tooth, leaving the edentulous, anterior-most portion lower than the rest of the bone.

The remaining teeth within the maxilla vary greatly in size from one large tooth in the middle of the right maxillary tooth row of nearly 6 mm to one in the back of only 2.5mm. In general, the maxillary teeth have smooth anterior surfaces, without the serrations present on the posterior edge.

The tight anterior angle of the maxilla creates an antorbital fossa that is similarly acute anteriorly. Posteriorly, the fossa seems to originate at the border with the antorbital fenestra making its borders nearly as extensive as the entire lateral surface of the maxilla itself, similar to *Sinornithosaurus* (Xu and Wu, 2001; Liu et al., 2004).

Two fenestrae perforate the maxilla. One, a small opening with distinct borders, is identifiable as the maxillary fenestra. It is oval in shape and positioned high in the posterior portion of the maxilla near the orbit. The borders of the second fenestra are less clearly defined, but it is still identifiable by position as the promaxillary fenestra. Without clean edges little can be concluded about its morphology, except that it appears to have been oval in shape as well and did not exceed the size of the maxillary fenestra by very much and could have been considerably smaller.

The same narrow ridge along the ventral surface of the maxilla noted for *Sinornithosaurus* (Xu and Wu, 2001) and *Velociraptor* (Barsbold and Osmolska, 1999) is clearly present. It is well defined, running below the antorbital fossa for the entire ventral extent of the maxilla to the posterior end of the posteroventral process. It is difficult to

discern the row of foramina in a groove figured by Xu and Wu (2001) for *Sinornithosaurus*, but at least two foramina are present along this ridge.

It is difficult to determine if the maxilla of *Wulong* has the pitted appearance seen in the two specimens of *Sinornithosaurus*. The maxillary and lacrimal which show the distinctive excavations are crushed enough in D2933 that the texture of the bone is obscured.

Nasal As in *Sinornithosaurus millenii* the nasals are long and very narrow. In *S. millenii* they reach half the length of the skull (Xu and Wu, 2001). In D2933, the nasals are truncated caudally at a crack, but they probably approximate this ratio. This same crack has destroyed the dorsal articulation with the frontal, so the condition of the posterior articular surface remains unknown. The anterior of the bone shows the expected medial prong where it separates to surround the posterior margin of the naris, while the ventral process extends very far anteriorly to meet the long maxillary process of the premaxilla. This ventral process is longer than in *S. "haoiana"*, or the more poorly preserved process on the holotype

Lacrimal Lacrimal is "T-shaped" in lateral view, as in other deinonychosaurs. The top bar of the "T" is angled somewhat ventrally, and the anterior arm is longer than the posterior. An excavation at the juncture of the rostral and descending processes appears to be the pneumatic fossa noted in several taxa of coelurosaurs. (Currie and Dong, 1993). The antorbital fenestra is "D-shaped" with a straight back wall and ventral border meeting at the ventral end of the lacrimal. These

result in a more triangularly-shaped fenestra than that of *S.millenii* and perhaps slightly more so that of *S.haoiana*.

Frontal A major break in the posterior skull crosses the jugal and surangular and obscures much of the frontal. A flat bone with a very straight edge which may be the rear part of the left frontal has been pushed up and over the corresponding section of the right frontal and parietal. This in combination with extreme lateral flattening of this, the widest portion of the skull, makes interpretation of the frontoparietal contact problematic. The lateral section of the sinusoidal rostral demarcation of the short oval supratemporal fossa seen in *Sinornithosaurus* by Xu and Wu (2001) is possibly visible as part of this region (see RESF in Fig. 7 for this shape, and compare with fig. 6). The shape of this curve strongly resembles the S-shaped curve of *S. millenii*, as well as the line of fusion seen in *Deinonychus*.

Parietal Little can be determined because only the broad dorsal shelf of this bone may be observed. With the postorbital displaced ventrally (see below) the parietal seems to be in close contact with the posterior bones of the scleral ring. This is likely a consequence of lateral crushing, as is the unclear nature of the posterior parietal where it abuts the squamosal.

Squamosal Like the parietal the squamosal's position is clear but little can be determined about its anatomy. The paraoccipital process overlies the interpreted position of the c-1 vertebra. The prequadratic process is buckled against dorsal portion of the quadrate. The post-orbital or anterior process is the best preserved portion of the

squamosal; it is long and very slender where it reaches to contact the post-orbital. The position of the medial or parietal process is difficult to determine. A shelf above the prequadratic process as in *Velociraptor* (Barsbold, 1999) is suggested by a ridge, but crushing makes this determination questionable.

Post-Orbital The post-orbital is triradiate and relatively small. It is surprisingly equilateral, with none of the sharpened or down-swept processes seen in *Velociraptor* (Barsbold, 1999) or in unenlagiines such as *Buitreraptor* (Makovicky, 2005). The ventral process does extend longer than the others imparting a “Y” shape, closer to that seen in *S. haoiana* than in *S. millenii*.

Occipital Several small bones at the caudal end of the skull are likely the occipital bones, but other than their position behind and slightly below the main part of the parietal, little information can be gleaned. Their separation into at least two separate pieces is reminiscent of the condition of the otoccipital in the Eichstatt specimen of *Archeopteryx* (Wellnhofer, 1988; Whetstone, 1983).

Scleral Bones At least five bones interpreted as part of the sclerotic ring are preserved in semi-articulation within the orbit. Individually flat and sub-circular in shape they comprise a tight hemicircle. It is difficult to compare with certainty but they appear similar to those described as “sub-rectangular” in *Sinornithosaurus* (Xu and Wu, 2001). They lie posteriorly and superiorly in the orbit.

Jugal The main body of the jugal extends horizontally and with a uniform height, without the caudal slope of *Dromaeosaurus* (Currie, 1995). The anterior portion of the jugal where it would have articulated with the maxilla is poorly preserved, having been compressed with a mass of bone probably representing the remains of the palate. A slight dorsal bend may be discernible as it meets the much better preserved maxilla. Along the visible portion it is longer and more slender than in *Bambiraptor* (Burnham, 2000), but does not approach the extreme thinness interpreted for *S. millenii* (Xu and Wu, 2001). In most regards it resembles that found in *Sinornithosaurus* “*haoiana*” and *Velociraptor* (Barsbold, 1999). The sub-orbital margin appears even straighter than in these animals.

Quadratojugal The quadratojugal is distinctly “L” shaped, differing from the “T” shape of most dromaeosaurids (Currie, 1995). The ascending process is about 6 mm and the jugal process is 5 mm long. A comparison with *S. millenii* demonstrates that the ascending process is remarkably tall and slender, while the jugal process is similar in shape and length. The posteroventral process is truncated in this specimen as it is in the two *Sinornithosaurus*. Likely the *S. millenii* specimen is missing the median section of its ascending process. In any case, D2933 is more similar to *S. “haoiana”* which has a quadratojugal with a 7 mm ascending process and a 3.6 mm jugal process. Though the bone’s general shape is poorly preserved in *Microraptor*, the similarity to *Sinornithosaurus* is so strong as to consider this character synapomorphic. The length of the jugal process, however, exceeds that of even the much larger *Sinornithosaurus* specimens. Such a long jugal process is a unique character of *Wulong*.

Quadrate The right quadrate is preserved close to life position. It has rotated to show a slightly posterolateral view, and now is abutted by the surangular anteriorly rather than ventrally. Due to its lateral exposure the shape of the condyles are not as apparent as they are in *S. millenii*, but there does appear to be both a lateral and medial condyle. Only the ventral portion is fully exposed, but the curvature that would make up the caudal portion of the prequadrate foramen is just slightly visible facing the quadratojugal and is particularly shallow. The preserved portion resembles that seen in *Sinornithosaurus*.

Lower Jaw The low, rectangular jaws are preserved in near-articulation. Because they are still in position only the right lateral surface is visible, except for the medial surface of the left dentary. This means that the medial jaw bones are not visible, so as with the cranial bones, elements not described below are not distinguishable. Though the right jaw is slightly abducted, it seems clear from its length and the position of the left mandible that the lower jaws would have sat comfortably within the premaxillae as in *Velociraptor* (Barsbold 1999).

Dentary The dentary shows the usual dromaeosaurid condition of being long and labiolingually narrow. Its short dorsoventral height gives it the impression of being even more gracile than previously described taxa. The double line of foramina on the lateral side of the right dentary is readily apparent and the Meckel's line is equally visible, running anteroposteriorly along the medial side of the left dentary. The posterior end of the dentary is bifurcated; the ventral section extends posteriorly, while the dorsal process is visible up to where it is overlain by the jugal process of the maxilla. No third

process is visible as described for *Sinornithosaurus* by Xu and Wu (2001), but it is difficult to tell whether it was present in life because the dorsal portion is less well preserved and it may be obscured.

Surangular The long surangular is imperfectly preserved, suffering from the crushing seen throughout the skull and being crossed by the large dorsoventral crack. It abuts the condyles of the quadrate. The prominent crest on the surangular visible here is present in *S. millenii* (Xu and Wu, 2001).

Angular The angular is crushed similarly to the surangular. This exposed portion curves anteriorly upward towards the bifurcated dentary. Only its overall shape can be discerned which seems very similar to that of the angular in other dromaeosaurids.

Teeth The teeth of D2933 are broadly comparable to those in the other identified taxa of microraptorinae. There are four teeth in the premaxilla and only room for 9-10 in the maxilla as in *S. millenii* (Xu and Wu, 2001). Getting an accurate tooth count for the dentary is problematic as not all are present and the lateral angle precludes direct viewing of all alveoli. Eleven teeth are visible in place in the right dentary, and at least 9 in the left, but there appears to be room for around 15 teeth on each side. Like *M. zhaoianus* (Xu et al, 2000), the premaxillary teeth of D2933 have no serrations. In most maxillary and dentary teeth present, denticles are visible on the posterior (concave, distal) surfaces only. None of the premaxillary teeth show the lingual groove present in *Sinornithosaurus*. The posterior teeth in the dentary appear to have more denticles than those located anteriorly. Whereas the anterior maxillary teeth of *S. "haoiana"* do

occasionally possess posterior denticles, they do not seem to occur in D2933 until the middle of the maxilla. Importantly, in a few teeth, faint denticles are visible on the anterior side near the point. This strongly distinguishes it from *Microraptor*, which has no anterior serrations, a feature shared by other groups diverging near the base of Paraves, some of whom have lost serrations all together, such as *Sinovenator* (Xu et al, 2002), *Anchiornis* (Hu et al 2009) and of course, *Archaeopteryx* (Wellnhofer, 2009). Among microraptorines, *Hesperonychus* preserves no teeth (Longrich and Currie, 2009) and *Graciliraptor* has perhaps the condition closest to D2933, with anterior maxillary teeth lacking serrations and more caudal teeth with anterior denticles, though these remain smaller than the posterior serrations (Xu and Wang, 2004). The teeth have a relatively smooth root to crown transition, distinguishing them from the “waisted” teeth in *Microraptor* and distancing them from the more troodontid-like condition.

Rest of Axial Column:

Vertebrae The cervical series of D2933 is preserved in situ which allows around nine or ten vertebral bodies to be identified, in keeping with the number expected in dromaeosaurs (Norell and Makovicky, 2004). There is very little additional information to be gleaned as the delicate processes and struts have been collapsed medio-laterally, preserving little morphology (Fig.8). The atlas and axis are present, but any significant anatomy is obscured by crushing and the posterior portion of the skull.

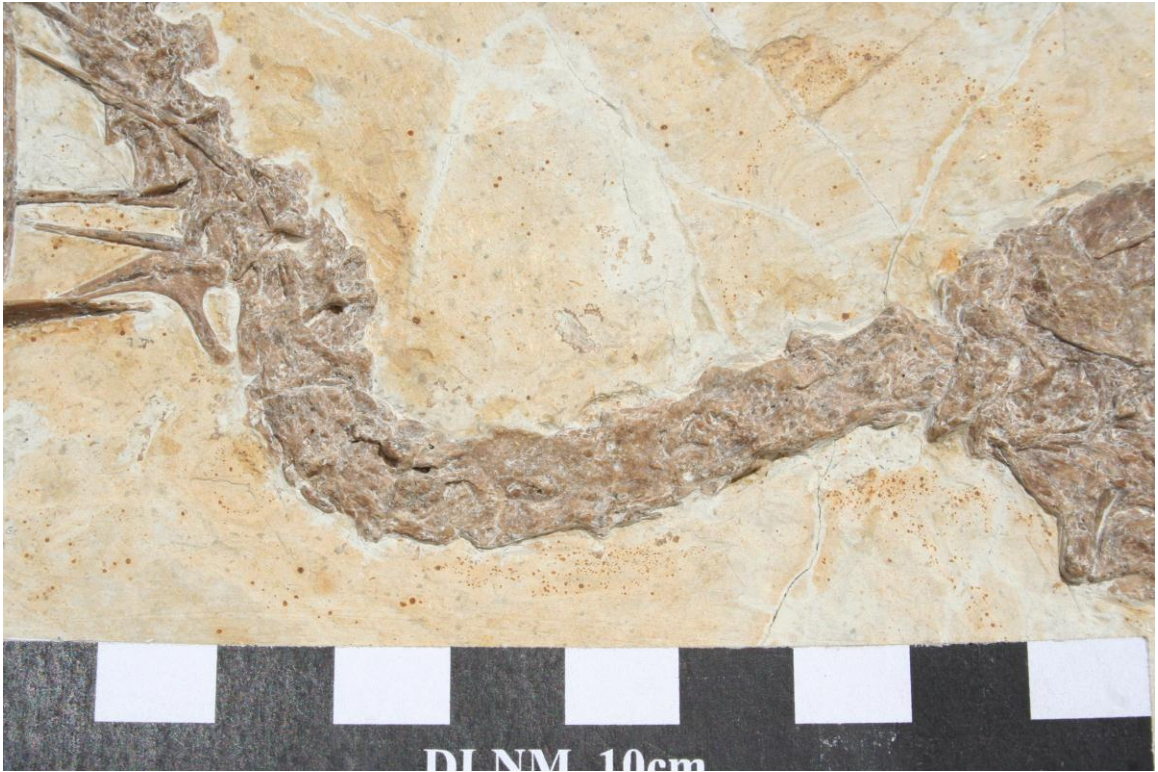


Figure 8. Cervical vertebral column, note poor preservation.

The dorsal vertebrae are very square in lateral profile (Fig.9). Details of the neural arches are difficult to discern, but the border with the centra is very clear due to a complete lack of fusion between arch and centrum. The centra are shallow with a slightly concave ventral surface in lateral profile.



Figure 9. Dorsal vertebral column. Note the feathers above the posterior dorsals. For a close-up view please see the following figure.

The neural spines are short relative to their anteroposterior length and squared off with a slight expansion at the top in lateral view. The very blade-like and laterally compressed spines maintain a very consistent morphology throughout the series. They are slightly off-set posteriorly from the center of the centra. The dorsal expansion gives the ventral part of the blade a pinched look, much more constricted than in *Microraptor* (Hwang et al., 2002).

A foramen opens on the laterally on the side of the dorsal vertebral bodies (Fig.10). This is most likely a pneumatic foramen leading to a pleurcoel. It is clearly a biological structure repeated in all the dorsals and not a relic of taphonomic alteration. This foramen is oval in shape, relatively large, and smooth-edged. They open on the

anterior part of the centrum and sit above the midline. Uniquely, the foramina in the more posterior dorsal vertebrae are inclined downward towards the front, so that in the second dorsal this inclination is slight, but by the sixth and seventh it is dipping anteriorly at an angle of more than 45 degrees. The anterior dorsals have some division of these pneumatic openings with a thin strut between them, but posterior dorsals have a single opening.

Though raised, stalk-like parapophyses on the dorsal vertebrae are diagnostic characters of dromaeosaurids (Norell and Makovicky, 2004), they are not visible on this specimen. This may partially be the result of taphonomic crushing obscuring detail, as in the cervical series, but they are mostly obscured by the overlying ribs, which remain partially articulated with the anterior dorsals.

In general, the dorsals are all very similar along the spinal column with slight anterior to posterior trends from short to slightly taller neural spines, mostly squared-off neural spines to ones with a longer posterior expansion at their dorsal edge, and increasing anterior inclination of the pneumatic foramina.

The sacral series is somewhat disarticulated. The arches remain unfused to the centra and there is no evidence of the fusion of the vertebral ribs to the ilia. The centra of at least three sacra are visible: two in articulation and partly in place within the ilial cavity and one which has fallen out to the posterior (Fig. 11). The vertebrae are poorly preserved but the bones are uniform in size and similar in dimensions to the centra of the dorsals. Along with the posterior centrum, there is a jumble of bone which probably represents sacral ribs and arches.

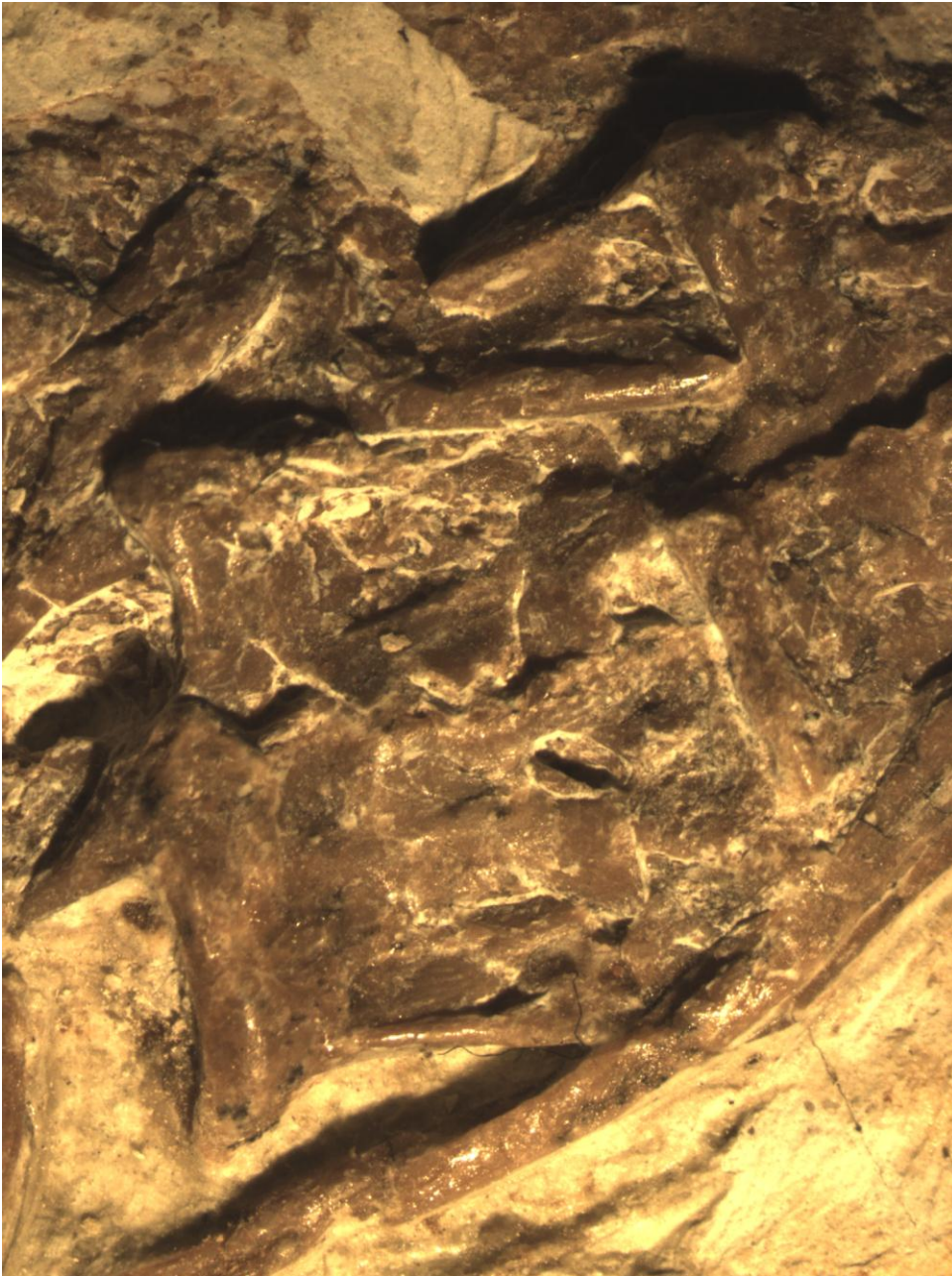


Figure 10. 7th dorsal vertebra, showing lack of fusion, inclined anterior pneumatic foramen, rib articulated to 6th dorsal extends below. Dorsal to top, ventral to bottom of photograph. Vertebra is approximately one centimeter in length.

The shape of this mass along with radiographic evidence indicates a fourth centrum may be present beneath the visible elements. The disarticulation of the sacrals was probably caused by the same taphonomic processes that caused the rotation of the proximal

caudals. *Sinornithosaurus millenii* has a visible sacral series of five fused vertebrae (Xu et al., 1999), which is also in accord with the length of the sacral series in *S. "haoiana"*.

The caudal series is complete to its posterior end, with 29 or 30 caudals present, including the very small, possibly incompletely ossified distal-most caudal which is barely more than twice the width of the accompanying ossified elongate chevrons and prezygophyses (Fig. 11). A caudotheca composed of the caudals and these rod-like elements extends from the third caudal to the tip of the tail, with some ends extending all the way to the ilium (Fig. 11). The anterior extension suggests that there was some flexibility to these elements; if they were fragile it seems unlikely that the tail could have moved in a practical manner. The first three caudals have been rotated 90 degrees to the animal's right and are preserved in ventral view. Their ventral aspect is marked by a shallow but wide groove running anteroposteriorly along the body of each vertebra, with highest relief at the four corners and a fainter sulcus in the middle running laterally. The centra of the first five caudals are of similar dimensions to the dorsals. At least one proximal caudal (ca 4) preserves a non-elongate chevron (Fig.11). This chevron is oriented dorsoventrally as opposed to along the tail. There is some posterior deflection of the distal end. The chevron is 11 mm long and 2 mm wide, far shorter and wider than the elongate elements composing the rods of the caudotheca. At least the first three caudal vertebrae have transverse processes (Fig.11). They are thin dorsoventrally, broad anteroventrally, long and point slightly posteriorly. At their lateral ends they are slightly hooked posteriorly. The transverse processes widen as they move posteriorly, with the second wider than the first and the third wider than the second. These processes are each

a third longer than the width of the centrum. I can find no other dromaeosaurids described with this trait, and it is certainly unique within microraptorinae. At least one other dromaeosaurid specimen, MOR 660, has very long transverse processes on the single preserved anterior caudal, so the distribution and function of this condition within dromaeosauridae may be worthy of further investigation. Following the fifth caudal the vertebral centra increase in length until the eighth where they achieve a stable average length of about 19 mm. There is a gradual decline in length until around the 23rd caudal vertebra where there is a sharp decline in length leading to the under 10 mm long 28th vertebra.

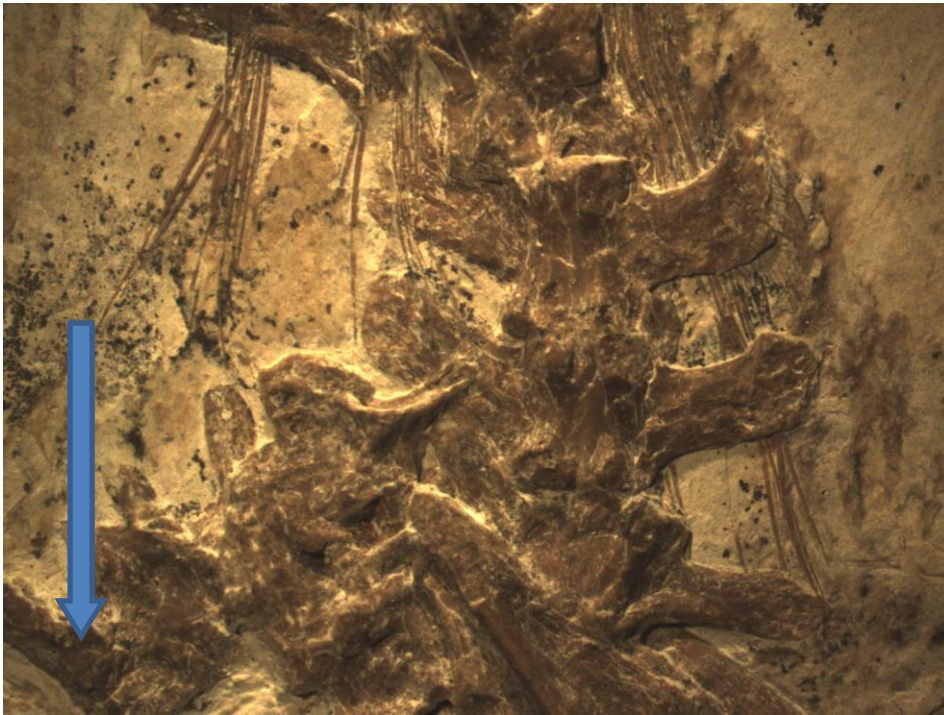


Figure 11. Proximal portion of the tail showing proximal caudals with elongate transverse processes and the delicate proximal ends of the elongate chevrons. Note possible sacral centrum in lowest left, indicated by arrow.

In *Microraptor* the tail is composed of 24-26 caudal vertebrae (Hwang et al 2002) far fewer than in D2933. The tail of *Wulong* is further differentiated by the fact that the mid-caudals are less than three times the length of the dorsals (Fig.12), more in line with the symplesiomorphic state in dromaeosauridae than the derived state in *Microraptor* of mid-caudals equaling between 3 and 4 times the length of the dorsals (Xu 2004, Turner 2012). For this reason it is very unfortunate that better tail remains are not present for either adult *Sinornithosaurus*. It should be noted that the mid-caudals are short only in comparison to *Microraptor*; they are still long compared to most theropods.



Figure 12. 19th caudal vertebra, showing gracile shape of middle caudals.

Zheng et al. (2009) considered possession of middle caudals having a length more than twice that of the dorsals to be a diagnostic character for *Tianyuraptor*. As this state is identified here as well as in *Microraptor* (Hwang, 2002), I suggest that it is no longer useful. As *Tianyuraptor* by all accounts appears to be a valid taxon I suggest that further specimens will reveal better diagnostic characters.

Ribs and Gastralria Not all of the ribs are preserved, only 10-13 ribs present of a predicted 22-24. In form the ribs preserved are elongate, rather straight with a well-developed head. They are broadly similar to those of *Sinornithosaurus*. Four ventral or sternal ribs are present, three still articulated to the distal ends of their ribs. The proximal ends of these ribs are expanded slightly. Only one possible uncinat process is preserved.

Pectoral Girdle and Forelimbs:

Pectoral Girdle: The pectoral girdle of D2933 is well preserved and fully articulated though it has detached from the axial column by several centimeters (see Fig.13, and drawing in Fig. 3). In detaching, the left side was twisted caudally and to the right. This results in a pectoral girdle that appears to have been rotated 180 degrees. The animal is lying left side down, thus the forelimb lying cranially is the right side and that laying caudally the left. This can be seen in the shape of the sterna (see section below) as well as their position



Figure 13. Pectoral girdle and forelimbs. Note feathers extending from the ulna, and white coprolite above the radius.

apparently above the coracoids. The orientation of the pectoral girdle is further indicated by the position of the right glenoid fossa when rotated to the right side where it would face laterally. All elements are visible excepting the left scapula which is largely obscured by the coracoids, furcula, and right scapula as suggested by radiographic work (Fig.4).

The forearms of D2933 are exceedingly long in comparison to the rest of dinosauria. The ratio of total forelimb length to hindlimb length is 79.4% which compares favorably with the 80% recorded for *S. millenii* (Norell and Makovicky, 2004), and to the 85% estimated by Liu et al (2004) for *S. "haoiana"*. These ratios are among the longest recorded in non-avian dinosaurs. It is notable however that D2933 falls near

the range of the two *Sinornithosaurus* specimens rather than being significantly shorter or longer. The ratio is also close to the value of *Microraptor* which has a ratio of 77%. Because it shares this high ratio with its closest relative as well as another member of microraptorinae, in this instance phylogeny may play a stronger role in determining this ratio than ontogeny.

Scapulocoracoids The scapulocoracoids are preserved in ventral view (Fig.14). The right scapulocoracoid in particular is fortuitously preserved in antereolateral view showing both the glenoid and the broad square blade of the coracoid. The scapulocoracoids show the typical “L-shaped” morphology common to enantiornithines (Chiappe et al., 1999) and the microraptorines *Sinornithosaurus millenii* (Xu et al., 1999) and *Microraptor zhaoianus* (Hwang et al., 2002) and very similar to that observed in *Sinornithosaurus “haoiana”*. The scapulae and coracoids remain unfused and so will be discussed separately below.

The blade of the scapula is long and strap-like, but only 59 percent as long as the humerus. This relative length compares well with the ratio of 0.59 for *Sinornithosaurus millenii* and 0.66 for *S. “haoiana”*. This is in keeping with the ratio noted for microraptorines (Makovicky et al., 2005).

As noted above, the left scapula has been folded under the furcula, but both coracoids are visible in lateral view close to anatomical position. That this is the case can be further confirmed by the anterior orientation of the coracoid tubercle. These tubercles are large and slightly inclined towards the glenoid. One of the most distinctive features of this animal is the open condition of the coracoid fenestrae. The fenestrae of both

coracoids are visible and are very large relative to the size of the element, reducing the remaining coracoid to narrow struts, especially laterally. Tear-drop in shape, the supracoracoid fenestrae are 7.37 x 9.36 mm on the right and 6.75 x 8.63 mm on the left. The slightly smaller measurements of the left supracoracoid fenestra are taphonomic and due to the left coracoid's more oblique position prior to compaction. The open condition of the fenestra is not only very distinctive, but may serve to indicate basal lability in the condition of this opening within paraves. The coracoids are not preserved in *Mahakala* (Turner et al., 2011) but in other basal paravians such as *Anchiornis* (Xu et al., 2008; Hu et al., 2009), *Sinovenator* (Xu et al., 2002), and *Archeopteryx* (Wellnhofer, 2009) the coracoid possesses no such fenestra. *Bambiraptor* falls near the base of the Microraptoria (Senter, 2007), and it has no coracoid fenestra at all. Outliers to the dromaeosauridae also possess no structures described as coracoid fenestrae, though many have coracoid foramina; e.g. *Microvenator* (Mackovicky and Sues, 1998). Though this fenestra is also large in closely related *S. millenii* (Xu, 1999) no other microraptorine specimens yet described have complete scapulocoracoids preserved in dorsoventral view so the condition remains unknown in *Graciliraptor*, *Hesperonychus*, and *Tianyuraptor*. In no other dinosaur does it approach the distinctively large relative size found in D2933, but the enlarged size in general may emerge as a synapomorphy of a larger clade, such as that uniting *Wulong* and *Sinornithosaurus*, or even the microraptorinae itself. A coracoid foramen is also present in D2933 on the lateral portion of the coracoids, by the glenoid; this is not commented upon in papers describing the other members of Microraptorinae, but presumably is present.

Sternum The bony sterna are very small; smaller than the coracoids. They are lying in contact with the coracoids, with the left sternum flipped laterally so that the normally lateral side now faces medially giving a view of the posterior or dorsal side (Fig. 14). Fusion between the right and left sides is totally absent. The two bones are generally half-moon- or “D”-shaped with the medial edge convex. The lateral edge, which in life would have articulated with the sternal ribs, is slightly concave, scalloped, and ends with a marked lateral spine at the anterolateral corners. This spine appears to be a true continuation of the bony sternum and seems similar to that seen in *Microraptor* “*gui*”. It appears as a continuation of the anterior edge, and after coming to a point, curves back medially to the more linear lateral border. This only slightly concave lateral section has four indentations, possibly for articulation with ribs, which lend it its scalloped appearance. This contrasts with *S. “haoiana”* which has at least 5 visible, and with *Microraptor* “*gui*” which has no distinctive lateral indentations.

A small hole presents at the caudal end of both sterna, slightly medial of center, but it is difficult to determine whether this is an actual feature or the taphonomic result of thin bone at this point. There is a similar well-defined round hole penetrating the right sternum. The edges of convex surface appear rough indicating a cartilaginous extension may have existed beyond this point. In contrast, *Microraptor* and *Sinornithosaurus*, both possess large, generally co-ossified sterna (Xu, 1999; Hwang, 2002; Liu, 2004).

Furcula The furcula is complete. It is visible except for the right epicleidial process and a portion of the ramus (Fig. 14).



Figure 14. Close-up of pectoral girdle.

Crushing on the two rami in a 1 cm oblong on both sides shows that this element is highly pneumatized (Nesbitt, 2007), though a possible pneumatic foramen on the proximal dorsal edge of the bone is inconclusive. In spite of this crushing the furcula shows a degree of dorsoventral flattening similar to that found in *Microraptor* (Hwang et al., 2002) and *Sinornithosaurus*. The furcula is boomerang-shaped rather than U- or V-shaped, with an interclavicular angle of about 110 degrees. This is wider than in other microraptorines, but Makovicky and Currie (1998), Hwang et al (2002), Lipkin et al (2007) have found variable angles within species so this difference may not be deeply significant. The furcula does not possess a keel, hypostyle, or hypocleidium. It maintains a gentle, shallow angle and is smooth and continuous at the symphysis. D2933 shows neither a lateral expansion of the rami nor the slight notching at the epicleidial ends

visible in *confuciusornithids*. Rather, it keeps a very regular width as it approaches the ends, only narrowing in the last few millimeters to a rounded point. The exposed left epicleidium does not show the same ligament attachment scarring that is seen some theropods (e.g. *Suchomimus*; Lipkin et al 2007). The exposed right side is relatively long; the length of one side relative to the femur approaches $1/3$, which is similar to *Anchiornis* (Xuet al., 2009). The exterior shows the same juvenile bone surface texture mentioned for other elements. The overall morphology is very similar to that of *Sinornithosaurus*, *Microraptor*, and *Bambiraptor*, but noticeably distinct from the obtuse and keeled derived forms such as *Velociraptor* or the relatively robust and acutely-angled furculae of basal Avialae. In *Confuciusornis* such as DMHN D1877, the furcula is more strongly bowed into a “U” shape.



Figure 15. Close-up of forelimbs.

Humerus Both humeri are well preserved. The proximal portion of the right humerus in particular is visible and in good condition. The long axis of this proximal portion is inclined in towards the small humeral head by 38 degrees, forming an obtuse angle of 142 with the shaft of the humerus. The delta pectoral crest is short for a microraptorine, less than one third the length of the humerus, though it is unknown if this ratio will be affected by further growth. The internal tuberosity is well developed as in *Microraptor* (Hwang et al., 2002), being just under 50% the length of the deltapectoral crest. Its point is also distally located as in that animal. Both distal condyles are visible on the right humerus but crushing obscures most detail except that they are of comparable size and separated by a deep groove. A small ligament pit is present on the medial condyle where it is visible on the right distal humerus.

A small hole opens on the medial portion of the deltapectoral crest of both humeri, about a third of the way out from its proximal end. This may represent a foramen as recently suggested in *Microraptor* (Li et al., 2012, SOM), but it is difficult to interpret the amount of taphonomic breakage to a naturally thin spot in the bone. This thinning may presage the enlargement of the deltapectoral fossa seen in basal birds such as *Confuciusornis*.

Ulna and Radius The ulna is nearly as thick as the humerus and nearly twice as thick as the radius at their respective midshafts. The ulna and radius are sub-equal in length with the ulna only longer by the length of the olecranon. The forearm is long, with the radius 80% as long as the humerus. The ulna is straighter than either *Sinornithosaurus "haoiana"* or *Microraptor* (Xu et al., 2000).

Carpus The semi-lunate carpal is visible in both wrists, immediately proximal to metacarpals I and II (fig. 15). On the left wrist this carpal lies out of contact with the first metacarpal, though still abutting the MC II. This is possibly a consequence of hyperflexion associated with the post-depositional history of this fossil. Though the left semi-lunate is slightly rotated towards MCIII, the right is in place covering about half of both MC-I and MC-II. No other carpals, such as the ulnare are present.

In general, this wrist resembles that of *Deinonychus* (Ostrom, 1969b; Senter, 2006) though the semi-lunate carpal is reduced enough that it does not solidly contact the third metacarpal. A semi-lunate carpal capping the entire proximal end of metacarpal I and a large portion of metacarpal II is nearly identical to that described for *Microraptor* (Hwang et al., 2002). An ulnare as described by Ostrom, 1969 for *Dromaeosaurus* is not present in D2933.

Metacarpals and Manual Phalanges The first metacarpal is very short compared to the length of the second, a feature common in theropoda (Fig. 15). MT I is more expanded proximally than the other metacarpals and it also possesses a longer flange on the lateral side towards metacarpal II. Metacarpals II and III are almost identical in length. MT II is more robust than MT III, however.

Phalanx I-1 is long enough to approach the distal ends of the second and third metacarpals. It is slightly more gracile than these metacarpals and has a distal articulation with its ungual which would allow a great degree of rotation. Phalanx I-2 is by a slim margin the largest of the manual unguals. The second digit is more robust than the third. Phalanx II-1 is very wide, equaling or exceeding the metacarpals in width. The next

phalanx in the digit (II-2) is longer than the first, but much narrower, culminating in a very small head for articulation with an ungual only slightly smaller than that of digit I. In the third digit the first phalanx is one and a half times as long as the second phalanx. The second phalanx on both sides is damaged however, so this assessment is estimated from fragments and spacing. This is in sharp contrast to both *S. millenii* and *S. "haoiana"* where the first phalanx is only twice the length of the second. *Wulong* differs even more strongly from *M. zhaoianus* and *M. "gui"*, where the ratio is 2.5 and 4.2 respectively. If correct, the pIII-1/pIII-2 ratio in *Wulong* of only 1.5 is the lowest among microraptorines. It may be that this is not damage, but lack of ossification in distal III-1 and/or III-2. The symmetrical nature of the missing bone on the right and left might support this idea. The third phalanx of the third digit is long and very thin. That the manual unguals of digit I are only marginally larger than those of digit II is similar to other microraptorines. The ungual of the third digit is the smallest of the manus.



Figure 16. Pelvic girdle. Note lack of fusion in the pubis, short amount of tail without reinforcing ossified tendons, and distinctive ischia.

Pelvic Girdle:

Ilium Both ilia are preserved though the dorsal portion of the right ilium has been lost (Fig.16). The ilium is only mildly dolichoiliac, with a preacetabular process only marginally longer than the postacetabular process. The antiliac shelf is flat, slightly concave laterally, and extends anteriorly for half the length of the preacetabular process. Even allowing for postdepositional flattening this seems less reduced than in other dromaeosaurids, such as *Microraptor* (Hwang et al., 2002) and *Velociraptor* (Norell and Makovicky, 1997). The antiliac crest visible in medial ventral view on the holotype specimen of *Sinornithosaurus* is relatively larger than that of *Microraptor* but still smaller than that present in D2933. The interior of the left ilium visible in medial view

does not show the pitting characteristic of the same location in *S. millenii* (Xu et al., 1999). The ischiadic peduncle is well developed and half of its length extends below the blade of the ilium. A well-developed flattened surface on the ischiadic peduncle contributes to the acetabulum. A similar peduncle is described in *Microraptor zhaoianus* (Hwang et al., 2002), but is not apparent in *S. "haoiana"*.

Ischium The left ischium is entirely exposed and its extent is only about a third of the length of the pubis. The ischia are boot-shaped and thin mediolaterally. Proximal iliac and pubic processes are separated by a straight dorsal border. The distal portion has two posterior features: a very strong posterior process located most of the way down the body of the ischium and a well-developed posteroventral process at the distal end, as well as a sharply angled anterior obturator process extending towards the pubis. The large size of the posterior process of the ischium as well as its distal position lend the distal portion of the ischia a bulbous appearance, very much opposed to the straight, narrow appearance of *Microraptor*. The ventral border is notably concave. Though distinctively different from those of *Microraptor* the ischia of D2933 are still closer to those of microraptorines than to any other theropods. They most closely resemble those of the two specimens of *Sinornithosaurus*, especially in the ratio of their length to the length of the pubis, and in the morphology of the posterior region.

Pubis The pubes are rotated to the right, leaving the right pubis articulated and pulling the proximal end of the left forward and medially to rest beneath the last exposed dorsal. The pubes are fixed to one another though incompletely fused; the line of suture is

visible for almost the entire length. Exposed in anterior view, the pubis is relatively unrecurved with a fairly indistinct pubic boot. Midway down the shaft, close to where the line of fusion with the opposing pubis begins, there is a very prominent lateral tubercle. This shape is nearly identical to that seen in *Sinornithosaurus* and *Microraptor*, and very close to that of *Hesperonychus*, though further up the shaft and lacking the slight dorsal upturn of the tubercle in that specimen. The boot may have the characteristically microraptorine backward inflection by the medial rugosity hidden by its orientation, but if so it still appears greatly reduced. The straightness of the pubis appears similar to that found in the *Sinornithosaurus* specimens and very different from that seen in *M. "gui"*, or *Hespyronychus* (Longrich and Currie, 2009), where it has a pronounced posterior hook. Visible pubis morphology may be heavily influenced by the position of preservation however, which becomes apparent when compared with the shape in the *Sinornithosaurus* specimens. The curvature and size of boot are not visible in anterior view, which is also the case with D2933. The distal end of the pubis is rough, cancellous-looking bone, and if this is indeed caused by an incompletely ossified state (see discussion), the boot may have still be partially cartilaginous at the time of the animal's death. The length of the ischia relative to the pubis is much shorter in D2933 than in the *M. gui*. The ischium/pubis ratio is approximately 2/5, which is about the same in *S. "haoiana"*. This ratio is close to 2/3 in *M. "gui"*, and nearly 1/2 in *M. zhaoianus* (Hwang et al., 2002).

Hind Limbs:

Femur D2933 preserves both femora in articulation with the hips proximally and with both tibiae and fibulae distally (Fig. 17). The femora are complete, though the proximal portion of the left femur is obscured as it passes beneath the hips and the right femur. The femoral head possess the same ventral lip seen in *Microraptor* (Hwang et al., 2002) and both *Sinornithosaurus* species, though this lip is more strongly expressed in these last forms. Though the leg is still in articulation, parts of the ilium covers the anterior portion of the femoral head, thus the trochanters cannot be well distinguished. The shaft of the femur is straight in contrast to the bowed condition in *Microraptor* (Xu et al., 2003, Hwang et al., 2002).

Tibia The tibiae are long in relation to the femora (Fig. 17) having a tibia/femur ratio of 1.36. In *Troodon* the ratio of both the tibia to the femur and the IV MT to the femur change through ontogeny. These ratios are impossible to compare with those in other microraptorines as few animals preserve all elements in total length. From a straight line, the left tibia bows 1.5 mm and the right 2 mm. This minor bowing of the tibia, recorded as unique and functionally significant in *M. gui*, has been argued by some authors to be taphonomic (Padian and Dial, 2005). The tibiae of other theropods (e.g. *Troodon*) also bow slightly to the side.



Figure 17. Legs. Note long length of feathers, exceedingly long tibiae and section removed for histologic sectioning.

Fibula The fibula is very slender. A proximal head gives way after about 2 cm to a thin rod of nearly uniform width extending the length of the tibia. It is not fused to the tibia. The fibular head is its broadest part with a short crest extending below it. The tubercle of the iliofibularis is present and seems slightly distal to its position as recorded in *Microraptor* (Hwang et al., 2002). The fibula reaches the tarsus distally, where it would contact the calcaneum if that bone were in place.

Tarsals The right crus is preserved in posterolateral view and so the ascending process of the astragalus is not fully visible, making estimation of its length impossible. The astragalus is not fused to the calcaneum in either ankle, and neither tarsal is fused to the base of the tibia. The left calcaneum has disarticulated and come to rest by

the left 5th metatarsal, while the right has disarticulated and come to rest upon the left metatarsus (Fig. 3). The calcanea are small and very thin mediolaterally, with a flattened posterior edge.

Metatarsals and Pedal Phalanges The metatarsals are asymmetrical (Fig.18). All metatarsals are straight and relatively narrow, held tightly together with little lateral departure from one another. MTI is a tiny triangular splint in place against the posterior side of the tarsus in articulation with the first phalanx of digit one. MTIII is the longest with MTIV slightly longer than MTII. The head of the right MTII is visible in the lateral view, is triangular and one and a half times the anteroposterior width of the shaft. The proximal shaft of MTIII is severely constricted, but still visible in anterior/dorsal view. Despite this constriction, the metatarsals are unfused proximally. The length of MTIII is over half that of the tibiae. MTV is splint like and long; about half the length of the tarsus. The bowed shaft creates a visible space between it and MTIV. The lateral edge has a convex and flattened flange.



Figure 18. Hind feet. Note long feathers extending behind metatarsus.

As mentioned above, the feet cross a natural break in the slab. The state of the right digit II is the result of improper preparation after the separation of the slab. Since further in-depth preparation by the authors was not possible all data on this digit must come from the left side.

The left foot is gracile with the usual 2-3-4-5 phalangeal formula; it is remarkably preserved and articulated, including both bones of digit I which are very reduced and appressed to the lateral surface of digit II, with the ungual sitting partial atop the first phalanx of digit IV. Digit II has a very large claw and flexor tubercle and the articulations are strongly ginglymoid, though perhaps not as strongly as in *Sinornithosaurus*, or in velociraptorines. Digits III and IV are similar in size at about twice the length of digit II. The three phalanges of digit III are each longer than those of digit IV, especially the long

and robust phalanx III-1. The terminal unguals of digits III and IV are nearly identical and much smaller and less recurved than the large raptorial phalanx II-3.

Feathers:

Feathers are present across the entire body of *Wulong*; in places they are clearly preserved (Fig. 1 and see Fig. 2 for schematic drawing). Though the feathers appear original, to demonstrate that they were real and *in-situ* further preparation was performed in two places (by the primaries above the dorsals and by the tail feathers). This exposed continuations of the feathers beneath the newly removed laminae. This is a finding consistent with the feathers being actual fossil remains.

These feathers make up three main morphotypes, which broadly correspond to feather types II, III, and IV of Prum (1999). Well-preserved filamentous feathers (type II) similar to those described from *Sinornithosaurus* (Xu et al., 1999; Ji et al., 2001) and *Yutyrannus* are preserved below the mandible (Fig. 19) and above the proximal caudals and sacrum. They preserve a range of lengths.

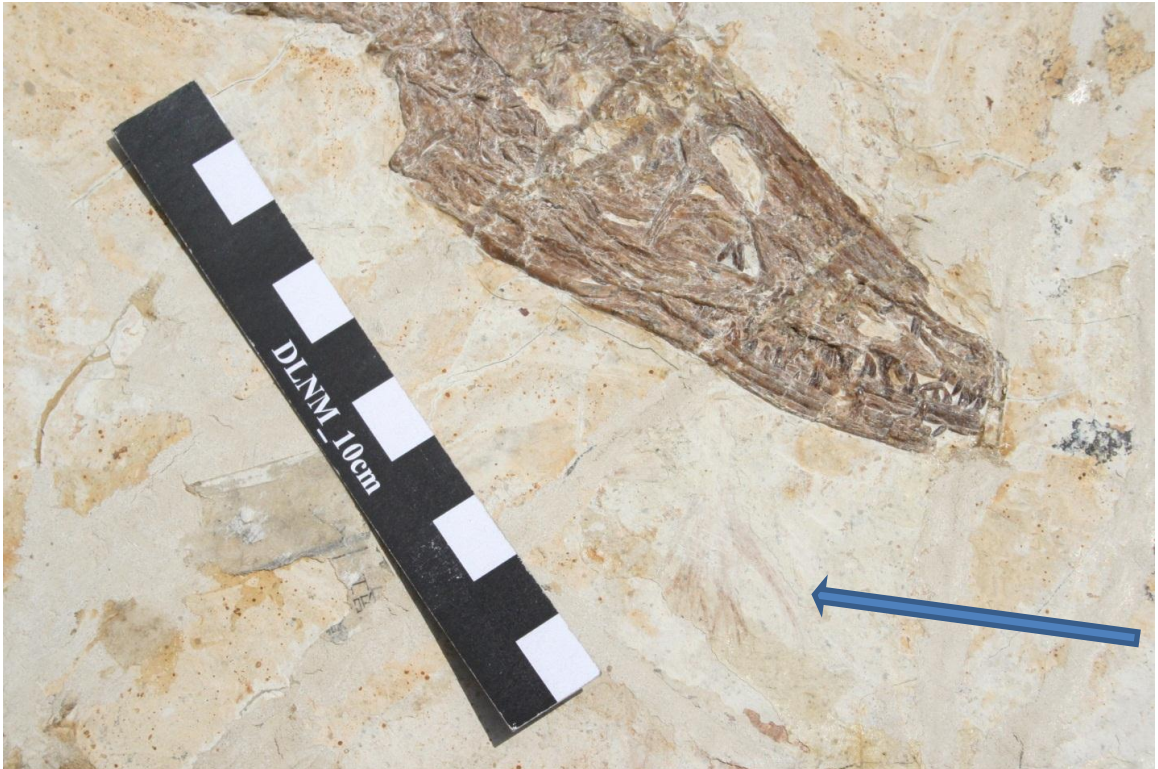


Figure 19. Feathers below head. Arrow showing filamentous feathers stemming from region of mandible.

Linear tufts of feathers with occasional hints of a central shaft (stage III and IV) are present over the fore- and hindlimbs. The best feather preservation is along back, between 9th and ~10th dorsal vertebrae. Here asymmetric feathers (possibly Prum's stage V) are especially visible in one spread stretching 54 mm above the dorsal vertebrae (Fig. 10). The preservation is good enough to preserve the herringbone pattern characteristic of feathers with cross-linked barbules, a feature of modern flight feathers. This same pattern is also visible in the feathers of the hindlimbs (Fig. 20).

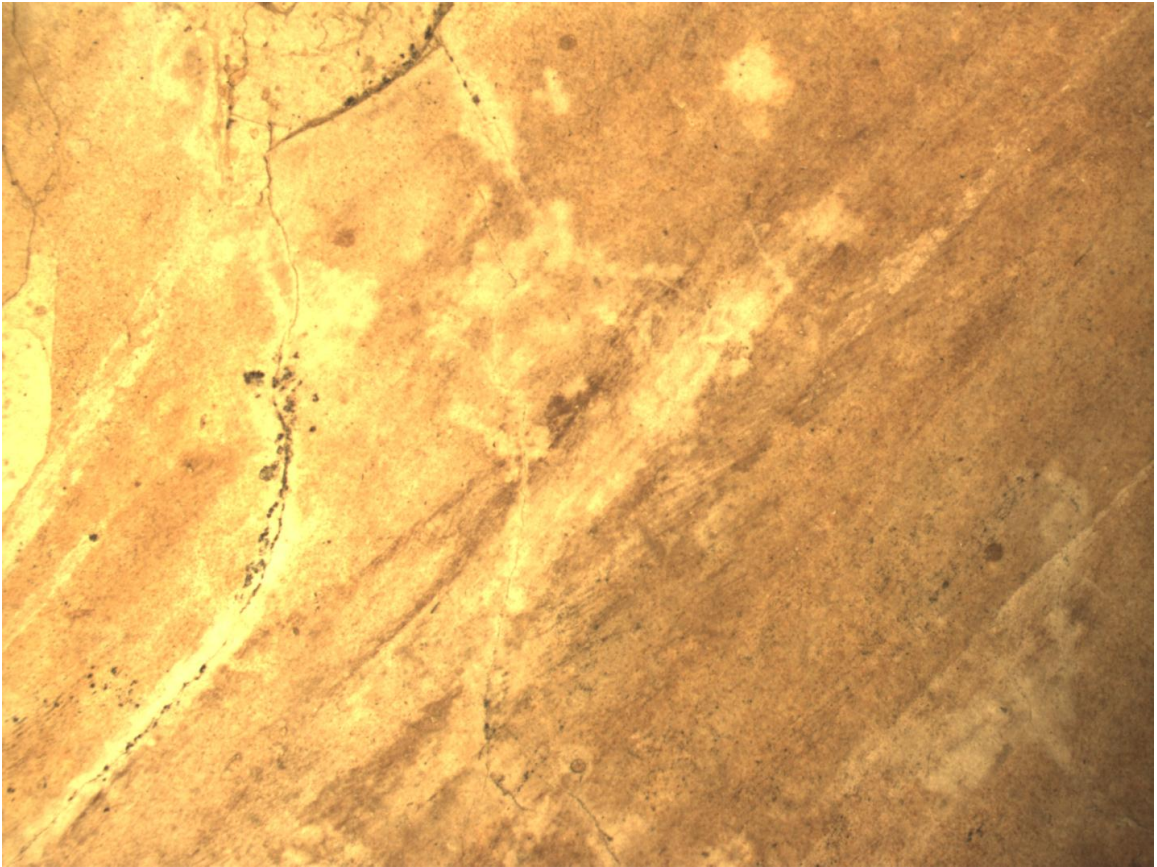


Figure 20. Texture of feathers stemming from hindlimb. Note herringbone pattern.

There are at least 5 feathers above the dorsals, all almost exactly 5.2 mm across. These feathers appear to originate at the left metacarpus, and their position is where feathers from the left manus might lie if the body had fallen on top of them. In the removal of the opposing slab and preparation they were likely destroyed where they would have been under the chest cavity and dorsal region, or perhaps they remain under the sediment. Thankfully, they are preserved above the dorsal vertebra where the tips of the feathers lay flat against the sediment (Fig. 21).

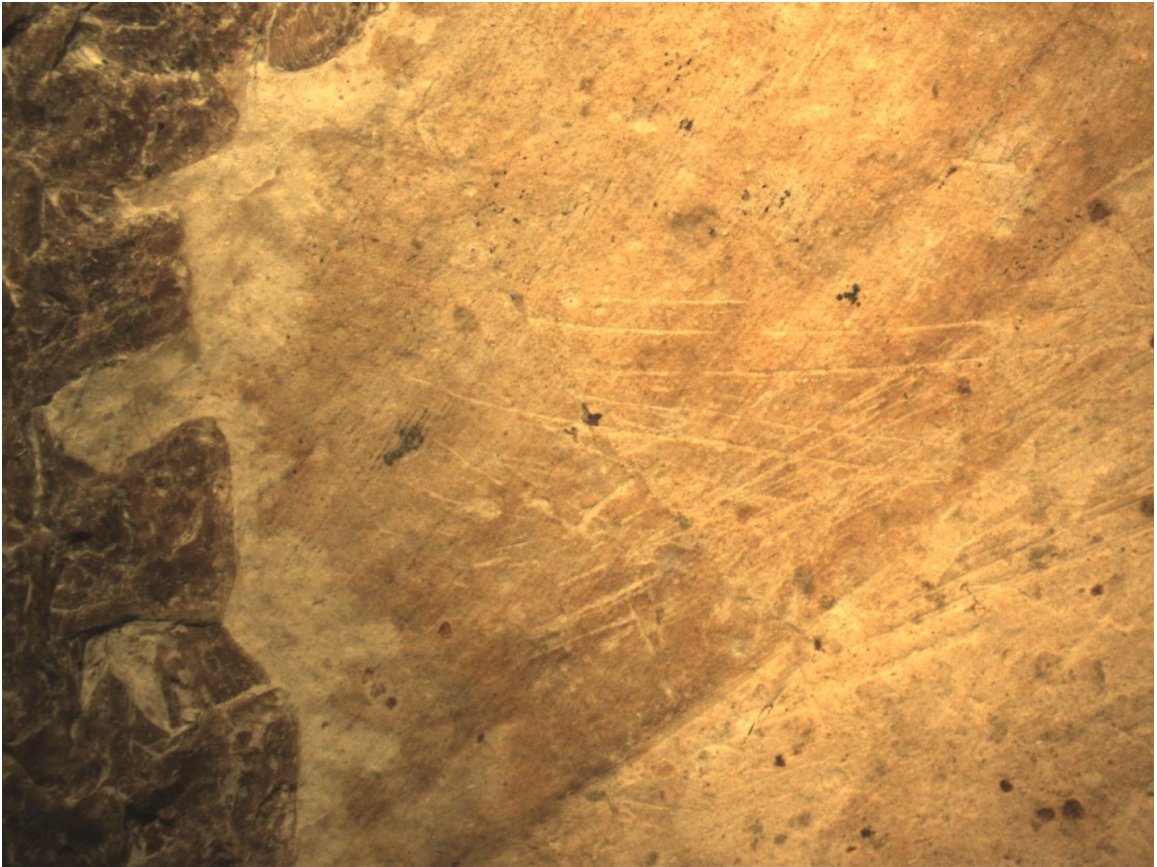


Figure 21. Possible primaries of right carpus, preserved above dorsal region. Scratches in center of photograph are toolmarks.

Measuring from the wrist extends their length from 54 mm to 111.1-139.8 mm long, making them the longest feathers on the body. They have the appearance and position of primary wing feathers. The remaining stage III and IV feathers originating from the limbs look like what would be called secondaries in modern birds, and are less obviously asymmetric, if at all. No alula is present.

Long distal tail feathers extend 127-153 mm beyond the last caudal vertebrae (Fig. 22). The tail feathers originate at about the 27th caudal. They extend caudally in at least two main strands; they do not splay out as in *M. "gui"* (IVPP V13352 and TNP

00996) but carry straight backwards. There is no evidence of a fan-like structure as in *Caudipteryx*; these rectrices are more similar to those of a quetzal or *Confuciusornis* than to a peacock.



Figure 22. Tip of tail and tail feathers

There does seem to be some lateral expansion at the distal most ends of the tail feathers before they are cut off at the end of the slab, but it is fairly minor and faintly preserved. If the suggestion of Hu et al (2009) is true that feathers first evolved distally and spread proximally then caudal distribution of feathers in *Wulong* may represent the state ancestral to the tail-fan seen in the *Microraptor* specimens.

Ontogenetic Indicators and Histology

D2933 has many gross osteological markers of immaturity. It has completely unfused dorsal and sacral vertebrae. Where the dorsal vertebrae are visible the sutures are completely open in lateral view (Figs. 9 and 10). The poorly preserved sacral vertebrae have separated post-mortem at the junction between the centra and the arches. In the shoulder, the line of suture between the scapula and the coracoid remains open, and the left scapula has disarticulated from the left coracoid. The suture between the left and right pubis is still visible. The astragali and the calcanea are unfused and the calcanea have dislocated from the ankle with the right resting on the left metatarsals and the left calcaneus resting above the left metatarsal 5 (Figs. 17 and 18). The sterna are small and the medial borders are not squared-off and flat for articulation for one another, they remain slightly concave and uneven (Fig. 14). The ends of the long bones in D2933 are poorly formed and poorly preserved, with a rough, porous and almost cancellous appearance consistent with incomplete ossification of the epiphyses. The exterior texture of the cortical bones is very porous, with a many parallel pits and grooves, generally trending along the diaphysis of the long bones, and contributing to an “unfinished” look (Fig. 23). This texture is very widespread in D2933 and is particularly conspicuous on the femora, tibiae, pubis, radius, ulna, and furcula.

In contrast, D2140, the holotype of *Sinornithosaurus “haoiana”*, exhibits only a few juvenile features. Both the dorsal and the sacral vertebrae are completely fused with the sutures completely obliterated from view.

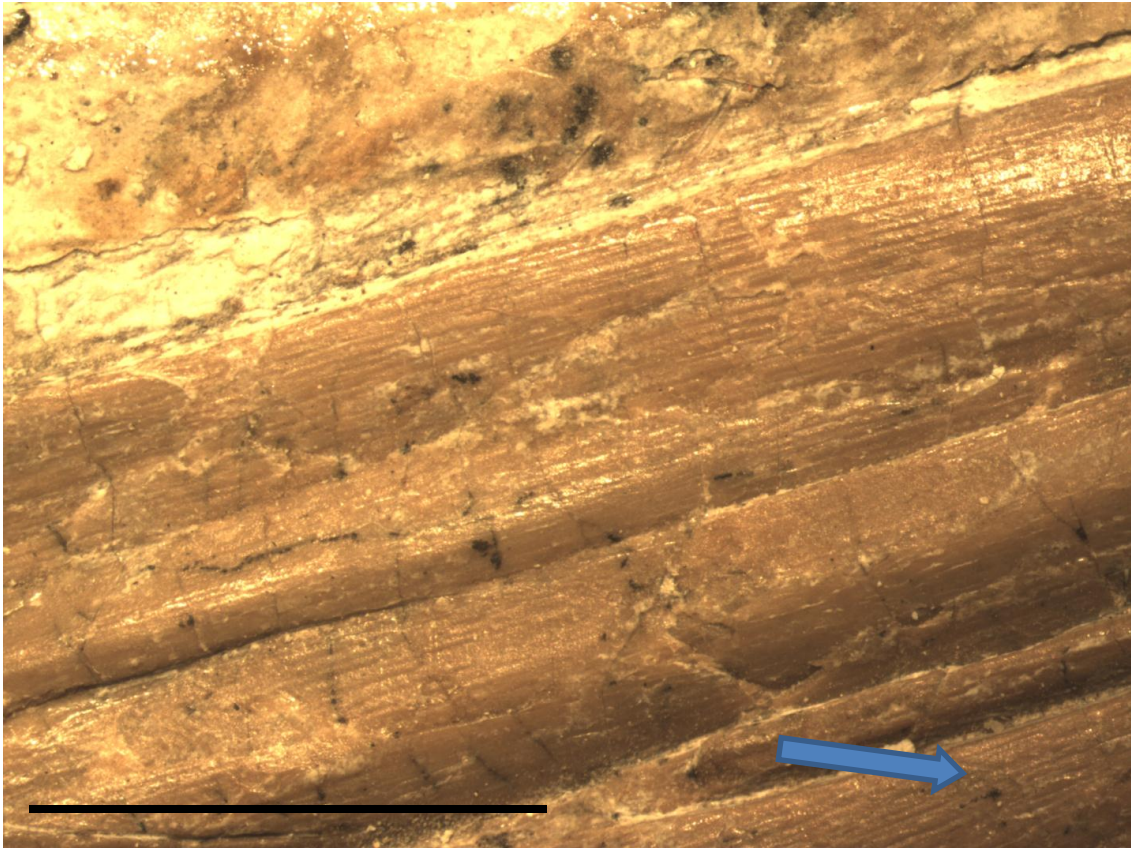


Figure 23. Close-up of right femur. Note juvenile or unfinished texture. Scale, 1 cm. Arrow points to triangle in lower right corner which is left femur.

The scapula and coracoid are completely fused with no obvious line of fusion remaining. The pubes are fused and the line of fusion barely visible, and then only proximally. The astraguli are fully fused to the calcanea and remain affixed to the distal tibiae, though there is no sign of their fusing to the tibia. The sterna are well-formed, large, and squared-off medially, though they remain free and not fused into a single sternum as in *Microraptor*. The ends of the long bones are well formed and preserved. They have a very distinct shape and smooth cortical bone except where roughened for muscle attachment. The exterior texture of the bones is largely smooth with little evidence of the

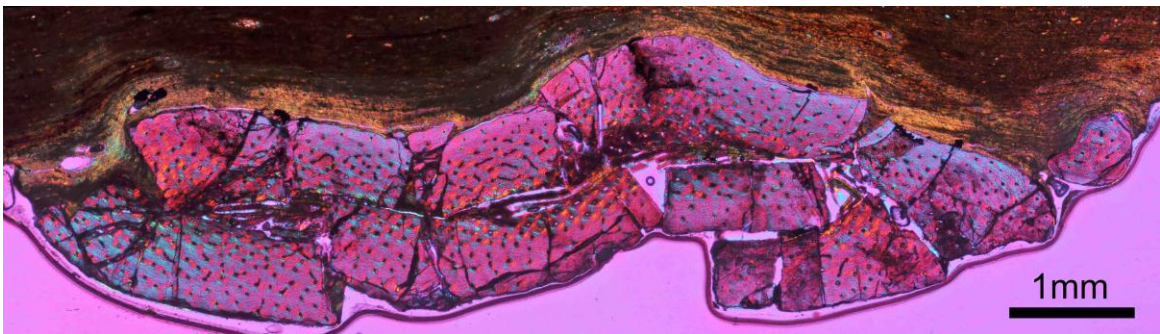
“unfinished” texture so widespread in D2933. The tibia of D2140 shows a very light remnant of this bone texture, but the remaining grooves are shallower and less dense than on any of the bones in D2933.

As related in the methods, D2933 was sampled for histological sectioning. In addition to D2933 the Dalian museum also allowed sampling of the holotype of *Sinornithosaurus “haoiana”* specimen D2140, for comparison with an apparently more mature, yet still closely related specimen. The histology of *Sinornithosaurus* is used here only for comparison; a more complete description is to follow in a subsequent paper. D2933 was sampled twice: from the mid-diaphysis of the tibia and fibula, and from the mid-diaphysis of the humerus. The tibia/fibula samples are complete cross-sections and the humerus sample is an isolated section of the lateral cortical bone collected to verify that the ontogenetic signal is not particular to the tibia/fibula. D2140 was also sampled twice: again from the mid-diaphysis of the tibia and fibula, and from the mid-diaphysis of the radius. The tibia does not preserve the entire circumference at the point of the sample. About 4/5 of the circumference is included. The fibula and the radius of D2140 are complete in cross-section.

The tibia of *Wulong* has a thin cortex, averaging slightly less than a millimeter in thickness. The medullary cavity would have been large but it has been collapsed by taphonomic crushing (Fig. 24).



A.



B.

Figure 24. Histological sample of D2933 mid-tibia and fibula in cross section. A under normal light and B under crossed polars. Fibula to upper right.

No trabeculae are preserved in the tibial midshaft. At the center a small amount of parallel fibered endosteal bone is visible. The endosteal bone is between 0.1 and 0.04 mm thick. This layer has detached from the inner surface of the bone and lies in thin slats between the collapsed cortical walls (Fig. 25). This endosteal bone is very thin, with only approximately $1/25^{\text{th}}$ the thickness of the normal cortical bone. However, the medullary surface of the endosteal bone is very regular, with no pitting or wavy layers. Along with the presence of the endosteal bone implies that deposition is currently outpacing resorption and there has been no major resorption from the medullary cavity, beyond that necessary to initially produce the hollow cavity. Some resorption may have occurred during the deposition of the inner layer, because the portion just superficial to the

endosteal bone contains a few truncated primary osteons which must have formed prior to the deposition of this newer type of bone. This may have simply been the resorption that occurred as the cortex migrated away from its initial diameter.

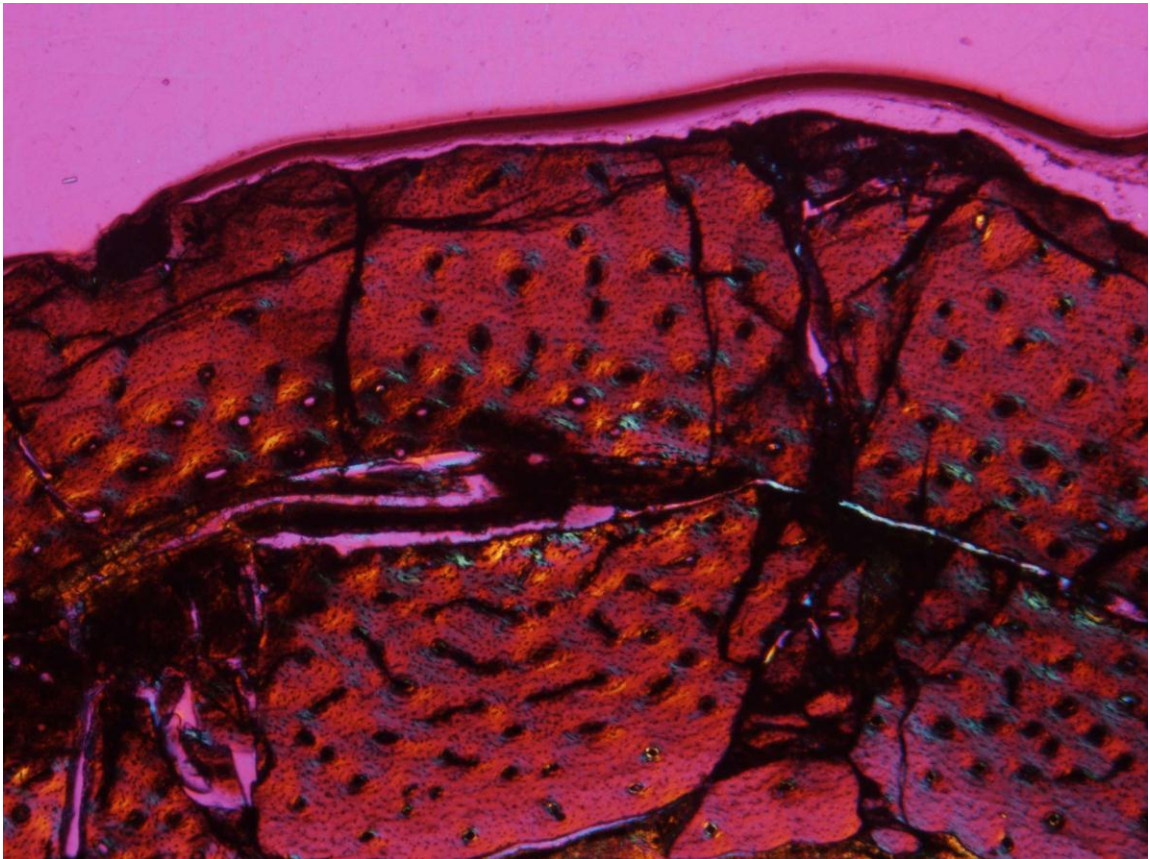


Figure 25. Detail of D2933 tibia under polarized light showing histovariability. Medullary cavity is compressed and visible in center of the photograph.

The cortical bone is fibrolamellar and interspersed with moderately densely-packed primary osteons (Fig. 26). The bone matrix is highly refringent. Radially, there appears to be no change in the size of the osteons, which maintain a similar size throughout the bone. All of the osteons appear to be primary with no secondary remodeling present, however, some of the Haversian canals appear open, so it is possible

that some of the osteons are still in the process of forming and remain partially open vascular canals. Some of this appearance may be due to growth of optically clear crystal in the vascular canals of some osteons. The density of vascular canals decreases appreciably to the exterior of the tibia, and there appears to be a coincident decrease in circumferential vascularity. The position of the osteocytes is also more regular, arranged into slightly arching lines rather than the more random positions of osteocytes in the inner cortex. This is subtle however and constitutes a change in emphasis, not a quality of difference, and so should not be taken to indicate any more slowing of growth than that already suggested by the more uniform fiber directions of the exterior cortex. The relative depth at which this more organized condition appears varies around the circumference of the tibia. There is no external fundamental system. The outside of the cortex contains occasional longitudinal vascular canals, imparting a slightly wavy look to the surface. This corresponds with the previously mentioned “unfinished” texture of the bone’s surface. There are no visible LAGs or annuli. LAGs are generally accepted as yearly markers in fossil archosaurs (Erickson, 2004). The presence and annual deposition of these structures is well established in most groups of tetrapods, including extant large-bodied, endothermic mammals (Kohler et al., 2012)

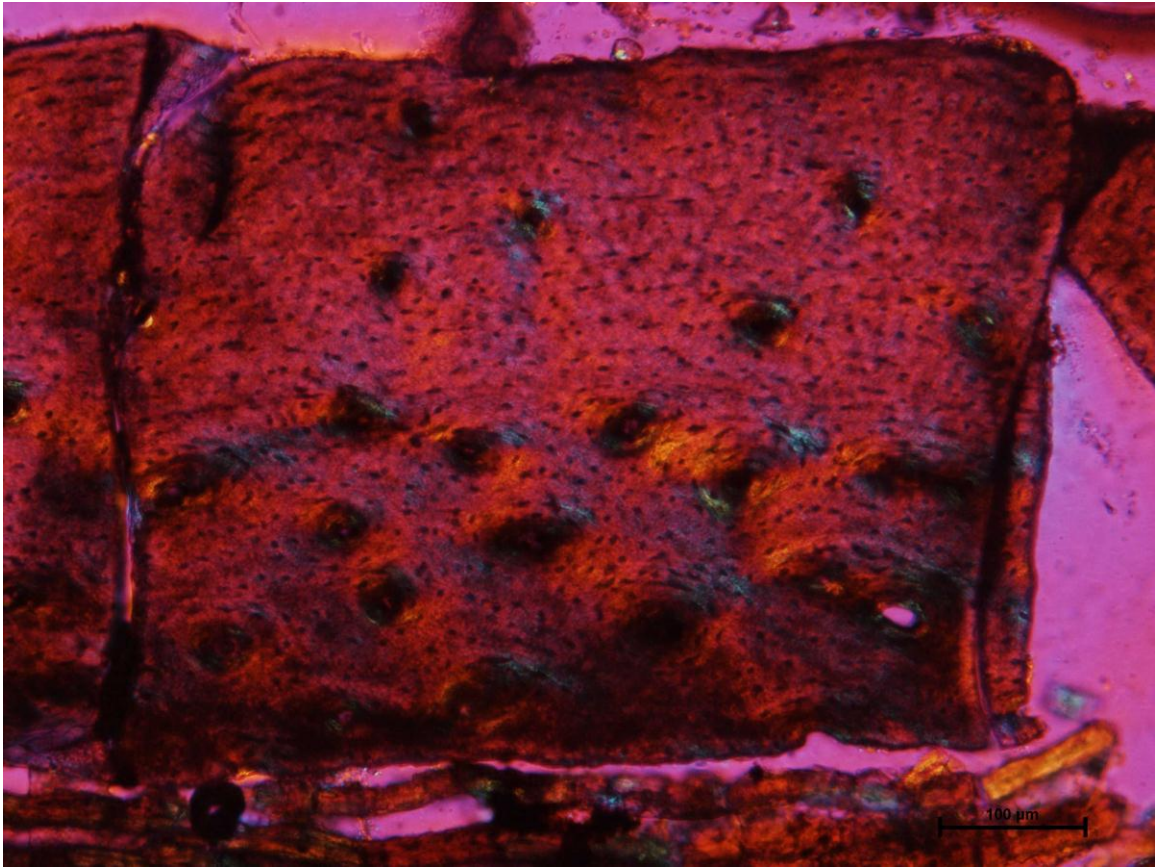


Figure 26. Close detail of D2933 tibia cross-section under polarized light, showing distinct periods of bone growth. Cortical surface to the top and endosteal bone visible at bottom.

Given the crushed nature of the bone, reliable backcasting to the centroid is difficult, but with no LAGs present, no external fundamental system, and only a minor slowing of growth as interpreted by the vascularity and osteon density of the outer cortex it is likely that this animal is less than a year old.

The fibula in *Wulong* was sampled along with the tibia. It is solid and lacks a medullary cavity. In cross section it is slightly comma-shaped in outline, showing primary fibrolamellar bone with little to no remodeling (Fig. 24). The outside shows particularly low vascularity. It may be possible to discern a single annulus close to the

exterior surface of the fibula. If this is an LAG then the age estimate from the tibia must be corrected upwards to just over one year. Alternatively, this could be a hatching line or other feature and not reflect a full year of growth.

A sample of the mid-diaphysis of the humerus was also sectioned (Fig. 27). It shows a signal similar to the tibia. There is no cancellous or endosteal bone preserved. Fibrolamellar bone with fairly regularly spaced primary osteons of equivalent size dominates the thin cortex. The more organized character of the matrix under polarized light seen in the tibia is less apparent in the humerus, thus the bone appears more uniform. The humerus does show a minor drop in vascularity in its outer cortex compared with the inner surface. Like the tibia, the humerus has wavy vascularization at the cortical surface.

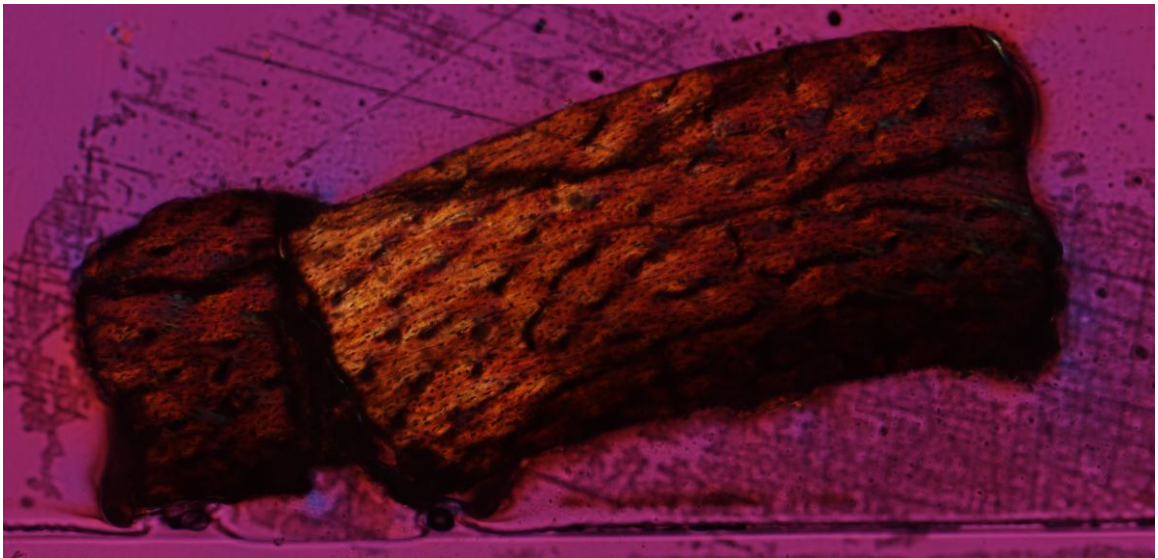


Figure 27. D2933 humerus thin-section under polarized light.

In the tibia of *Sinornithosaurus* by contrast, the thin cortex shows a different growth history. No cancellous bone appears. Endosteal bone is present and it is much thicker relative to the entire width of the cortex (Fig. 28). The endosteal bone composes about 1/8th the thickness of the cortex, around three times as thick compared to the total cortical bone thickness as in D2933. The endosteal bone cuts across a layer of secondary osteons, variably present along the inner edge of the cortex. This cross-cutting relationship implies that the endosteal bone was laid down at a later developmental stage than that present in *Wulong*, having undergone multiple waves of resorption and deposition.

The cortical bone of the tibia in D2140 is similar in general to that of D2933. It is dominated by moderately densely packed primary osteons in a matrix of fibrolamellar bone (Fig. 28) . Major differences include the presence of the secondary osteons close to the endosteal surface and a slightly reduced osteon density towards the periosteal surface. All primary osteons here appear to be fully formed as well, without any that might still be open vascular canals. Additionally, D2140 has one prominent lag running variably 1/2 to 3/4 of the way to the outside of the cortex. This LAG may be traced around the entire circumference of the tibia, and appears to be a double LAG on one side, possibly a consequence of cortical drift.

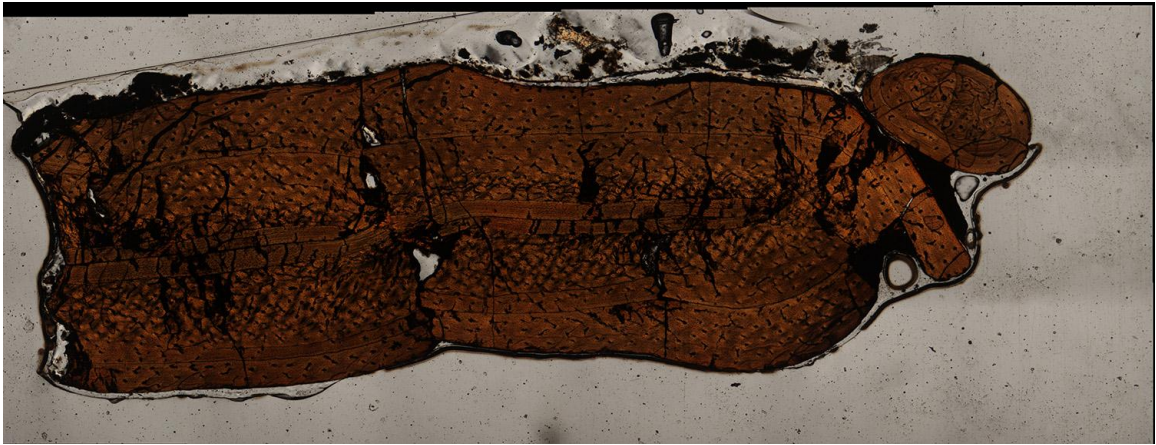


Figure 28. D2140 tibia and fibula in cross-section. Both sides of tibia are present, medullary cavity compressed at center, medial portion of tibia broken. Thick endosteal bone is visible at center. Note prominent arrest line at middle of cortical bone.

The fibula of *Sinornithosaurus* is slightly rounder than in D2933 (Fig. 28), but is also solid and lacks a medullary cavity. It is characterized by much more densely remodeled bone and shows at least one distinct LAG, and possibly another near the center of the bone, partly obscured by a localized but dense mass of overlapping secondary osteons. The outer layers are nearly avascular except in the section closest to the tibia where primary osteons remain in a slightly denser concentration. The vascularization present is longitudinal. The fibulae of the holotypes of *Wulong* and *S. "haoiana"* reinforce the dichotomy between the two specimens, helping to account for any error in aging due to expanding medullary cavity in the tibiae.

The radius of D2140 also conforms to the general histologic state of the tibia. One LAG is present. There is an even greater reduction in the number of osteons towards the outer cortex than in the tibia. Interestingly, there seem to be predominantly radial vascular canals in the outer section of the cortex rather than circumferential canals.

The age assessment of D2933 as a one year old animal is consistent with the available osteological evidence presented elsewhere. This animal is not perinatal, but it is still actively growing. In contrast with this is the D2140 *Sinornithosaurus*, which shows a much more adult signal. Not only does it show adult bone texture on the surface of its long bones and evidence a much more complete ossification of the epiphyses of its long bones and the end of its pubis, but most bones, such as the proximal tarsals and the sacrum are well fused. Histologically, it shows much more endosteal bone, a strong signal of secondary osteon formation, and very organized vascularity, the majority longitudinal but with the circumferential and radial component increasing exteriorly. There is at least one lag present in the middle of the cortex, and possibly one more very near the exterior. Though likely still growing, *Sinornithosaurus* “haoiana” was more mature osteologically than D2933, on both microscopic and gross scales.

Phylogenetic Results

Phylogenetic analysis using the matrix of Turner et al. (2012) with the addition of characters for D2933 (see Table 3) recovered *Wulong* as sister to *Sinornithosaurus* within a monophyletic microraptorinae (Figures 29-32). During this analysis the other interrelationships within the microraptorine clade remained unresolved. This close relationship with *Sinornithosaurus*, an animal with which is shared geography, but from whom it was separated by 4 or 5 million years, suggests one of three possibilities. First, that *Wulong* is a true clade, which diverged from the ancestor of the earlier *Sinornithosaurus* sometime before 120 mya. Second, that *Wulong* is part of an anagenetic

lineage leading from *Sinornithosaurus* or third, that D2933 indeed represents a juvenile of *Sinornithosaurus*. The last possibility is unlikely on the basis of diagnostic characters unlikely to change during juvenile-adult ontogeny (e.g. number of tail vertebrae are not known to vary during the ontogeny of an individual within archosaurs) as well as on the differences in plumage between D2933 and a suggested juvenile of *Sinornithosaurus*, NGMC-91 which does not have elongate tail feathers or the degree of pennaceous feathers on the limbs. Indeed the general differences between NGMC-91, widely regarded as a juvenile *Sinornithosaurus* (Turner et al., 2012), and D2933 suggest that they are unlikely to both be juveniles of the same taxon. Differences could be either taphonomic or developmental in ways not yet understood however, so the diagnostic autapomorphies of D2933 are important to distinguish it from its closest relative. If further research later reveals that the second possibility is likely and a cladogenic event cannot be demonstrated, I suggest keeping the species epithet as a morphospecies within *Sinornithosaurus*.

Table 3. Character matrix

Character matrix for D2933 – characters from Turner et al. 2012 Wulong_bohaiensis 0011????????????2100???111????10?11???????????????????? ?00?00100?11???000100?0?00?????????????????0?0???021??1112?? 1?????01101111010?1???10000?00?21?0???1110?3???1?00211200??? ?????01???????01111?0?0001?100???00?0???0?101111001?10?001?1 100?000???00?00???2?????010?????????????????0?????????0?0000?? 000?00????00?0?0????1?00?0???0000????????10??000????0101???? 0????????????????????????????0????????????000????????????101???000 ???0?11101000?????????0???110????0?1100010?1
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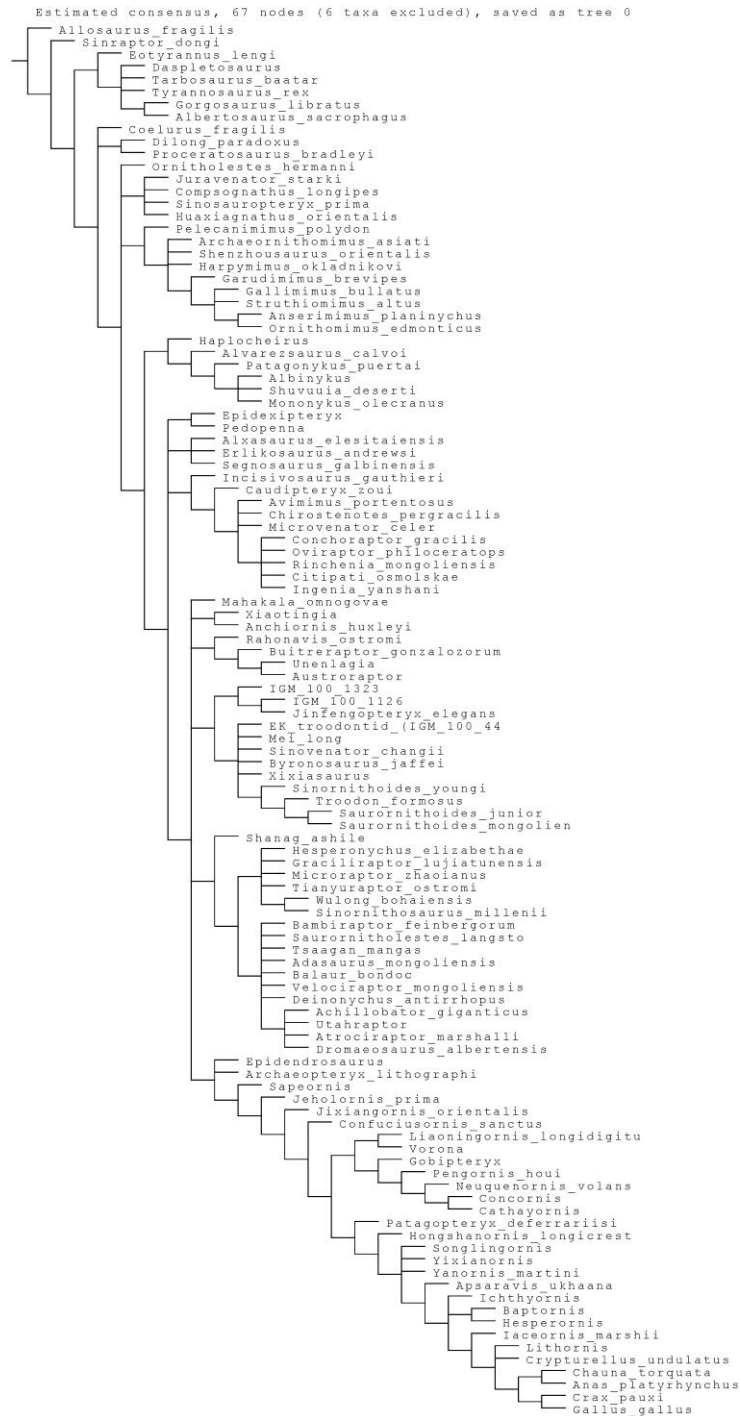


Figure 29. Strict Consensus tree of 474 characters and 112 taxa; CI=0.285, RI=0.706.

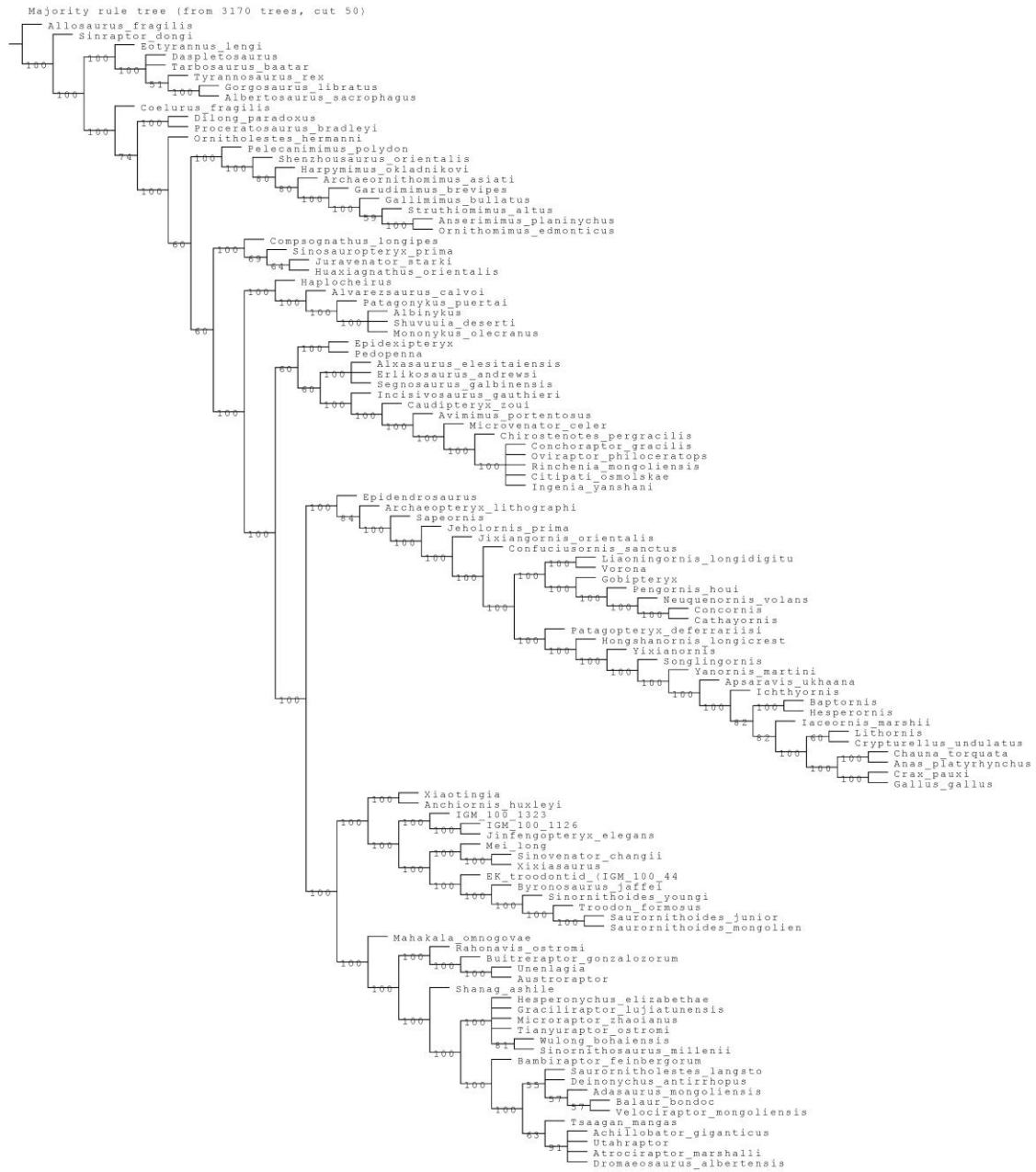


Figure 30. Majority-rule consensus tree from same matrix. A monophyletic microraptorinae was recovered in all trees.

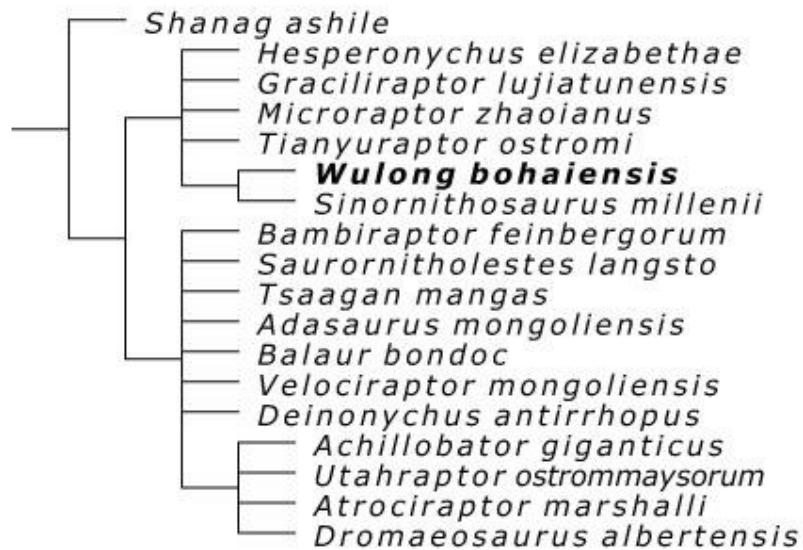


Figure 31. Detail of Fig. 29 Strict consensus tree of dromaeosaurid clade of Shanag, Velociraptor and all the descendents of their most recent common ancestor, derived from the phylogenetic analysis in this study, showing monophyly of microraptorinae, and the position of *Wulong*.

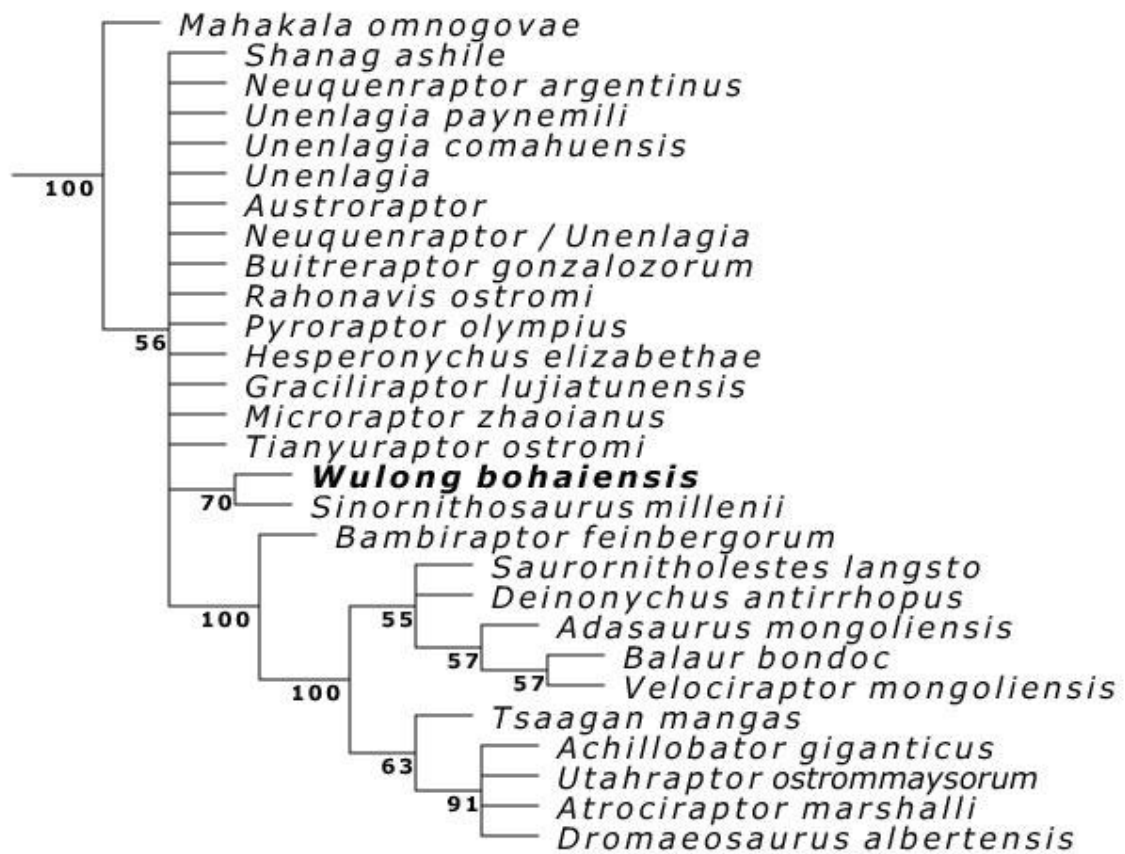


Figure 32. Detail of Fig. 30. Majority rule tree of dromaeosauridae, recovered from this study. Numbers equal bootstrap values for each resolved node.

DISCUSSION

Taxonomy

The dromaeosaurid status of D2933 is indisputable due to the presence of several features that define the group. The elongate chevrons and prezygapophyses that surround the animal's caudal vertebrae are unique to Dromaeosauridae among theropods. The presence of a recurved and dominantly-sized "raptorial" pedal ungual two, slotted into a ginglymoid second phalanx of the second toe with a proximally extended caudoventral heel is a defining feature of the clade, though this feature is also shared to some degree with Troodontids. Within the skull the T-shaped lacrimal, sinusoidal fronto-parietal boundary, and teeth with posteriorly dominant serrations also support this assignment.

Turner et al (2012) identify five synapomorphies uniting *Tianyuraptor*, *Microraptor*, *Graciliraptor*, *Hesperonychus*, and *Sinornithosaurus* within Microraptorinae. These are a small semilunate carpal, a subarctometatarsalian condition of the tarsus, the lateral face of pubic shaft possesses a prominent lateral tubercle about halfway down the shaft, the caudal chevrons have very elongated posterior extensions, and the combined length of metacarpal I plus phalanx I-1 is equal to or less than the length of metacarpal II. Of these *Wulong* possesses a semilunate carpal similar to that of *Microraptor* (Hwang et al., 2002), a prominent lateral tubercle of the pubis very similar to that of *Microraptor* and *Sinornithosaurus* but lacking the hook seen in *Hesperonychus*, caudal chevrons that are very elongate, and a metacarpal II with a length slightly greater than the combined length of its MC-I and phalanx I-1 combined. To these features I

suggest the addition of two new Microraptorine synapomorphies shared by *Wulong* with the members of this group; the exclusion of the maxilla from naris by the maxillary process of the premaxilla, and presence of a coracoid fenestra.

Wulong is distinguished by several autapomorphic features: it has a long jugal process of the quadratojugal; anteriorly inclined pneumatic foramina on the anterior half of dorsal centra, transverse processes of the proximal caudals significantly longer than width of centrum, the presence of more than 29 caudal vertebrae, and the large size of supracoracoid fenestra (>15% of total area). Additionally, there are many features that distinguish it from its closest well known relatives. *Wulong* is distinguished from the roughly contemporaneous *Microraptor* by anterior serrations on some teeth, having a less “waisted” root to crown transition on all teeth, having a fairly large promaxillary fenestra, having a bifurcated posterior dentary like that of *Sinornithosaurs*, having thirty or more caudal vertebrae as opposed to less than 26 in *Microraptor*, and having two long tail feathers instead of a splay of many. It further differs from the ~5 million year older taxon *Sinornithosaurus* by lacking the distinctive tooth groove found on the lingual side of premaxillary teeth in *Sinornithosaurus*, having a large promaxillary fenestra but lacking the thickened posterior rim, having no excavation on the posteroventral edge of the maxilla (as per Turner, 2012), and having long, pennaceous feathers.

The presence *Wulong* in the Jiufotang beds marks it as roughly contemporaneous with the similar *Microraptor* but separated by as much as 5 Ma from *Sinornithosaurus*, its closest relative, found in the underlying Yixian Formation (Zhou et al., 2003). This minor ghost lineage is explainable in several ways and it is difficult even to suggest the

most likely possibility in the absence of a more constrained stratigraphic context. Better stratigraphic information will only be available with the adoption of new collecting procedures; this certainly will be a necessary step in further understanding the relationships of these animals to one another.

Of course this group may not have originated here, especially in light of the North American member of the clade (Longrich and Currie, 2009), but it thrived and diversified, as apparently did other basal members of the sister groups troodontidae and avialia. Any attempt at recognizing these patterns of diversification raises the importance of ontogenetic information in determining make-up of fossil assemblages

Ontogenetic Assessment

As this animal is skeletally immature, the assignment of a new genus and species may require some defense. I have tried to identify autapomorphic features that are unrelated to ontogeny, following the method suggested by Choiniere et al. (2014). However I acknowledge that dinosaurs are incredibly labile in their skeletal ontogeny, particularly cranially, and I subsequently make this taxonomic assessment with appropriate caution. Both species of *Sinornithosaurus* (Xu et al., 1999; Liu et al., 2004) are reported from the Yixian Formation. All vetted specimens of *Microraptor* are from the Jiufotang. The largest specimen of *Microraptor* is sub-equal to D2933 in size, but comparison of histology to *Troodon* suggests that D2933 may only be 2/3 of its adult size as measured by linear dimensions putting it outside the adult size range of *Microraptor*.

One of the most interesting results of the study of D2933 has been more information on the timing of events previously used to assign ontogenetic status to coelurosaurs. This example can be highlighted through comparison with one of the only other sampled dinosaurs from lake sediments in China. Though this topic has received much attention in some groups (e.g. Tyrannosauridae, Carr and Williamson, 2004) it has not been systematically studied in Dromaeosaurids. This is unfortunate as ontogenetically related evolutionary pathways (e.g. neoteny) may have played a role in the basal paravian divergence that helped to set the pattern of modern birds. Certainly body size changes, which may be significantly influenced by life history and ontogeny, characterize this divergence (Turner et al., 2009).

The patterns and timing of ossification and fusion may vary greatly between taxa and elements may not always be homologous, so fusion alone is often a very rough and potentially misleading tool for the determination of ontogenetic age. Clearly age determination based on size has been long discredited, and anything less than all the consistency of available evidence should render the developmental status of a fossil tetrapod ambiguous. This should as far as possible always include histology, when the age is determined important, but other factors such as fusion, cortical bone texture, tooth status, and epiphyseal development should also be considered when appropriately known for the groups in question. These things are both necessary for further exploration of this topic and variable among clades, thus further analysis should be conducted whenever possible (preferably with larger sample sizes than here available).

In crocodilians, vertebral fusion proceeds from caudal to cranial (Brochu, 1996) and is unfinished in adult animals. In most modern birds fusion is complete well prior to reproduction. The crocodilian condition as regards reproductive maturity seems to predominate in most non-avian dinosaurs, in that they may be unfused past this period. This may not be universal, however, even within deinonychosauria, as *Troodon* apparently fuses its vertebral laminae to their centra prior to reproductive maturity (Varricchio, 2013; DJV, pers. comm).

The fusion of the calcaneus to the astragalus and of these proximal tarsals to the tibia is often used as ontogenetic characters. All indications from microraptorines are that the fusion of the small calcaneus onto the astragalus follows the pattern well established in other coelurosaurs (Carr and Williamson, 2004). The unfused condition may be more widespread in theropoda – many theropods are found with the proximal tarsals unfused – or it may be that it is one of the last elements to fuse and the general paucity of histologically sampled true adults keeps us from properly evaluating its timing.

Several authors have described a characteristic texture of juvenile cortical bone (e.g. Chiappe and Gohlich 2010; Tumarkin-Deratzian et al. 2007; Tumarkin-Deratzian 2009). In D2933 this highly porous texture with excavated striations parallel to the long bone shaft is externally visible across most long bones (Fig.23) and also present on the furcula, the distal ischium and the length of the pubis. The various holotypes of the *Sinornithosaurus* and *Microraptor* species do not show this texture, except to a small degree in the tibia of *S. "haoiana"*. The texture is clearly visible in *Graciliraptor*.

Texturally, the ends of several bones are rough and porous. This “unfinished” texture is characteristic of incomplete ossification, often present in the epiphyses of long bones while growth continues. Thus the rough texture observed in the tibia, ulna, and distal end of the pubis is not localized taphonomic wear but instead most likely a signal of the animal’s continued though slowing growth as reflected in the histology of its tibia and humerus.

D2933 possesses tiny, unfused, partially rounded sterna. Though it is unique, I have chosen not to interpret this distinctive morphology as a diagnostic feature of *Wulong* as it is likely ontogenetic. The sterna are one of the last bones to ossify in extant birds and in some ducks do not begin to ossify until after hatching (Mitgutsch, 2011). This possibility shows that the ossified or unossified state is not always a dichotomous presence/absence character and ontogeny must be accounted for. If this is a snapshot of the process of ossification it is interesting to note that though unfused, the facets for articulation of the ribs are already formed as are the laterally extending xiphoid processes, seen in other microraptorines (Hwang et al., 2002; Xu et al., 1999). The shield-like shape of the sternum apparently comes later, followed by the fusion of the left and right sides, if indeed this occurs. This pattern is identical to that observed in large ratites, including *Casuaris*, *Dromaeus*, and *Rhea* (Parker, 1868), birds which early in ontogeny also share a similarly-shaped pair of ossifications growing medially towards one another along a convex border. Interestingly in D2933, the articular processes are formed early in development, which should seem to suggest that the sterna were involved in the support of the pectoral girdle. In the aforementioned ratites, the connection with the ribs is not

ossified until well after hatching (Parker, 1868). A neonate of this taxon is unknown, but by one year the articulations are ossified but the connection between the sterna remain unfused. However, if this is not a feature of ontogeny and the sterna here represent the adult condition, it may indicate that *Wulong* was less well adapted to flying or gliding than was *Microraptor* with its large, well fused sternum.

Plumage

The most important recognition is that a wide range of feather types is present in a verified juvenile theropod. Though “fuzzy” (Stage I-II) feathers are found across the skeleton, they are particularly visible around the head and the pelvis. In regards to these sacrally located feathers, it should be noted in this interpretation that all modern birds have natal feather tracts, or “pterylae”, that run along certain areas of their body prior to the growth of feather quills (O’Connor, 1984). Several of these pterylae seem to be lost and gained throughout avian evolution, among these are the pterylae which run along the crus, which microraptorines and basal troodontids likely possessed on account of the adult, pennaceous feathers located in this region (Xu et al., 2001; Xu et al., 2009), though they are lost in most extant birds. This same region has very long feathers in D2933, which are elongate and pennaceous (stage III-IV), to the point where it is difficult to imagine they could have been kept from dragging on the ground. Some pterylae are present in all birds and seem to be strongly maintained through evolution (O’Connor, 1984); these include the mid-dorsal tract, which could account for the feathers seen here. This sort of feather growth can be seen in domestic turkey poults, among other birds.

The long feathers preserved above the lower dorsals in D2933 were folded under the body at death, originating from the folded left wing. These feathers are long pennaceous, preserved on echelon and are possibly assymetric (stage IV-V). Their origin at the distal wing seems most parsimonious both in comparison with modern birds' patterns of feather coverage and with the general state of the feathers on D2933 considered across the animal. Note that depending on the point of origin in the forearm this would significantly increase the minimum length of these primaries: by 300 percent! This indicates a wing with a chord of 16.5 cm and a span of (from glenoid to claw tip) of only about 48 cm. The simplified formula for a rectangular wing (S^2/SC) yields a rather low aspect ratio of only about 3, about half that of a red tailed hawk. Of course this animal is under no restrictions to follow the dictates of the modern bird wing.

One would expect feathers to be present in the juvenile morphs of deinonychosaurs due to their obvious presence in juvenile and even embryonic birds. Animals with integumentary structures appear to form these structures during embryonic development, even when the first versions are later replaced by more adult covering. Additionally, it would seem that whether or not presence of feathers in an embryo is tied to the juvenile's precociality, feathers would be useful for thermoregulation in small-bodied animals of any ontogenetic age as long as the animals were at least partially endothermic, especially in light of a recent study reporting the globally and locally cool conditions of the Early Cretaceous (Amiot, 2011). However, it should be noted that feather growth does not appear to be a major factor governing the onset of thermoregulation; rather it works to reduce the energetic cost associated with maintaining

the heat generated (O'Connor, 1984 and studies cited therein). This would suggest that this reasoning can only be invoked in the event that dinosaurs possessed some degree of endothermy. Another possibility, as in modern birds, is that the young gain heat from a brooding parent who then must leave for some period to forage. In these cases, natal down helps them to stay warm in the parents' absence (O'Connor, 1984, and studies cited therein). This would, of course, require that the young gain heat from their parents, which is interesting in light of solid evidence for brooding *posture* in theropods (Norell et al., 1995; Dong and Currie, 1996).

The presence of the long tail feathers is not unique within the Jehol Biota, reminiscent of *Confuciusornis* and similar to the recently described elongate feathers in *Microraptor* (Li, 2012), but without the distal “fan” seen in that taxon. Feathers of a similar length (>13.5 cm) are noted in another specimen from the same general locality, BPM 1 3-13 (Norell et al., 2002). Though this specimen is not well enough preserved for diagnosis, I cannot rule out synonymy with D2933 on the basis of these tail feathers and its relatively high tail to body length ratio. Conversely, tail plumes observed in specimens of *Microraptor* imply that this may be a synapomorphy of a larger group. As neither specimen of *Sinornithosaurus* preserves the distal tail the condition in this animal remains unknown, though the generally “downy” consistency of its integumentary structures might imply that it lacked these pennaceous feathers.

There is some disagreement about the correlation of long tail plumes to sexual dimorphism. At least two recent studies agree that in the Yixian bird *Confuciusornis* presence of long tail feathers is statistically uncorrelated with size (Chiappe et al., 2008;

Peters and Peters, 2009, 2010). Peters and Peters' further claim that tail feathers' "presence as such is not a reliable sexual character in the vast majority of extant bird species" is weakened by the facts that they evaluated pintailed birds at the familial level, missing some of the species level diversity and have omitted taxa initially defined as pintailed, e.g. Trogonidae (Balmford et al., 1993). These studies indicate clearly that presence/absence of tail feathers is currently of little use in referring a specimen to a sex, and concordantly there is no basis to assess the gender of D2933. It is important to remember that ornamental feathers may function for species recognition, communication, threat display, or any of many signaling functions beyond sexual selection and mate choice. The size and position of the rectrices suggests that dinosaur feathers were at least in part used for signaling in support of some recent suggestions (Xu et al., 2012; Xu et al. 2009; etc.) and in contrast to others (e.g. Chatterjee et al., 2007). Ultimately, on the basis of current evidence it is impossible to rule out a purely functional interpretation of the tail feathers. There is little data on how theropods may have used their distal tails and such an analysis is beyond the scope of the current study. Two tail feathers of the length found in D2933 without the spray of additional plumage found in some *Microraptor* could not assist with flight in the ways currently modeled for that taxon (M. Habib, pers. com.), but this does not rule out other functions.

In modern birds development of ornamental feathers is generally timed to co-occur with sexual maturity. Even in sexually isomorphic birds such as *Egretta thula*, the snowy egret, the presence of ornate feathers follows the breeding season and they do not occur during the juvenile molts (Parry, 2012). Resplendent quetzals (*Pharomachrus*

mocinno) from Central America possess flight primaries and can fly at around 3 weeks, but do not develop their long tail plumes until around their third year (Skutch, 1944). Tails are long, over a meter in some males (Labastille et al., 1972). In several types of birds with long tails, definitive plumage may come in during the second prealternate molt at the end of the first year, but extreme structures may take much longer to develop, growing sequentially longer with each molt. In general, larger, longer-lived birds tend to delay mating longer than smaller birds and in accord with this show a delayed mature plumage (Proctor and Lynch, 1993). These same large birds tend to also delay mating, up to five years in some gulls (Proctor and Lynch, 1993). Possession of such developed ornamental structures in a relatively somatically immature individual demonstrates that nonavian dinosaurs had a very different strategy of plumage development. Even if unlike in many birds the long rectrices grew in during only one molt, it is still clear that the appearance of these features is not tracking with somatic maturity, and may precede sexual maturity as well. I expect further research to uncover that within non-avian dinosaurs reproductive and other signaling traits developed earlier in ontogeny, but whether this is part of a selectively advantageous functional life history or developmental “baggage” as a consequence of other life history traits, I do not hazard to guess.

Conclusions

Wulong bohaiensis is recognized as a new species of microraptorine dromaeosaurid on the basis of several autapomorphies and a combination of characters distinct from other members of that clade. Phylogenetic analysis finds it to be a well

supported sister group of *Sinornithosaurus*. The holotype is skeletally immature, and bone histology reveals no LAGs. Multiple feather types are preserved in the holotype of *Wulong*, including branched filamentous and symmetrical pennaceous feathers (stages II-IV of Prum, 1999) and possibly of asymmetrical feathers as well (Prum's stage V). Most interesting are the elongate feathers extending from the tip of the tail. The position and length of these feathers suggests that they are ornamental in nature. Though I cannot rule out other unsuspected functional explanations for the tail plumes, their presence in an animal whose osteological characteristics indicate that it was a very young juvenile suggest an as yet unexpected diversity of ornamental and/or functional trajectories for feathers within dinosauria. Larger sample sizes and better control for ontogenetic age and stratigraphic position will be required, but the discovery of stage IV and possibly V body feathers and elongate tail feathers in a yearling nonavian dinosaur suggest that future work may reveal the early evolutionary history of moulting patterns, the timing of sexual and display maturity, and the development of ornamental plumage.

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