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# FIRST NON-AVIAN THEROPOD (DROMAEOSAURIDAE, MICRORAPTORINAE) FROM THE BIRD-BEARING LOWER CRETACEOUS XIAGOU FORMATION OF THE CHANGMA BASIN, GANSU PROVINCE, NORTHWESTERN CHINA

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## ABSTRACT

Lacustrine sediments of the Lower Cretaceous (lower Aptian) Xiagou Formation exposed near the village of Changma in the Changma Basin of northwestern Gansu Province, China have yielded more than 100 avian partial skeletons, many of which also preserve remnants of soft tissues such as feathers and skin. Collectively, these fossils characterize a rich avifauna dominated by the crownward ornithuromorph *Gansus yumenensis* Hou and Liu, 1984. Despite this wealth of Early Cretaceous bird material, no skeletal remains of other dinosaurs have been described from Changma to date. Here we report the first non-avian dinosaur body fossil from the Xiagou Formation of the Changma Basin. Consisting of an articulated left pectoral girdle and forelimb lacking the carpus and manus, the specimen pertains to a new dromaeosaurid theropod taxon, ***Jian changmaensis*, gen. et sp. nov.** Phylogenetic analysis recovers *Jian* within Microraptorinae, expanding the definitive fossil record of this clade to include northwestern China. The new Changma microraptorine constitutes an additional similarity between the theropod faunas of the Xiagou Formation of the Changma Basin and penecontemporaneous strata of the Jehol Group of northeastern China. In particular, the Changma theropod assemblage closely resembles that of the Sihedang locality of the Jehol Group in that both include representatives of Microraptorinae and are overwhelmingly dominated by single ornithuromorph taxa that phylogenetic analyses have repeatedly resolved as close relatives. This raises the possibility that the two sites were deposited under comparable paleoenvironmental settings that are otherwise poorly represented at known Jehol localities.

Key Words: Early Cretaceous, *Gansus yumenensis*, *Jian changmaensis*, microraptorine, paleobiogeography, paleoenvironment, phylogeny, Sihedang.

Fig. 1.—Location of the type locality of *Jian changmaensis,* gen. et sp. nov., in the Changma Basin of northwestern Gansu Province, China.

## INTRODUCTION

In 1981, paleontologists searching for fossil fishes in a Lower Cretaceous (lower Aptian, ~124–120 Ma; Li and Yang 2004; You et al. 2006; X. Li et al. 2013; Suarez et al. 2013, 2017; Zhang et al. 2016; S. Li et al. 2020; Zheng et al. 2021; Wang 2024) exposure of the Xiagou Formation near the village of Changma in the Changma Basin of northwestern Gansu Province, China (Fig. 1) serendipitously discovered an isolated avian distal hind limb that was subsequently designated as the holotype of the ornithuromorph *Gansus yumenensis* Hou and Liu, 1984, the first Mesozoic bird to be found in China. Initiated in 2002, renewed paleontological explorations of the Changma Basin have yielded more than 100 additional articulated and three-dimensionally preserved avian partial skeletons, many preserving soft tissues including feathers, ungual sheaths, and skin. The large majority of these specimens are referable to *G. yumenensis* (Ji et al. 2006; You et al. 2006; Barden et al. 2011; Li et al. 2011; Wogelius et al. 2011; Nudds et al. 2012; Moyer et al. 2014; Wang et al. 2016; O'Connor et al. 2022; Zhao et al. 2022; Monfroy et al. 2023), though a few pertain to Enantiornithes (You et al. 2005; Harris et al. 2006; Lamanna et al. 2006, 2009; Ji et al. 2011; O'Connor et al. 2012, 2016, 2025; M. Wang et al. 2015; Bailleul et al. 2019; Atterholt et al. 2025) or other ornithuromorph taxa (You et al. 2010; Wang et al. 2013; O'Connor et al. 2022). Despite this abundance of Early Cretaceous bird material, no non-avian dinosaur body fossils have previously been described from the Xiagou Formation of the Changma Basin, although sauropod and ornithopod footprints have been documented (Xing et al. 2017). Here we describe the first non-avian dinosaur (herein defined as dinosaurs that are phylogenetically positioned outside the clade Aves, which is in turn defined as all descendants of the common ancestor of *Archaeopteryx lithographica* Meyer, 1861, and *Passer domesticus* Linnaeus, 1758, sensu Sereno 1999) skeletal specimen from the Changma Basin—initially reported in an abstract by Lamanna et al. (2010)—and demonstrate that it pertains to a new taxon closely related to *Microraptor zhaoianus* Xu et al., 2000, a four-winged, likely volant dromaeosaurid from the Jehol Group of northeastern China (Xu et al. 2000, 2003; Hwang et al. 2002; Pei et al. 2014; Kiat et al. 2020; Chotard et al. 2025; Grosmougin et al. 2025; Wang and Pei 2025).

**Institutional Abbreviations**.—**AMNH**, American Museum of Natural History, New York, United States of America; **BMNHC**, Beijing Museum of Natural History, Beijing, China; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **DNHM**, Dalian Museum of Natural History, Dalian, China; **GSGM**, Gansu Geological Museum, Lanzhou, China; **HG**, Paleontological Center, Bohai University, Jinzhou, China; **IGM**, Mongolian Institute of Geology, Ulaanbaatar, Mongolia; **IMMNH**, Inner Mongolia Museum of Natural History, Hohhot, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **JPM**, Jinzhou Paleontological Museum, Jinzhou, China; **LVH**, Department of Land and Resources of Liaoning Province, Shenyang, China; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, United States of America; **MDE**, Musée des Dinosaures, Espéraza, France; **MML**, Museo Paleontológico de Lamarque, Lamarque, Argentina; **MPC**, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Argentina; **MUCPv**, Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén, Argentina; **NGMC**, National Geological Museum of China, Beijing, China; **PBMNH**, Palm Beach Museum of Natural History, Palm Beach, United States of America; **SMP**, State Museum of Pennsylvania, Harrisburg, United States of America; **STM**, Shandong Tianyu Museum of Nature, Shandong, China; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

## SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Dromaeosauridae Matthew and Brown, 1922
Microraptorinae Xu, 2002

### *Jian changmaensis*, gen. et sp. nov.

(Figs. 2, 3)

**Holotype**.—GSGM-D050, an articulated partial left pectoral girdle and forelimb consisting of the complete scapulocoracoid, humerus, radius, and ulna (Figs. 2, 3; Tables 1, 2).

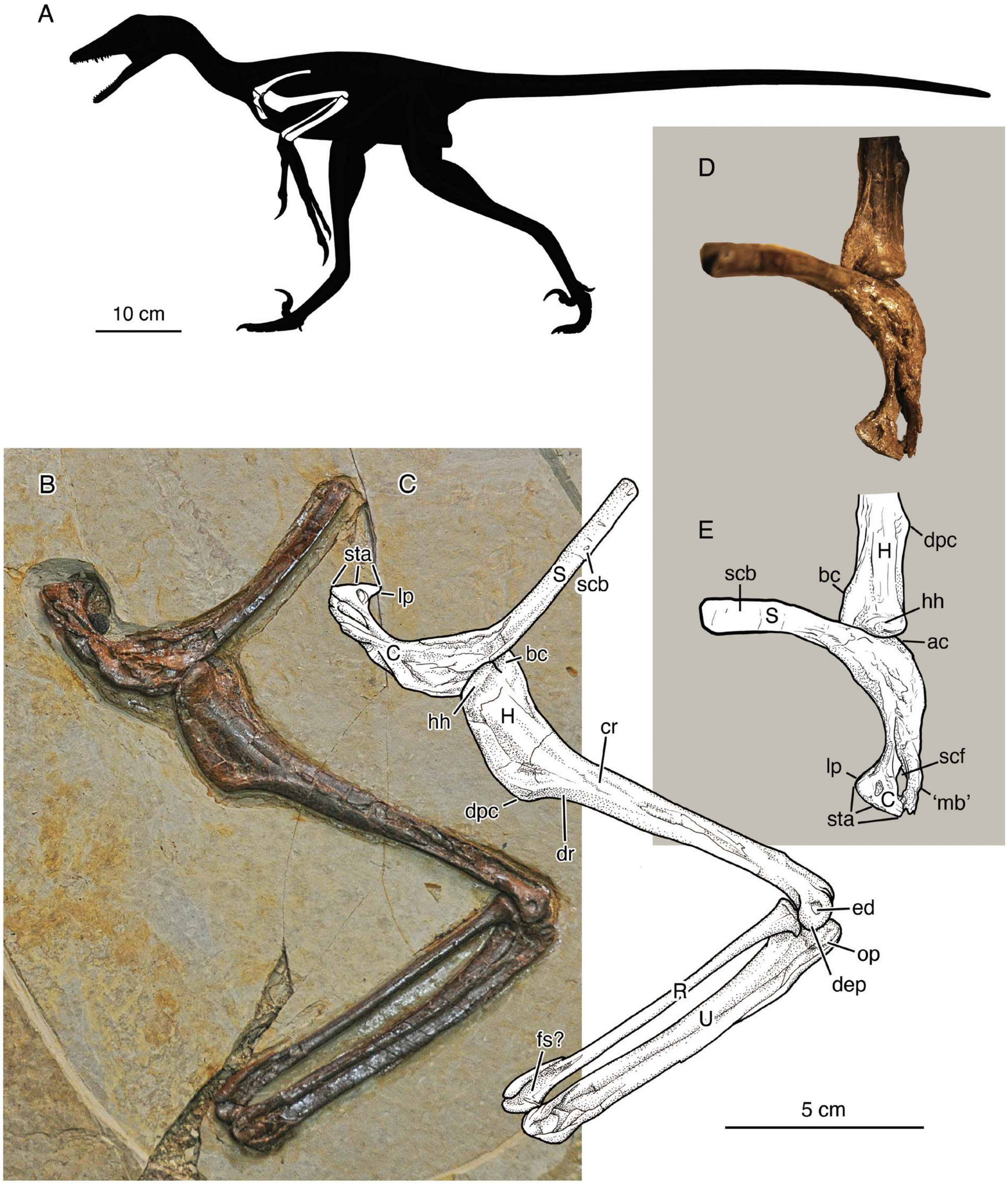

Fig. 2.—Holotype of *Jian changmaensis*, gen. et sp. nov. (GSGM-D050), an articulated partial left pectoral girdle (scapulocoracoid) and forelimb (humerus, radius, and ulna). **A**, silhouette of generalized microraptorine dromaeosaurid theropod (courtesy Scott Hartman) showing skeletal elements preserved; **B**, photograph of specimen as preserved, exposed primarily in dorsomedial (scapulocoracoid), caudodorsal (humerus), and dorsal (radius and ulna) views; **C**, interpretive line drawing of **B**; **D**, detail photograph of scapulocoracoid and proximal end of humerus in caudodorsal view, showing supracoracoid fenestra and other structures; **E**, interpretive line drawing of **D**. Abbreviations: **ac**, acromion; **bc**, bicipital crest; **C**, coracoid; **cr**, caudal ridge; **dep**, dorsal epicondyle; **dpc**, deltopectoral crest; **dr**, dorsal ridge; **ed**, epicondylar depression; **fs?**, fossa for M. supinator?; **H**, humerus; **hh**, humeral head; **lp**, lateral process; **'mb'**, 'medial bar'; **op**, olecranon process; **R**, radius; **S**, scapula; **scb**, scapular blade; **scf**, supracoracoid fenestra; **sta**, sternal articulation; **U**, ulna.

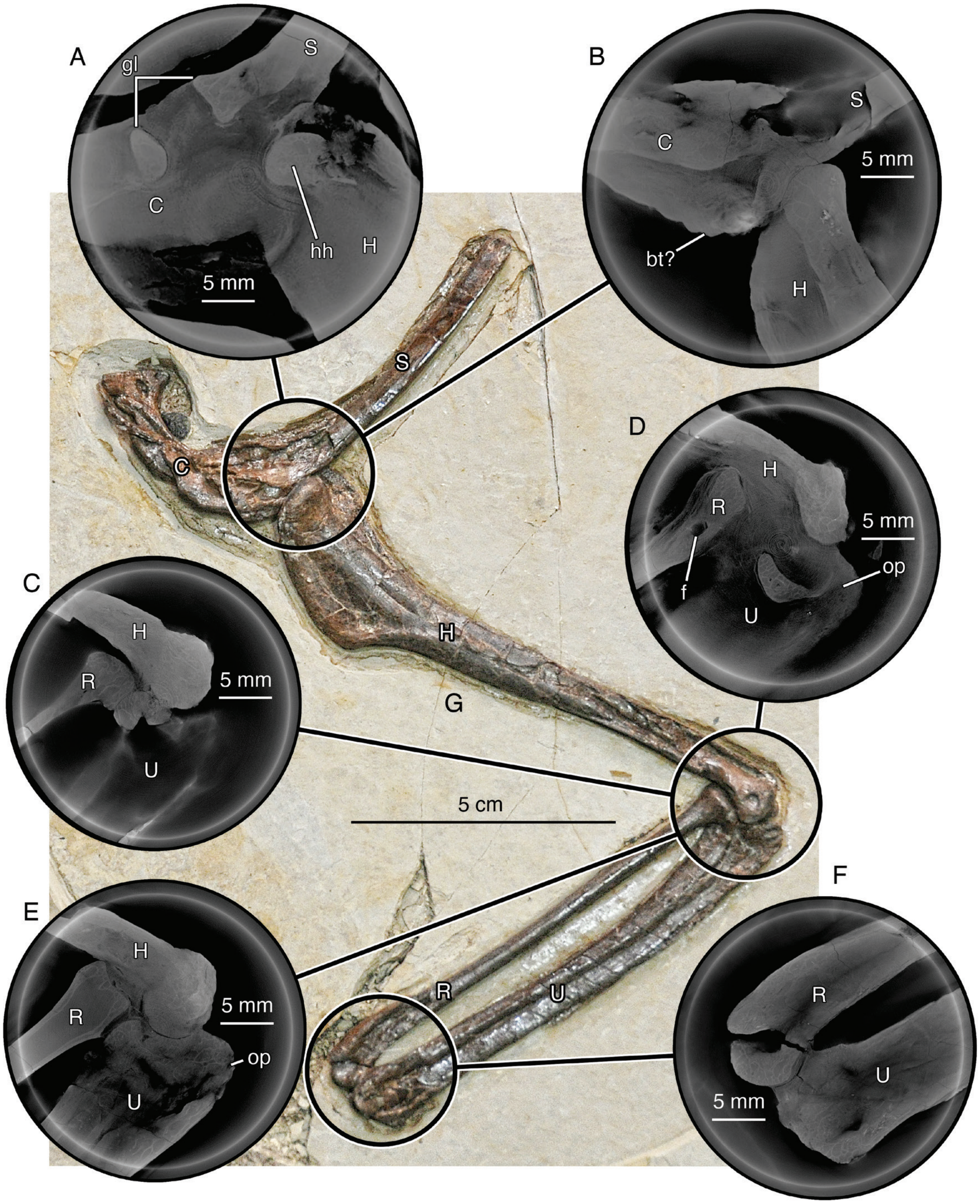

Fig. 3.—Computed laminography (CL) images of left pectoral girdle and forelimb of *Jian changmaensis*, gen. et sp. nov. (GSGM-D050). **A–B**, glenoid region showing omal ends of scapula and coracoid and proximal extreme of humerus; **C–E**, articulated distal humerus and proximal radius and ulna ('elbow region'); **F**, articulated distal radius and ulna; **G**, photograph of specimen showing approximate locations of images in **A–F**. The CL image in **A** is lateral to that in **B**; **A** reveals the projected rim of the glenoid, whereas **B** shows the probable biceps tubercle. Image **C** shows large internal cavities in the radial and ulnar shafts. In **D**, the concave ventral cotyle of the ulna and the autapomorphic radial foramen are visible; **E** is a more central 'slice' that shows the thin cortical wall of the radius. Image **F** illustrates the concave facet on the craniodistal ulna that receives the radius. Abbreviations: **bt?**, biceps tubercle?; **C**, coracoid; **f**, foramen; **gl**, glenoid; **H**, humerus; **hh**, humeral head; **op**, olecranon process; **R**, radius; **S**, scapula; **U**, ulna.

**Diagnosis**.—Medium-sized (intermediate in skeletal dimensions between adult specimens of *Microraptor zhaoianus* and *Sinornithosaurus millenii* Xu et al., 1999; see Table 2) microraptorine dromaeosaurid theropod characterized by the following three autapomorphies: (1) a coracoid that is proportionally longer relative to the humerus than in any other microraptorine (~36% humerus length; the next closest individuals are the immature *Microraptor* IVPP V31612, with a value of ~35%, and IVPP V12811, the holotype of *Sinornithosaurus*, with a value of 33%) (Table 2); (2) humeral distal condyles developed on the cranial surface of this bone (Figs. 2B–C, 3E; a local autapomorphy within Microraptorinae, shared with non-microraptorine theropods such as the therizinosaur *Erlikosaurus andrewsi* Barsbold and Perle, 1980, and Aves); and (3) a well-developed foramen on the ventral aspect of the proximal radius (Figs. 3D, S1). In addition to its possession of the aforementioned autapomorphies, *Jian* may be further differentiated from the microraptorine *Changyuraptor yangi* Han et al., 2014, and the probable microraptorine *Zhenyuanlong suni* Lü and Brusatte, 2015, by its much smaller body dimensions (see Table 2), and from *Microraptor* in having a coracoid that is proportionally much longer relative to the scapula (Table 2) and in lacking a proximal fenestra of the humerus (present in at least some *Microraptor* specimens, see, e.g., Turner et al. 2012: fig. 24c; Pei et al. 2014). Notably, the proximal humeral fenestra is absent in IVPP V31612, a juvenile specimen recently referred to *Microraptor* sp., suggesting that the lack of this structure may be related to ontogenetic immaturity (Wang and Pei 2025). However, GSGM-D050 shows no signs of immaturity, such as incomplete ossification of the periosteum and poorly ossified epiphyses (features that are both present in IVPP V31612), suggesting that GSGM-D050 was ontogenetically mature, or nearly so, at the time of its death (see also below). Therefore, the absence of a humeral fenestra in *Jian* and the presence of this structure in mature individuals of *Microraptor* would appear to constitute a genuine taxonomic distinction between these genera rather than a consequence of ontogeny. *Jian* also differs from *Sinornithosaurus* in having a supracoracoid fenestra that more closely approaches the sternal margin of the coracoid (compare Figs. 2D–E to Xu et al. 1999: fig. 4c) and a proportionally longer ulna (humerus:ulna proximodistal length ratio is 1.14 in GSGM-D050 versus 1.22–1.25 in *Sinornithosaurus*; see Table 2). *Jian* differs from the probable microraptorine *Tianyuraptor ostromi* Zheng et al., 2009, in being substantially smaller in body size and in having a proportionally shorter scapula (scapula:humerus length ratio is 0.68 in *Jian* versus 0.88 in *Tianyuraptor*; Table 2) and a supracoracoid fenestra of the coracoid, and from *Wulong bohaiensis* Poust et al., 2020, in being larger in size and in possessing a much mediolaterally narrower and less craniocaudally extensive supracoracoid fenestra. Finally, *Jian* differs from *Zhongjianosaurus yangi* Xu and Qin, 2017, in being much larger in body dimensions, in having a proportionally shorter scapula and antebrachium (relative to humerus length; Table 2), and in lacking the autapomorphies of the humerus and ulna proposed for that taxon.

**Etymology**.—The genus name is for the Jiān (鹣), a one-winged bird in Chinese mythology, in reference to the bird-like, possibly volant nature of this microraptorine taxon and the skeletal composition of its holotype (an isolated partial pectoral girdle and forelimb). The specific name is for Changma (昌马), the locality where the holotype was discovered.

**Locality and horizon**.—Near the village of Changma (39°51.322'N, 96°46.773'E), Changma Basin, northwestern Gansu Province, People's Republic of China (Fig. 1); Lower Cretaceous (lower Aptian; Li and Yang 2004; You et al. 2006; X. Li et al. 2013; Suarez et al. 2013, 2017; Zhang et al. 2016; S. Li et al. 2020; Zheng et al. 2021; Wang 2024) Xiagou Formation.

## DESCRIPTION AND COMPARISONS

**Terminology**.—Given the bird-like morphology of the dromaeosaurid pectoral girdle and forelimb (Fig. 2A; see also, e.g., Norell and Makovicky 1997, 1999; Xu et al. 1999; Burnham et al. 2000: fig. 3.1), in describing the osteology of *Jian changmaensis*, we follow the directional terminology for the avian skeleton developed by Baumel and Witmer (1993). However, in so doing, our study contrasts with many other anatomical analyses of non-avian theropods; for instance, what has been termed the anterior, cranial, or distal margin of the coracoid in many non-avian theropod studies is herein termed the caudal (= sternal) margin; similarly, the surface of the humerus, radius, and ulna that is typically described as lateral in non-avian theropods is here regarded as the dorsal surface. For additional clarity, a diagrammatic representation of the directional terminology employed herein is provided as Figure 4.

**Preservation and exposure**.—Like nearly all fossil vertebrate specimens from the Xiagou Formation of the Changma Basin, GSGM-D050 is preserved partially articulated and embedded in a slab of yellowish-gray mudstone (Fig. 2B). Consequently, individual elements of the specimen are exposed in only some views. The scapulocoracoid is largely visible in dorsomedial view, while the humerus is in caudodorsal view and the radius and ulna are in dorsal view. Micro-computed laminographic (µCL) scans of selected areas of the specimen performed at the IVPP during 2019 (160 kV µCL system at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences [CAS], IVPP, CAS, Beijing, China; see Liu et al. 2015 for specifications) allowed for additional osteological details to be discerned (Figs. 3, S1). (CL may be preferable to the more commonly used computed tomography [CT] in the cases of compression fossils such as GSGM-D050; see Liu et al. 2015; Wei et al. 2017.) Due to the size of GSGM-D050, the entire specimen could not be simultaneously scanned at appropriate resolution; therefore, we performed three separate scans that imaged the epiphyses (but not the diaphyses) of the preserved elements. The glenoid region was scanned at a voxel size of 15.99 µm, whereas the two areas comprised by the distal humerus and proximal radius and ulna (i.e., the 'elbow') and the distal radius and ulna, respectively, were scanned at 12.99 µm. Though essentially complete and three-dimensionally preserved, all elements of GSGM-D050 are slightly diagenetically crushed, as is common in vertebrate fossils from lacustrine sediments. This compression does not appear to have affected the overall lengths of the elements, but it has obscured some three-dimensional morphological details.

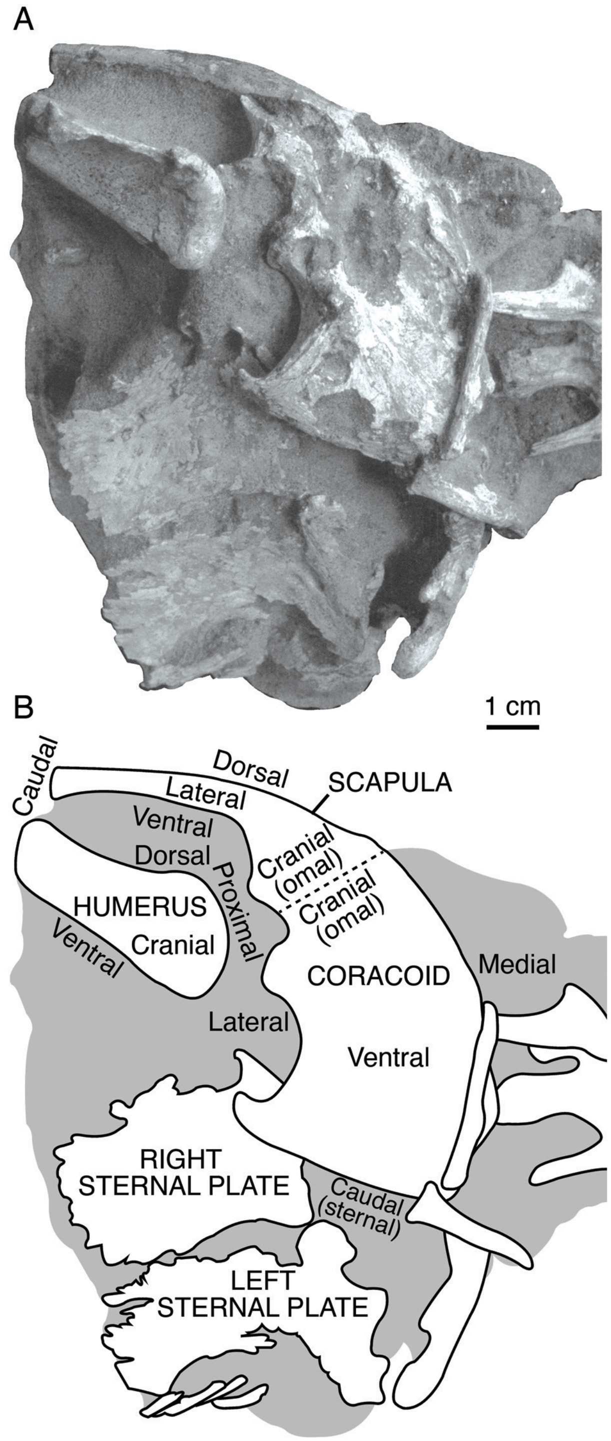

Fig. 4.—Diagrammatic representation of the osteological terminology employed for the dromaeosaurid pectoral girdle and proximal forelimb. **A**, cranial thoracic region of *Velociraptor mongoliensis* (IGM 100/976) in right ventrolateral view (modified from Norell and Makovicky 1999: fig. 2); **B**, interpretive line drawing of **A** with surfaces/margins of the scapula, coracoid, and humerus as described herein indicated. Dashed line indicates approximate location of synostosis between scapula and coracoid.

**Body dimensions and ontogenetic stage**.—*Jian* is a medium-sized representative of Microraptorinae (Table 2). In all examined dimensions, the holotype (GSGM-D050) is intermediate in size between the exceptionally small-bodied microraptorines *Wulong bohaiensis* (the holotypic specimen of which is immature), *Zhongjianosaurus yangi*, and small specimens of *Microraptor zhaoianus,* and the largest known specimens of the larger-bodied *Sinornithosaurus millenii*. It is close in size to (though slightly larger than) NGMC 91 (Ji et al. 2001, 2002), a subadult microraptorine referred to *Sinornithosaurus* (Turner et al. 2012), and LVH 0026, a large individual of *Microraptor* (the holotype of '*Microraptor hanqingi*' Gong et al., 2012, regarded by Pei et al. [2014] as a junior synonym of *M. zhaoianus*). The holotypic specimens of *Changyuraptor yangi* and the probable microraptorines *Tianyuraptor ostromi* and *Zhenyuanlong suni* are substantially larger. (We follow many previous authors [e.g., Senter et al. 2004; Turner et al. 2007a, 2012; Pei et al. 2014; Xu and Li 2016; Agnolín et al. 2019] in regarding '*Microraptor gui*' Xu et al., 2003, '*M. hanqingi*,' and '*Cryptovolans pauli*' Czerkas et al., 2002, as subjective junior synonyms of *M. zhaoianus*, and Turner et al. [2012] in considering '*Sinornithosaurus haoiana*' Liu et al., 2004, as a junior synonym of *Si. millenii*. As such, we consider *M. zhaoianus* and *Si. millenii* to be the only presently valid species of *Microraptor* and *Sinornithosaurus*, respectively.)

The scapula and coracoid are firmly co-ossified, with no line of synostosis visible externally or in the CL scans, suggesting that the individual represented by GSGM-D050 was osteologically mature, or nearly so, at the time of its death (Wu et al. 2021). Again, this assertion is corroborated by the smooth periosteal surface of all preserved elements, indicating that ossification was complete (i.e., the cortical bone is 'finished,' lacking the pitted and grooved surface texture generated by the vascular canals of an actively growing element) (e.g., Tumarkin-Deratzian et al. 2007).

**Scapulocoracoid**.—As noted above, the scapula and coracoid are fully fused and exhibit smooth, 'finished' surface texture. A slight medial expansion of the costal (= internal) margin of the scapulocoracoid (i.e., the medial margin of the scapula and the dorsal margin of the coracoid), directly opposite the point of contact of this compound element with the humeral head, probably marks the junction between the scapula and coracoid, which would have passed through the glenoid fossa. A fully fused scapulocoracoid also occurs in many other dromaeosaurids, including some other microraptorines (e.g., *Microraptor* [Hwang et al. 2002], *Zhongjianosaurus* [Xu and Qin 2017]), but not in *Wulong* (Poust et al. 2020), the probable microraptorine *Tianyuraptor* (Zheng et al. 2009), or the unenlagiines *Buitreraptor gonzalezorum* Makovicky et al., 2005, and *Unenlagia comahuensis* Novas and Puerta, 1997 (Novas et al. 2018). In at least *Wulong* and *Tianyuraptor*, this lack of fusion is most likely due to ontogenetic immaturity (Wu et al. 2021). Both the scapula and coracoid of *Jian* are almost completely preserved, but their edges are damaged, the former element in the acromial region and the latter throughout the length of its medial margin. The cranial half of the scapulocoracoid is strongly arched medially, lending the element a 'J'-shaped contour in dorsomedial view (Figs. 2B–C). Consequently, in this view, the long axes of the scapula and coracoid intersect at an angle only slightly greater than 90°, lower than in many other theropods, including other maniraptorans (e.g., *Microraptor*, reported to be ~105° [Hwang et al. 2002]). CL scans reveal that the glenoid fossa is laterally oriented and deeply concave, defined by well-developed projections of both the scapula and coracoid (Fig. 3A). The margin of the glenoid that projects from the coracoid is tapered, whereas the margin that projects from the scapula is more ridge-like.

The scapula is characterized by a slightly dorsoventrally expanded cranial end and an essentially straight, strap-like blade with parallel dorsal and ventral margins. Though long, it is shorter than the humerus, as in other dromaeosaurids (e.g., *Bambiraptor feinbergorum* Burnham et al., 2000 [Burnham 2004], *Deinonychus antirrhopus* Ostrom, 1969 [Ostrom 1969], other microraptorines and probable microraptorines [Xu et al. 1999; Hwang et al. 2002; Zheng et al. 2009; Han et al. 2014; Xu and Qin 2017; Poust et al. 2020]) (Figs. 2B–C; Table 1). The acromial process is damaged but was almost certainly dorsoventrally low and in contact with the craniomedial edge (i.e., the medial part of the omal end) of the coracoid cranially. It is unclear whether the margin of this process was laterally everted. The uncrushed scapular blade is elliptical in cross section, with the long axis of the ellipse oriented dorsoventrally, and it gradually thins in mediolateral dimension caudally, such that the dorsal edge grades from a rounded surface cranially to an acute ridge caudally. In dorsal view, the scapular blade is straight, not gently sigmoid as in *Bambiraptor* (Burnham 2004: fig. 3.14b). The caudal end of the blade is very slightly ventrally expanded, as in *Deinonychus* (Ostrom 1969), and rounded in lateral and medial views.

Compared to those of most other non-avian theropods, the coracoid of *Jian* is extremely elongate (in craniocaudal [i.e., omal to sternal] length) relative to its mediolateral width (Fig. 2). The coracoid is proportionally longer even than in most other dromaeosaurids, such as *Achillobator giganticus* Perle et al., 1999 (Perle et al. 1999), *Bambiraptor* (Burnham 2004), *Buitreraptor* (Gianechini et al. 2018; Novas et al. 2018), *Deinonychus* (Ostrom 1969, 1974), *Luanchuanraptor henanensis* Lü et al., 2007 (Lü et al. 2007), *Saurornitholestes langstoni* Sues, 1978 (Jasinoski et al. 2006: figs. 6a–b), and *Tianyuraptor* (Zheng et al. 2009), more closely resembling, though still exceeding, *Sinornithosaurus* (Xu et al. 1999) and *Wulong* (Poust et al. 2020). Although, as noted above, the cranial (i.e., omal) margin of the coracoid is difficult to distinguish from that of the scapula, it is clear that the former element is more than one-half the length of the latter (Tables 1, 2). To our knowledge, the only other dromaeosaurid specimens in which this condition has been reported are the holotypes of *Sinornithosaurus* (IVPP V12811; Xu et al. 1999) and *Wulong* (DNHM D2933; Poust et al. 2020) and an immature specimen referred to *Microraptor* (STM5-50; Zheng et al. 2014). The caudolateral (= sternolateral) portion of the coracoid is strongly expanded into a subtriangular, laterally pointed lateral process, rendering the lateral margin of the bone strongly concave in ventral or dorsal (i.e., external or internal) view. The sternolateral corner of the coracoid is similarly expanded in *Microraptor* (O'Connor et al. 2015, 2019; Wang and Pei 2025) and *Wulong* (Poust et al. 2020). Immediately cranial to this process, the coracoid narrows dramatically in mediolateral dimension, though how much so cannot be definitively determined due to the broken condition of the medial margin of the element.

The most conspicuous feature of the coracoid is a large, elliptical fenestra that is approximately half the craniocaudal length of the bone itself (Figs. 2D–E; Table 1). This fenestra was probably mediolaterally wider in life than it is as preserved, having been diagenetically compressed to a degree that is difficult to ascertain. Both the lateral and medial margins of the fenestra are composed of smooth, finished bone, demonstrating that it is not a taphonomic artifact. The fenestra is completely open caudally but partly closed cranially by a dorsoventrally thin crest that extends medially from its craniolateral margin. The only other theropods in which a comparable fenestra occurs are the microraptorine dromaeosaurids *Microraptor* (Xu et al. 2003; Gong et al. 2012; Turner et al. 2012: fig. 24c; Grosmougin et al. 2025; Wang and Pei 2025), *Sinornithosaurus* (Xu et al. 1999: 262, fig. 4c; Turner et al. 2012: fig. 24b; A.W.P., pers. obs.), *Wulong* (Poust et al. 2020), and *Zhongjianosaurus* (Xu and Qin 2017) from the Lower Cretaceous Jehol Group of northeastern China (though note that Moutrille et al. [2025] recently reported the presence of a similar fenestra in the Mongolian Late Cretaceous eudromaeosaurian *Shri rapax* Moutrille et al., 2025). In these microraptorine taxa, this opening has been termed the supracoracoid fenestra (Xu et al. 1999, 2003; Turner et al. 2012; Wang and Pei 2025). The occurrence of this distinc-

TABLE 1. Measurements (mm) of the holotypic specimen of *Jian changmaensis,* gen. et sp. nov. (GSGM-D050). * = element incomplete, measurement as preserved; ~ = measurement approximate.

| Element/dimension | Measurement |
|---|---|
| **Scapulocoracoid** | |
| Craniocaudal length, dorsomedial (= omomedial) margin of coracoid–caudal end of scapula | 73.2 |
| Dorsoventral depth, ventromedial corner of coracoid–craniodorsal edge of scapula | ~40 |
| **Scapula** | |
| Craniocaudal length | ~69 |
| Mediolateral width, mid-blade | 4.9 |
| Dorsoventral depth, mid-blade | 6.1 |
| Mediolateral width, caudal | 3.3 |
| Dorsoventral depth, caudal | 6.1 |
| **Coracoid** | |
| Craniocaudal (i.e., omal to sternal) length | ~37 |
| Mediolateral width, ventral | ~15* |
| Craniocaudal length, supracoracoid fenestra | 18.6 |
| Mediolateral width, supracoracoid fenestra | 3.1* |
| **Humerus** | |
| Proximodistal length | 101.6 |
| Proximodistal length, deltopectoral crest | ~33 |
| Proximodistal length, bicipital crest | ~22 |
| Craniocaudal width, proximal (bicipital crest–deltopectoral crest) | ~25 |
| Craniocaudal width, midshaft | 8.2 |
| Craniocaudal width, distal (distodorsal condyle) | 8.2 |
| **Radius** | |
| Proximodistal length | 84.9 |
| Craniocaudal width, proximal | 5.8 |
| Craniocaudal width, midshaft | 3.2 |
| Craniocaudal width, distal | 7.3 |
| **Ulna** | |
| Proximodistal length | 89.2 |
| Craniocaudal width, proximal | ~11 |
| Craniocaudal width, midshaft | 7.2 |
| Craniocaudal width, distal | 10.9* |

tive structure in *Jian* supports the referral of the new Gansu form to Microraptorinae. Among other well-supported microraptorine or probable microraptorine taxa (following the systematic revision of Turner et al. [2012] and the phylogenetic hypothesis presented by Han et al. [2014]) in which this condition can be confidently evaluated, only *Tianyuraptor* does not possess a similarly fenestrated coracoid (Zheng et al. 2009). As in *Sinornithosaurus*, the supracoracoid fenestra of *Jian* is proportionally smaller than that of *Wulong*, which effectively divides the coracoid of this latter taxon into craniocaudally elongate lateral and medial struts (Poust et al. 2020). Regrettably, the presence or absence of the supracoracoid fenestra cannot be ascertained in the remaining microraptorines (*Changyuraptor* [Han et al. 2014], *Graciliraptor lujiatunensis* Xu and Wang, 2004 [Xu and Wang 2004], and *Hesperonychus elizabethae* Longrich and Currie, 2009 [Longrich and Currie 2009; Rhodes and Currie 2020]) or the relatively large-bodied probable microraptorine *Zhenyuanlong* (Lü and Brusatte 2015).

As in *Bambiraptor* (Burnham et al. 2000; Burnham 2004), no coracoid foramen is evident, but based on the condition in other microraptorines (e.g., *Microraptor*, Wang and Pei 2025: fig. 3c; *Sinornithosaurus*, Xu et al. 1999: fig. 4c; *Wulong*, Poust et al. 2020: fig. 6) it likely was present but has been obscured by crushing. The presence or absence of the biceps tubercle cannot be definitively determined due to the minimal exposure of the ventral surface of the coracoid, though a large ventral projection near the glenoid fossa, visible in CL images, may correspond to this structure (Fig. 3B). Two diamond-shaped pits, one larger and deeper than the other, occur on the dorsal surface, caudolateral to the supracoracoid fenestra, and are interpreted as taphonomic artifacts. A dark, subcircular structure lodged beneath the lateral edge of the coracoid appears to represent carbonized plant matter.

**Humerus**.—The humerus is well preserved, especially proximally, and (as noted above) is considerably longer than the scapula (Table 1), as in all other microraptorines or probable microraptorines for which this condition can be reliably assessed (i.e., *Changyuraptor* [Han et al. 2014], *Microraptor* [Xu et al. 2003], *Sinornithosaurus* [Xu et al. 1999], *Tianyuraptor* [Zheng et al. 2009], *Wulong* [Poust et al. 2020], and *Zhongjianosaurus* [Xu and Qin 2017]) plus some other dromaeosaurids (e.g., *Bambiraptor*, *Buitreraptor*). The humerus has been disarticulated and caudally deflected from the scapulocoracoid (Figs. 2B–E, 3A–B), but the two elements otherwise remain close to their relative in vivo positions. As is also the case for the scapulocoracoid, the surface texture of the humerus is smooth. Overall, the humerus is moderately elongate, with its proportions generally resembling those of the corresponding element in *Dakotaraptor steini* DePalma et al., 2015 (DePalma et al. 2015), *Deinonychus* (Ostrom 1969), *Dineobellator notohesperus* Jasinski et al., 2020 (Jasinski et al. 2020, 2023), *Diuqin lechiguanae* Porfiri et al., 2024 (Porfiri et al. 2024), *Luanchuanraptor* (Lü et al. 2007), Microraptorinae (Fig. 5) (Xu et al. 1999, 2003; Ji et al. 2001; Czerkas et al. 2002; Hwang et al. 2002; Liu et al. 2004; Xu and Wang 2004; Zheng et al. 2009; O'Connor et al. 2011, 2019; Gong et al. 2012; Li et al. 2012; Turner et al. 2012; Xing et al. 2013; Han et al. 2014; Pei et al. 2014; Xu and Qin 2017; Poust et al. 2020; Grosmougin et al. 2025; Wang and Pei 2025), *Sa. langstoni* (Jasinoski et al. 2006: figs. 6e–f), *U. comahuensis* (Novas and Puerta 1997; Turner et al. 2012), *Unenlagia paynemili* Calvo et al., 2004 (Calvo et al. 2004), and *Zhenyuanlong* (Lü and Brusatte 2015), but differing markedly from the elongate, gracile humeri of *Bambiraptor* (Burnham et al. 2000) and *Buitreraptor* (Makovicky et al. 2005; Gianechini et al. 2018; Novas et al. 2018) and the shorter, more robust humeri of *Austroraptor cabazai* Novas et al., 2008 (Novas et al. 2008), *Balaur bondac* Csiki et al., 2010 (Csiki et al. 2010; Brusatte et al. 2013), and *Shri rapax* (Moutrille et al. 2025) and the similarly stout humerus referred to *Variraptor mechinorum* Le Loeuff and Buffetaut, 1998 (MDE-D 158; Le Loeuff and Buffetaut 1998) (regarded as a nomen dubium by Allain and Taquet [2000] and Turner et al. [2012]). Proximally, the oval, dorsoventrally elongate humeral head projects strongly caudally. A portion of its articular condyle (that would have resided within the glenoid fossa of the scapulocoracoid) is visible in caudal view; moreover, as shown by the CL scans, the condyle extends onto the cranial surface, where it is dorsoventrally narrower (Fig. 3A). The humeral head grades distally into the remainder of the bone via a low, dorsoventrally broad ridge. Though obscured from view, the cranial surface of the humerus appears to be broadly concave between the humeral head and the dorsal margin of the deltopectoral crest. The latter is subtriangular and extends slightly less than one-third the length of the bone (Table 1). The deltopectoral crest projects cranially, with its cranial apex situated near its distal margin. Although prominent, the crest is proportionally smaller and less cranially projected than in Unenlagiinae (i.e., *Austroraptor* [Novas et al. 2008], *Buitreraptor* [Makovicky et al. 2005; Gianechini et al. 2018; Novas et al. 2018], *Diuqin* [Porfiri et al. 2024], *U. comahuensis* [Novas and Puerta 1997; Calvo et al. 2004; Turner et al. 2012], *U. paynemili* [Calvo et al. 2004]). The proximal end of the deltopectoral crest lacks the foramen present in *Zhongjianosaurus* (Xu and Qin 2017), possibly *Wulong* (Poust et al. 2020), and many specimens of *Microraptor* (Li et al. 2012; Turner et al. 2012: fig. 24c; Pei et al. 2014). The proximodistal extent of the crest along the humerus resembles that in most other microraptorines and probable microraptorines (Fig. 5) (Ji et al. 2001; Hwang et al. 2002; Xu et al. 2003; Zheng et al. 2009; Gong et al. 2012; Pei et al. 2014; Xu and Qin 2017; Poust et al. 2020; Grosmougin et al. 2025; Wang and Pei 2025) and some non-microraptorine dromaeosaurids (e.g., *Dineobellator* [Jasinski et al. 2020, 2023]; *Sa. langstoni* [Jasinoski et al. 2006: figs. 6e–f]), appearing intermediate between the proximally restricted deltopectoral crest of *Bambiraptor* (Burnham et al. 2000; Burnham 2004) and the more distally extended crests of *Austroraptor* (Novas et al. 2008), *Deinonychus* (Ostrom 1969), and *Variraptor* (MDE-D 158; Le Loeuff and Buffetaut 1998). The caudodistal margin of the crest is buttressed by a robust dorsal ridge that grades distally into the humeral shaft. The bicipital crest (= internal tuberosity) is rounded in caudal view and proximodistally elongate, extending distally to approximately two-thirds the length of the deltopectoral crest. The bicipital crest appears to be separated from the ventral edge of the humeral head by a narrow longitudinal sulcus, though the depth of this structure may be exaggerated by taphonomic distortion. Immediately distal to the deltopectoral crest, the caudal surface of the humeral midshaft is marked by a low, dorsoventrally narrow, longitudinally oriented ridge.

The distal one-third of the humerus, especially the shaft, is badly crushed and thus difficult to reliably interpret. The crushing of the shaft is presumably attributable to its hollow nature, which is also revealed by the CL scan (Fig. 3E). The dorsal epicondyle is moderately developed and dorsally embayed by a marked, subcircular epicondylar depression. The distal condyles are located primarily on

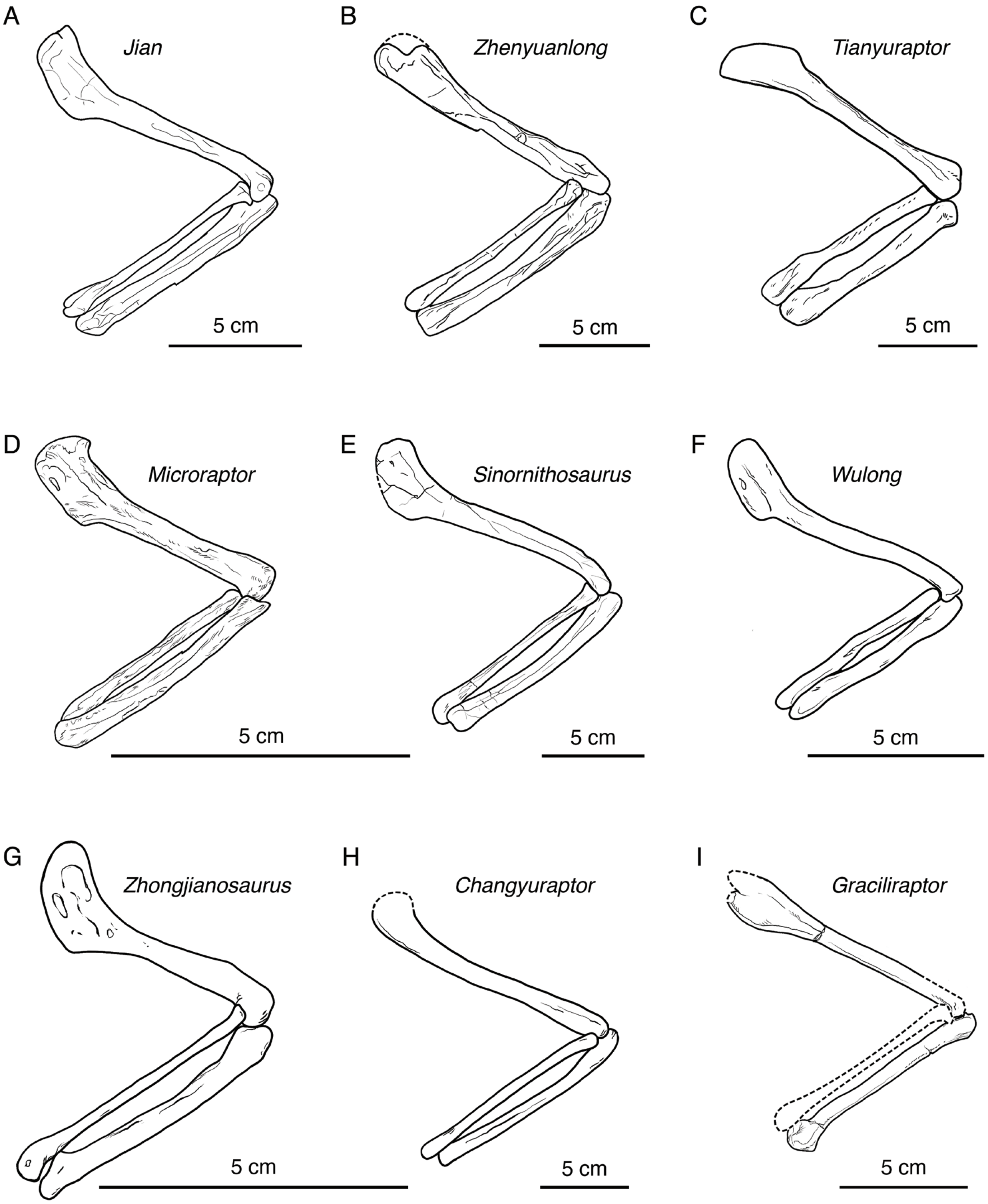

Fig. 5.— Comparison of left forelimb (minus carpus and manus) osteology of Microraptorinae and probable Microraptorinae, primarily in dorsal view. Drawings scaled to same humerus length and in some cases (**B–D**, **H**, **I**) reversed from right side for ease of comparison; missing portions reconstructed with dashed lines. Note that most source specimens are compressed and that, as such, the perspectives from which they are depicted often vary at least slightly. Figure is intended primarily to illustrate proportional differences in bone length and robusticity between species. **A**, *Jian changmaensis*, gen. et sp. nov. (GSGM-D050). **B**, *Zhenyuanlong suni* (JPM-0008, after Lü and Brusatte 2015: fig. 3a). **C**, *Tianyuraptor ostromi* (STM-1, after Zheng et al. 2009: fig. 1). **D**, *Microraptor zhaoianus* (BMNHC PH881, after Pei et al. 2014: fig. 9). **E**, *Sinornithosaurus millenii* (DNHM D2140, drawn from unpublished photo by A.W.P.). **F**, *Wulong bohaiensis* (DNHM D2933, after Poust et al. 2020: figs. 1a, c, 3a, 6). **G**, *Zhongjianosaurus yangi* (IVPP V22775, after Xu and Qin 2017: figs. 1, 3b–c). **H**, *Changyuraptor yangi* (HG B016, after Han et al. 2014: figs. 2a–b). **I**, *Graciliraptor lujiatunensis* (IVPP V13474, after Xu and Wang 2004: fig. 2a).

the cranial surface of the bone (Fig. 3E), a condition that resembles that in birds but differs from that in other microraptorines, in which the humeral condyles are craniodistally oriented (Pei et al. 2014; Poust et al. 2020; Wang and Pei 2025).

**Radius**.—The radius remains articulated with the humerus and ulna and is very well preserved proximally but moderately crushed distally. It is a rod-shaped element with craniocaudally and dorsoventrally expanded proximal and distal ends. The proximal extreme is dorsally embraced and slightly obscured from view by the craniodorsal process of the ulna. Despite this, the proximal end is three-dimensionally preserved and has a cylindrical form as in animals that are capable of significant pronation and supination (VanBuren and Bonnan 2013). CL images reveal that the ventral surface of the proximal radius is pierced by a well-developed subcircular foramen that has not been described in other dromaeosaurids (including other microraptorines) and that we therefore regard as an autapomorphy of *Jian* (Fig. 3D). This foramen lies within a larger, oval, proximodistally elongate fossa (Fig. S1). The radial shaft is much craniocaudally narrower than that of the ulna, and appears elliptical in cross section, especially proximally, with the long axis of the ellipse oriented dorsoventrally. A radial shaft that is much narrower than that of the ulna is present in most other microraptorines (Figs. 5D–H) (e.g., Xu et al. 2000, 2003; Ji et al. 2001, 2002; Czerkas et al. 2002; Hwang et al. 2002; Norell et al. 2002; Liu et al. 2004; Xu and Wang 2004; O'Connor et al. 2011, 2019; Gong et al. 2012; Li et al. 2012; Xing et al. 2013; Han et al. 2014; Pei et al. 2014; Xu and Qin 2017; Poust et al. 2020), the probable microraptorine *Zhenyuanlong* (Fig. 5B; Lü and Brusatte 2015), the unenlagiines *Austroraptor* (Currie and Paulina Carabajal 2012) and *Buitreraptor* (Gianechini et al. 2018; Novas et al. 2018), and the halszkaraptorine *Natovenator polydontus* Lee et al., 2022 (Lee et al. 2022), but not in most other dromaeosaurids (e.g., *Bambiraptor* [Burnham 2004; Senter 2006], *Dakotaraptor* [DePalma et al. 2015], *Deinonychus* [Ostrom 1969; Senter 2006], *Halszkaraptor escuilliei* Cau et al., 2017 [Cau et al. 2017], *Mahakala omnogovae* Turner et al., 2007 [Turner et al. 2007c, 2011], *Pyroraptor olympius* Allain and Taquet, 2000 [Allain and Taquet 2000; Turner et al. 2012]) and the short-forelimbed probable microraptorine *Tianyuraptor* (Fig. 5C; Zheng et al. 2009). Though crushed, the distal end of the radius widens and bends caudally towards the ulna as in *Microraptor*, *Sinornithosaurus*, and *Wulong*. The distodorsal end is embayed by a shallow, longitudinally oriented furrow that may correspond to the origin site of the M. supinator, as has been proposed for *Buitreraptor* (Novas et al. 2018).

**Ulna**.—Like the radius, the ulna is better preserved proximally than distally, though it is dorsoventrally crushed throughout much of its length. It is longer than the scapula but shorter than the humerus (Table 1), as in most other microraptorines except *Zhongjianosaurus*, in which the ulna is slightly longer than the humerus (Xu and Qin 2017). Importantly, however, the ulna of GSGM-D050 is proportionally longer than those of *Sinornithosaurus* and *Wulong* (Table 2), taxa that otherwise resemble the new Changma form in the extraordinary length of the coracoid. The proximally-projecting olecranon process is well developed. As is evident in the CL scans (Figs. 3C–E), the ventral cotyle is deeply concave and preserved in articulation with the ventral condyle of the humerus, which strongly suggests that the proximal articular surface of the ulna is differentiated into two distinct cotyles. As noted above, the small, subtriangular craniodorsal process is preserved in contact with the proximodorsal extreme of the radius. As in other maniraptorans, the ulnar shaft is gently bowed caudally away from that of the radius, especially proximally. The distal end is broken but clearly forms a convex, semilunate surface that is also present in *Graciliraptor* (Xu and Wang 2004) and *Zhongjianosaurus* (Xu and Qin 2017). Like other elements of GSGM-D050, the surface of the ulna is composed of smooth, finished cortical bone. In contrast to *Dakotaraptor* (DePalma et al. 2015), *Dineobellator* (Jasinski et al. 2020, 2023), *Rahonavis ostromi* Forster et al., 1998 (Forster et al. 1998, 2020), and at least some specimens of *Velociraptor mongoliensis* Osborn, 1924 (Turner et al. 2007b), no ulnar papillae (= 'quill knobs') are evident on its caudal edge (either via visual or tactile examination), though if present such structures would presumably be minute and thus difficult to detect.

## PHYLOGENETIC ANALYSIS

To elucidate the systematic position of *Jian changmaensis* within Paraves, we conducted a phylogenetic analysis using the character-taxon matrix presented by Pei et al. (2020) in their analysis of potential volant capabilities in Pennaraptora, which was itself sourced from Brusatte et al. (2014) in their study of evolutionary rates across the dinosaur-bird transition. We initially added three taxa to this data matrix: the new Changma theropod and two other microraptorines, *Wulong bohaiensis* (Poust et al. 2020) and *Zhongjianosaurus yangi* (Xu and Qin 2017). The resulting matrix consisted of 167 theropod operational taxonomic units (OTUs) and 853 morphological characters, and included, for the first time in a published, quantitative phylogenetic analysis, all putative members of Microraptorinae (*Changyuraptor yangi*, *Graciliraptor lujiatunensis*, *Hesperonychus elizabethae*, *J. changmaensis*, *Microraptor zhaoianus*, *Shanag ashile* Turner et al., 2007a, *Sinornithosaurus millenii*, *Tianyuraptor ostromi*, *W. bohaiensis*, *Yurgovuchia doellingi* Senter et al., 2012, *Zhenyuanlong suni*, *Z. yangi*, and IVPP V22530, a fragmentary possible microraptorine from the Aptian–Albian Bayan Gobi Formation of Nei Mongol, China [Pittman et al. 2015]) (see Supplementary Information). The matrix was analyzed with equally weighted parsimony using TNT

TABLE 2. Comparison of selected length measurements (mm) of the holotypic specimen of *Jian changmaensis*, gen. et sp. nov. (GSGM-D050) versus those of other dromaeosaurids. -- = measurement not reported or not possible due to insufficient preservation; * = element incomplete, measurement as preserved; ~ = measurement approximate or estimated; $^{a1}$ = listed measurement is average of left and right elements; $^{a2}$ = listed measurement is average of slab and counterslab. Anatomical abbreviations: S, scapula; C, coracoid; H, humerus; R, radius; U, ulna. Institutional abbreviations see text.

| **Taxon** | **Specimen** | **S** | **C** | **H** | **R** | **U** | **S/C** | **S/H** | **C/H** | **H/R** | **H/U** | **Source(s)** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Microraptorinae** | | | | | | | | | | | | |
| ***Jian changmaensis*** | **GSGM-D050** | **~69.0** | **~37.0** | **101.6** | **84.9** | **89.2** | **1.86** | **0.68** | **0.36** | **1.20** | **1.14** | **This paper** |
| *Changyuraptor yangi* | HG B016 | -- | -- | 148.9 | -- | 126.1 | -- | -- | -- | -- | 1.18 | Han et al. 2014 |
| *Graciliraptor lujiatunensis* | IVPP V13474 | -- | -- | -- | -- | -- | -- | -- | -- | -- | ~1.16 | Xu and Wang 2004 |
| *Microraptor zhaoianus* | BMNHC PH881 | -- | -- | 45.0$^{a1}$ | 41.0 | 44.7 | -- | -- | -- | 1.10 | 1.01 | Pei et al. 2014 |
| *Microraptor zhaoianus* | CAGS-20-7-004 | -- | -- | 61.7$^{a1}$ | ~48.0 | 53.8 | -- | -- | -- | 1.29 | 1.15 | Hwang et al. 2002 |
| *Microraptor zhaoianus* | CAGS-20-8-001 | 43.0 | 16.0 | 62.9 | ~48.3 | ~53.5 | 2.69 | 0.68 | 0.25 | 1.30 | 1.18 | Hwang et al. 2002 |
| *Microraptor zhaoianus* | IVPP V12330 | -- | -- | -- | -- | 35.0 | -- | -- | -- | -- | -- | Xu et al. 2000 |
| *Microraptor zhaoianus* | IVPP V13320 | -- | -- | 54.1$^{a1}$ | 43.5$^{a1}$ | 45.1$^{a1}$ | -- | -- | -- | 1.24 | 1.20 | Grosmougin et al. 2025 |
| *Microraptor zhaoianus* | IVPP V13352 | -- | -- | 82.0 | 69.8 | 70.3 | -- | -- | -- | 1.17 | 1.17 | O'Connor et al. 2011 |
| *Microraptor zhaoianus* | IVPP V13475 | -- | -- | 42.0 | 34.5 | -- | -- | -- | -- | 1.22 | -- | Gianechini and Apesteguía 2011 |
| *Microraptor zhaoianus* | IVPP V13972 | -- | -- | 89.4 | 75.9$^{a2}$ | 79.0$^{a2}$ | -- | -- | -- | 1.18 | 1.13 | O'Connor et al. 2011 |
| *Microraptor zhaoianus* | LVH 0026 | 57.4$^{a1}$ | 27.3 | 93.1$^{a1}$ | 79.5 | 82.5 | 2.10 | 0.62 | 0.29 | 1.17 | 1.13 | Gong et al. 2012 |
| *Microraptor* sp. | IVPP V31612 | 32.3$^{a1}$ | 14.2 | 41.0 | 32.2 | 32.8 | 2.28 | 0.79 | 0.35 | 1.27 | 1.25 | Wang and Pei 2025 |
| *Microraptor* sp. | STM 5-4 | -- | -- | 82.3 | 60.2 | -- | -- | -- | -- | 1.37 | -- | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-5 | -- | -- | 77.8$^{a1}$ | -- | 75.4 | -- | -- | -- | -- | 1.03 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-9 | -- | -- | 89.0 | 85.2 | 84.2 | -- | -- | -- | 1.05 | 1.06 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-75 | -- | -- | 51.5$^{a1}$ | 51.2 | 53.9 | -- | -- | -- | 1.01 | 0.96 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-93 | -- | -- | 74.9 | 58.1$^{a1}$ | 64.7$^{a1}$ | -- | -- | -- | 1.29 | 1.16 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-109 | -- | -- | 80.6 | 67.2 | 73.2 | -- | -- | -- | 1.20 | 1.10 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-142 | -- | -- | 98.1$^{a1}$ | 79.7$^{a1}$ | 83.1$^{a1}$ | -- | -- | -- | 1.23 | 1.18 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-150 | -- | -- | 60.1$^{a1}$ | 51.2 | 52.0 | -- | -- | -- | 1.17 | 1.16 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-172 | -- | -- | 63.0$^{a1}$ | 58.8$^{a1}$ | 57.4$^{a1}$ | -- | -- | -- | 1.07 | 1.10 | Grosmougin et al. 2025 |
| *Microraptor* sp. | STM 5-221 | -- | -- | 61.9$^{a1}$ | 52.3$^{a1}$ | 51.7$^{a1}$ | -- | -- | -- | 1.18 | 1.20 | Grosmougin et al. 2025 |
| *Sinornithosaurus millenii* | DNHM D2140 | 84.4 | -- | 129.5 | -- | 105.3 | -- | 0.65 | -- | -- | 1.23 | Liu et al. 2004; Han et al. 2014 |
| *Sinornithosaurus millenii* | IVPP V12811 | 85.0 | 44.0 | 134.0 | 116.0 | 110.0 | 1.93 | 0.63 | 0.33 | 1.16 | 1.22 | Xu et al. 1999, 2000; Ji et al. 2001 |
| *Sinornithosaurus millenii* | NGMC 91 | -- | -- | 90.8 | 71.3 | 72.4 | -- | -- | -- | 1.27 | 1.25 | Ji et al. 2001 |
| *Wulong bohaiensis* | DNHM D2933 | 44.8 | 23.9$^{a1}$ | 76.0$^{a1}$ | 61.4 | 64.0$^{a1}$ | 1.87 | 0.59 | 0.31 | 1.24 | 1.19 | Poust et al. 2020 |
| *Zhongjianosaurus yangi* | IVPP V22775 | 33.0 | -- | 43.0 | 42.0 | 44.0 | -- | 0.77 | -- | 1.02 | 0.98 | Xu and Qin 2017 |

TABLE 2. Continued

| Taxon | Specimen | S | C | H | R | U | S/C | S/H | C/H | H/R | H/U | Source(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Probable Microraptorinae** | | | | | | | | | | | | |
| *Tianyuraptor ostromi* | STM-1 | -- | -- | -- | -- | -- | -- | 0.88 | -- | -- | -- | Zheng et al. 2009 |
| *Zhenyuanlong suni* | JPM-0008 | -- | -- | 121.1 | 96.6 | 102.9 | -- | -- | -- | 1.25 | 1.18 | Lü and Brusatte 2015 |
| **Possible Microraptorinae** | | | | | | | | | | | | |
| *Daurlong wangi* | IMMNH-PV00731 | 112.0 | -- | 120.0 | 90.0 | 96.0 | -- | 0.93 | -- | 1.33 | 1.25 | Wang et al. 2022 |
| **Halszkaraptorinae** | | | | | | | | | | | | |
| *Halszkaraptor escuilliei* | MPC-D 102/109 | -- | -- | -- | 39.0 | 39.3 | -- | -- | -- | -- | -- | Cau et al. 2017 |
| **Unenlagiinae** | | | | | | | | | | | | |
| *Austroraptor cabazai* | MML 220 | -- | -- | 232.0* | 161.0 | 188.0 | -- | -- | -- | 1.44* | 1.23* | Currie and Paulina Carabajal 2012 |
| *Buitreraptor gonzalezorum* | MPCA 245 | ~103.0 | 45.0 | 135.0 | 95.0 | 110.0 | 2.29 | 0.76 | 0.33 | 1.42 | 1.23 | Makovicky et al. 2005 |
| *Diuqin lechiguanae* | MUCPv 1401 | -- | -- | 200.0* | -- | -- | -- | -- | -- | -- | -- | Porfiri et al. 2024 |
| *Rahonavis ostromi* | UA 8656 | 82.2 | -- | -- | 126.5 | 132.3 | -- | -- | -- | -- | -- | Forster et al. 1998, 2020 |
| **Eudromaeosauria** | | | | | | | | | | | | |
| *Bambiraptor feinbergorum* | AMNH 001 | 85.0 | 22.0 | 102.5$^{a1}$ | 85.0 | 94.0$^{a1}$ | 3.86 | 0.83 | 0.21 | 1.21 | 1.09 | Burnham 2004 |
| *Dakotaraptor steini* | PBMNH.P.10.113.T | -- | -- | ~320.0 | ~320.0 | 360.0 | -- | -- | -- | 1.00 | 0.89 | DePalma et al. 2015 |
| *Deinonychus antirrhopus* | AMNH 3015 | ~190.0 | -- | ~237.0 | ~172.0 | 186.0 | -- | 0.80 | -- | 1.38 | 1.27 | Ostrom 1969, 1976 |
| *Deinonychus antirrhopus* | MCZ 4371 | -- | -- | 254.0 | 192.0 | 208.0 | -- | -- | -- | 1.32 | 1.22 | Ostrom 1976 |
| *Dineobellator notohesperus* | SMP VP-2430 | -- | -- | 185.8* | -- | 101.0* | -- | -- | -- | -- | 1.84* | Jasinski et al. 2020 |
| *Linheraptor exquisitus* | IVPP V16923 | ~160.0 | -- | ~155.0 | 110.0 | -- | -- | 1.03 | -- | 1.41 | -- | Xu et al. 2010 |
| *Shri rapax* | MPC-D 102/117 | 149.0 | 61.4 | 151.7 | 111.5 | 117.1 | 2.43 | 0.98 | 0.41 | 1.36 | 1.30 | Moutrille et al. 2025 |

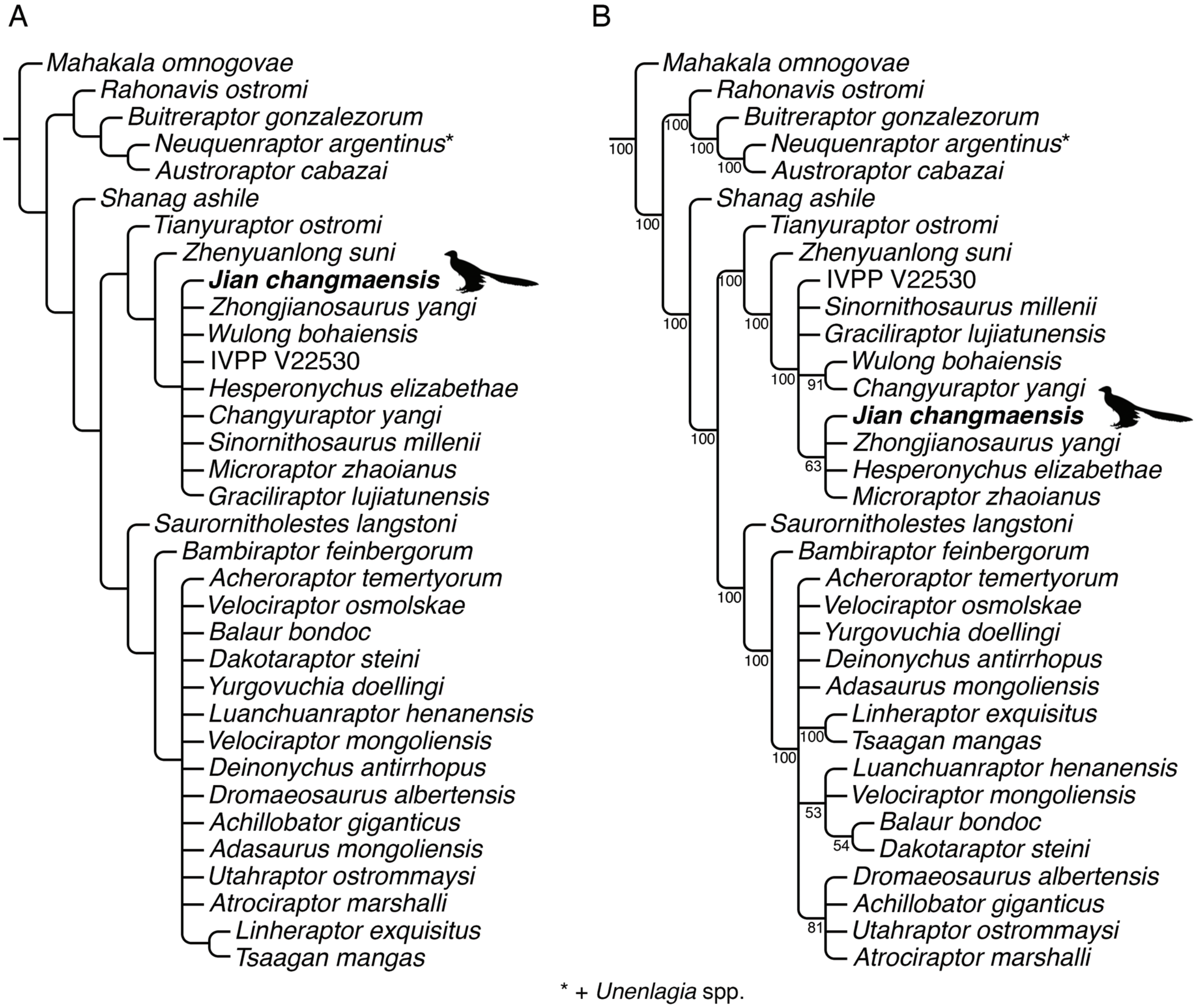

Fig. 6. Hypothesized phylogenetic position of *Jian changmaensis*, gen. et sp. nov. Topology of Dromaeosauridae as represented in the strict (**A**) and 50% majority-rule (**B**) consensuses of 810 most parsimonious trees (MPTs) of 3,452 steps recovered by parsimony analysis of 167 included theropod operational taxonomic units (OTUs) and 853 active morphological characters. Complete topologies are presented as Figs. S2A and S2B, respectively. Note, in both trees, the recovery of a monophyletic Microraptorinae that includes *Jian* and the systematically controversial dromaeosaurids *Tianyuraptor ostromi* and *Zhenyuanlong suni*. Microraptorine silhouettes adjacent to *Jian* by Emily Willoughby and courtesy of PhyloPic.org.

(Tree analysis using New Technology) version 1.5 (Willi Hennig Society Edition; Goloboff et al. 2008; Goloboff and Catalano 2016) with *Allosaurus fragilis* Marsh, 1877, designated as the outgroup. A traditional search (tree bisection-reconnection swapping algorithm, random seed ten, 1,000 replications, ten trees saved per replication) yielded 810 most parsimonious trees (MPTs) of 3,452 steps. The full strict and 50% majority-rule consensus topologies of these MPTs are shown in Figures S2A and S2B, respectively. The portion of each topology that constitutes Dromaeosauridae is reproduced herein as Figures 6A (strict consensus) and 6B (majority-rule consensus). Both the strict and 50% majority-rule consensus trees support a monophyletic Microraptorinae that includes all taxa listed above with the exceptions of *Shanag*, which is recovered as the outgroup to Microraptorinae + Eudromaeosauria (i.e., *Shanag* is hypothesized as the earliest branching member of Serraraptoria of Wang and Pei 2025), and *Yurgovuchia*, which is resolved within Eudromaeosauria. *Tianyuraptor* is postulated as the earliest diverging microraptorine, a relationship supported by five synapomorphies (character states 113:0, 234:2, 297:0, 420:0, and 833:0; see Supplementary Information), all of which are ambiguous in *Jian*. This is followed by the divergence of *Zhenyuan-*

*long*, which is positioned as the sister taxon of all more derived microraptorines, a clade containing *Changyuraptor*, *Graciliraptor*, *Hesperonychus*, *Jian*, *Microraptor*, *Sinornithosaurus*, *Wulong*, *Zhongjianosaurus*, and IVPP V22530. This clade is supported by eight synapomorphies (character states 20:1, 144:1, 161:1, 184:1, 199:1, 227:0, 438:1, and 742:0; see Supplementary Information), only one of which (438:1, radius width at midshaft less than half that of ulna) can be scored for (and is present in) *Jian*. In the strict consensus tree, all nine members of this derived microraptorine clade form an unresolved polytomy. In the 50% majority-rule tree, however, there is some structure within this clade: instead of a nine-part polytomy, this tree depicts a five-part polytomy consisting of *Graciliraptor*, *Sinornithosaurus*, IVPP V22530, a subclade consisting of *Changyuraptor* and *Wulong* (recovered in 91% of the MPTs), and a polytomous subclade comprised of *Hesperonychus*, *Jian*, *Microraptor*, and *Zhongjianosaurus* (recovered in 63% of the MPTs). Removing OTUs that are known from exceptionally fragmentary material (*Hesperonychus*, *Shanag*, and IVPP V22530) to generate a reduced consensus changes the strict consensus tree only by finding a relationship between *Changyuraptor* and *Wulong* (strict consensus of 620 trees of 3,444 steps; Fig. 7). The 50% majority-rule consensus of these reduced trees posits further topological structure within derived Microraptorinae: *Graciliraptor* forms one part of a three-part polytomy, with the other two parts consisting of (1) a polytomous clade containing *Jian*, *Microraptor*, and *Zhongjianosaurus* (recovered in 85% of the trees), and (2) a clade comprised by *Sinornithosaurus* + (*Changyuraptor* + *Wulong*) (recovered in 69% of the trees).

The phylogenetic results herein cast light on the probable affinities of several systematically controversial dromaeosaurids. First, two taxa that have occasionally been regarded as representatives of Microraptorinae, *Shanag* (see Longrich and Currie 2009) and *Yurgovuchia* (see Ding et al. 2020: fig. 6), are recovered elsewhere within Dromaeosauridae (as the sister taxon of Microraptorinae + Eudromaeosauria [i.e., the basalmost serraraptorian] and as a eudromaeosaurian, respectively). Conversely, other dromaeosaurids whose possible microraptorine affinities have been debated—namely *Tianyuraptor*, *Zhenyuanlong*, and IVPP V22530—are herein supported as members of the latter clade, as was previously concluded by Senter et al. (2012) for *Tianyuraptor*, by Gianechini et al. (2018) for *Tianyuraptor* and *Zhenyuanlong*, and by Pei et al. (2020) for all three forms (although *Tianyuraptor* and *Zhenyuanlong* are not supported as microraptorines in the more recent analyses of Wang et al. [2022] and Wang and Pei [2025], instead forming a clade that is closer to Eudromaeosauria than Microraptorinae with another Jehol Biota dromaeosaurid, *Daurlong wangi* Wang et al., 2022). Support for the placement of *Zhongjianosaurus* as a member of Microraptorinae (Xu and Qin 2017) has been also recently found by Wang and Pei (2025).

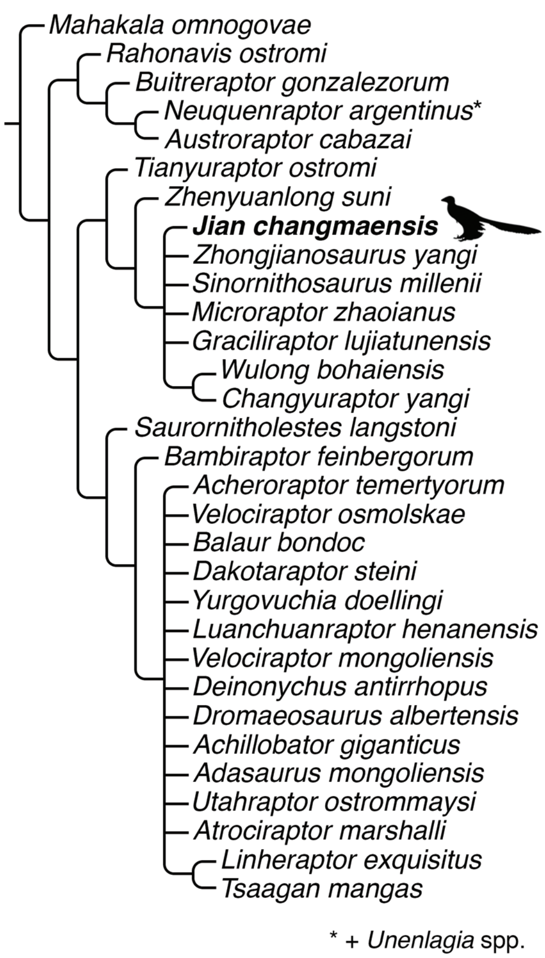

Fig. 7. Recovered topology of Dromaeosauridae in reduced strict consensus tree generated by removing operational taxonomic units that are known from exceptionally fragmentary material (*Hesperonychus elizabethae*, *Shanag ashile*, and IVPP V22530), which differs from the original strict consensus tree (Fig. 6A) only by finding a relationship between *Changyuraptor yangi* and *Wulong bohaiensis*.

Finally, at the request of one of this paper's reviewers, we added the recently described Mongolian Late Cretaceous dromaeosaurids *Kuru kulla* Napoli et al., 2021, and *Shri devi* Turner et al., 2021, to the phylogenetic data matrix (thus yielding 169 OTUs) and re-performed both analytical iterations (i.e., the full analysis plus the analysis excluding *Hesperonychus*, *Shanag*, and IVPP V22530) under the same parameters. As expected, *Kuru* and *Shri devi* were recovered within Eudromaeosauria. Moreover, the inclusion of these two taxa had no effect on the topology or taxonomic content of Microraptorinae as reported above and as depicted in Figures 6, 7, and S2, except for slightly altering support values for derived microraptorine nodes within the 50% majority-rule consensus trees generated by both the full analysis (91% vs. 87% for *Changyuraptor* + *Wulong*; 63% vs. 57% for *Hesperonychus* + *Jian* + *Mi-*

*croraptor* + *Zhongjianosaurus*) and the reduced analysis (85% vs. 87% for *Jian* + *Microraptor* + *Zhongjianosaurus*; 69% vs. 65% for *Sinornithosaurus* + (*Changyuraptor* + *Wulong*)). Note that the data matrix provided as Supplementary Information herein includes *Kuru* and *Shri devi*; as such, in order to replicate the results shown in Figures 6, 7, and S2, users must first deactivate these two OTUs prior to performing the analysis.

## DISCUSSION

The largely complete theropod pectoral girdle and forelimb GSGM-D050 constitutes the first skeletal remains of a non-avian dinosaur to be reported from the richly fossiliferous Changma Basin locality of the Lower Cretaceous (lower Aptian) Xiagou Formation of northwestern Gansu Province, China. The morphology of the specimen indicates a close relationship with the probably volant microraptorine dromaeosaurid *Microraptor zhaoianus* from the approximately coeval Jehol Group of northeastern China (Xu et al. 2003; Pei et al. 2020). Character states including a coracoid that is proportionally more elongate than those of other microraptorines, the development of the distal condyles on the cranial surface of the humerus, and a prominent foramen on the proximoventral face of the radius—plus other differences with established microraptorine genera and species—indicate that GSGM-D050 represents a new taxon, *Jian changmaensis*, gen. et sp. nov. The discovery of *Jian* increases the phylogenetic diversity of fossil vertebrates from the Changma locality, which is dominated by smaller-bodied ornithothoracine birds, in particular the ornithuromorph *Gansus yumenensis* (Hou and Liu 1984; You et al. 2006; Wang et al. 2016), and provides further evidence that the Xiagou Formation vertebrate fauna was in many ways similar to that of the Jehol Group. The preservation of GSGM-D050 resembles that seen in most specimens of *G. yumenensis* and other Changma birds, i.e., incomplete but articulated and preserved in three dimensions. Below, we discuss the implications of *Jian* for the paleobiogeography of Microraptorinae and the relationships of the Changma Basin theropod fauna to that of the Jehol Group.

### Microraptorine Paleobiogeography

The occurrence of *Jian* expands the paleobiogeographic distribution of indisputable members of Microraptorinae—following the definition of the clade presented by Turner et al. (2012:111)—to include the early Aptian of northwestern Gansu Province, China, and northwestern China more generally. All other unquestioned and probable Early Cretaceous members of the group have been recovered from Barremian–Aptian sediments of the Jehol Group of northeastern China (e.g., Xu et al. 1999, 2000, 2003; Xu and Wang 2004; Zheng et al. 2009; Han et al. 2014; Lü and Brusatte 2015; Xu and Qin 2017; Ding et al. 2020; Pittman et al. 2020; Poust et al. 2020; Wang and Pei 2025). Nevertheless, the results of our phylogenetic analysis shed light on the affinities of several putative microraptorines and support previous inferences that the Early Cretaceous distribution of the clade may have been even broader than that indicated by *Jian* and its Jehol Group counterparts (Pittman et al. 2015; Ding et al. 2020).

Namely, as in the phylogenetic analysis of Pei et al. (2020), specimen IVPP V22530, a fragmentary partial skeleton consisting of an incomplete left hind limb and a few additional elements that may pertain to the same individual, is herein recovered as a member of Microraptorinae. Hailing from the Aptian–Albian Bayan Gobi Formation of Inner Mongolia (China), approximately 500 km west of Jehol Group exposures (Pittman et al. 2015), IVPP V22530 helps to bridge the ~2,000 km geographic gap between *Jian* and Jehol Group microraptorines. Moreover, depending on the precise age of the Bayan Gobi Formation within the Early Cretaceous, IVPP V22530 might represent the stratigraphically youngest Asian microraptorine yet discovered.

The only other widely recognized microraptorine taxon from outside northeastern China is the diminutive *Hesperonychus elizabethae*, definitively known only from an articulated partial pelvis from the Upper Cretaceous (upper Campanian) Dinosaur Park Formation of Alberta, Canada (Longrich and Currie 2009). *Hesperonychus* can be assigned to Microraptorinae based on its possession of, among other character states, a strongly developed lateral tubercle on the distal pubis, which was more recently interpreted as an osteological correlate for the attachment of pubogastralial ligaments (Rhodes and Currie 2020). Due to the lengthy stratigraphic gap between microraptorines from the Early and the Late Cretaceous, further fossil discoveries are needed to clarify the evolutionary history of Microraptorinae from, at minimum, the Albian through middle Campanian, as well as to establish the potential distribution of this intriguing dromaeosaurid clade beyond eastern Asia and western North America.

### Xiagou and Jehol Theropod Faunas Compared

Because they are from the only Lower Cretaceous geologic units in China to have produced an abundance of associated fossil bird specimens, the avifaunas of the Xiagou Formation of Gansu Province and the Jehol Group of Liaoning and neighboring provinces have been frequently compared in the literature (e.g., You et al. 2006; Zhou et al. 2014). The discovery of *Jian*, a microraptorine dromaeosaurid closely related to Jehol microraptorines such as *Changyuraptor yangi*, *Graciliraptor lujiatunensis*, *Microraptor*, *Sinornithosaurus millenii*, *Wulong bohaiensis*, and *Zhongjianosaurus yangi*, adds another similarity between the theropod dinosaur assemblages of the two units.

The avifauna of the Xiagou Formation of the Changma Basin differs markedly from those of nearly all Jehol

Group localities in that only ornithothoracine birds have been recovered and fossils of crownward ornithuromorphs (primarily those of *G. yumenensis*) greatly outnumber those of other stem lineages (You et al. 2006). Indeed, in the collections of Changma bird fossils assembled to date, specimens of ornithuromorphs are approximately ten times as abundant as are those of enantiornithines, the only other birds recorded thus far (M.C.L., J.K.O., pers. obs.). Based on biostratigraphic arguments, the Xiagou avifauna was initially considered to be slightly younger than the most recent avian assemblages of the Jehol Group (Lamanna et al. 2006; You et al. 2006). This, in turn, led many of the present authors (M.C.L., D.-Q.L., H.-L.Y., J.K.O.) to speculate that the Xiagou Formation might capture the initial stages of the eventual rise to dominance of ornithuromorphs over enantiornithines and other stem birds, which ultimately culminated in the extinction of all non-neornithine birds at the Cretaceous–Paleogene boundary (e.g., You et al. 2006, 2010).

More recently, however, two important discoveries have necessitated a reevaluation of this hypothesis. First, chemostratigraphic evidence now suggests that the bird-bearing quarries in the Xiagou Formation of the Changma Basin were deposited during the early Aptian, approximately 124–120 Ma (Suarez et al. 2013). Consequently, the Xiagou avifauna appears to be at least roughly contemporaneous with those of the upper Yixian and Jiufotang formations of the Jehol Group, which are also widely regarded as early Aptian in age based primarily on radiometric dates (He et al. 2004; Chang et al. 2009, 2017). Most of these early Aptian Jehol bird localities are numerically and taxonomically dominated by enantiornithines, and also include earlier-diverging avian taxa such as *Jeholornis prima* Zhou and Zhang, 2002a, *Sapeornis chaoyangensis* Zhou and Zhang, 2002b, confuciusornithids, and jinguofortisids. Nevertheless, and secondly, one such, relatively recently-discovered locality—Sihedang, near the city of Lingyuan in western Liaoning Province, variously assigned to either the Yixian Formation or the Jiufotang Formation (see Yao et al. 2019)—appears to resemble Changma in that specimens of near-ornithurine Ornithuromorpha are far more abundant than are those of Enantiornithes and more stemward birds.

Comparison of the fossil vertebrate faunas of Changma and Sihedang as described to date reveals numerous similarities (see Tables S1 and S2 and references therein). Both are characterized by the presence of sinemydid turtles, microraptorine dromaeosaurids, enantiornithines, and, most strikingly, multiple ornithuromorph taxa, including the most derived, skeletally modern birds yet known from the Early Cretaceous. The Changma fauna includes at least one osteoglossomorph fish and an undescribed salamander, whereas that of Sihedang includes a choristodere, at least five pterosaurs, an ankylosaur, a therizinosaurian theropod, the early diverging pygostylian *Sapeornis*, a confuciusornithid, and a eutherian mammal, but these discrepancies could well be due to the fact that paleontological explorations of both localities are still in their early stages (e.g., the first bird from Sihedang was only published in 2014). For example, there are, at present, five named species of Enantiornithes from Changma (Table S1) but only three from Sihedang (Table S2); nevertheless, additional specimens pertaining to this clade have been recently discovered at the latter locality, suggesting that the observed enantiornithine diversity of Sihedang will increase substantially in the near future (Wang and Zhou 2019). The same effect may explain the present lack of pterosaurs from Changma, which were not recognized from the Jehol Group for many decades after the first fossils were described from that unit (Wang et al. 2005).

Why the fossil vertebrate faunas of Changma and Sihedang exhibit numerous similarities (e.g., the numerical and possibly taxonomic dominance of derived ornithuromorphs over other birds) but that the latter differs markedly from those of other Jehol Group localities is not well understood. Perhaps, as originally hypothesized for Changma (Lamanna et al. 2006; You et al. 2006), the two sites are indeed geologically more recent than the remaining Jehol vertebrate localities, and their faunal commonalities are therefore due primarily or even wholly to this younger age. Given the uncertain stratigraphic position of the Sihedang site—which, again, has been assigned to both the Yixian Formation (e.g., Zhou et al. 2014; Lü and Brusatte 2015; Wang and Zhou 2019) and the Jiufotang Formation (e.g., X.-L. Wang et al. 2012; Liu et al. 2014; Shao et al. 2018; X. Wang et al. 2018; Zhang et al. 2019) in previous works (see Yao et al. 2019)—plus recent arguments that the Xiagou Formation is actually late early Aptian to early Albian in age (Zheng et al. 2021; M. Suarez, C. Suarez, pers. comms. to M.C.L.), this remains a possibility. Nevertheless, the aforementioned early Aptian chemostratigraphic dates for this latter formation (Suarez et al. 2013) cast doubt on this hypothesis, as does the possibility that Sihedang may pertain to the Yixian Formation, which underlies the Jiufotang Formation and would therefore be older than the stem bird-dominated avifaunas of sites in the latter unit.

In our view, a more likely (though not mutually exclusive) alternative is that, as argued by some previous authors (e.g., Zhou et al. 2014; Hu and O'Connor 2017; O'Connor et al. 2022; O'Connor 2025), the Changma and Sihedang sites represent a specific paleoenvironment that is otherwise poorly represented in known Jehol Group localities; as such, the distinctive faunas of both sites would be due entirely or at least primarily to environmental and/or ecological rather than temporal differences. By extension, the Changma and Sihedang avifaunas would not signify the rise to dominance of ornithuromorphs over more archaic birds (contra, e.g., You et al. 2006, 2010) but instead would constitute avian assemblages that were adapted to this particular habitat. At present, however, only limited paleoenvironmental information exists for both localities, with the only significant exception being a paleoclimatic study of the Changma fossil quarries that used the results of clumped isotope analyses to argue for seasonally warm, arid conditions and a mean annual air temperature of 20.2°C during the time of deposition (Suarez et al. 2017). Consequently, coupled with continued paleontological explorations of both Changma and Sihedang, additional paleoenvironmental and stratigraphic analyses of these localities will be needed to enable a definitive test of this hypothesis, and, in turn, shed light on the evolutionary and ecological significance of their respective fossil assemblages. In the meantime, when viewed in light of the occurrence of other microraptorine dromaeosaurids (*Zhongjianosaurus* and probably *Zhenyuanlong*) at Sihedang, the new Changma microraptorine *Jian* provides further evidence of similarity between the theropod faunas of these extraordinary Cretaceous bird-bearing sites.

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## SUPPLEMENTARY INFORMATION

Supplementary Information accompanies this paper at https://www.morphobank.org/permalink/?P6280. It consists of the phylogenetic data matrix in TNT (Tree analysis using New Technology; Goloboff et al. 2008; Goloboff and Catalano 2016) format, plus a PDF file that contains the following sections:

Supplementary Data on Phylogenetic Analysis;
Supplementary Figures (i.e., Figures S1 and S2);
Supplementary Tables (i.e., Tables S1 and S2); and
Literature Cited in Supplementary Information.