



PISCIVORY IN THE FEATHERED DINOSAUR *MICRORAPTOR*

Lida Xing,^{1,2,3} W. Scott Persons IV,^{3,4} Phil R. Bell,⁵ Xing Xu,² Jianping Zhang,¹ Tetsuto Miyashita,² Fengping Wang,⁶ and Philip J. Currie³

¹School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

²Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, Beijing 100044, China

³Department of Biological Sciences, University of Alberta, 11455 Saskatchewan Drive, Edmonton, Alberta T6G 2E9, Canada

⁴E-mail: persons@ualberta.ca

⁵Pipestone Creek Dinosaur Initiative, Clairmont, Alberta T0H 0W0, Canada

⁶Qijiang District Bureau of Land and Resources, Chongqing 401420, China

Received December 4, 2012

Accepted March 20, 2013

The largest specimen of the four-winged dromaeosaurid dinosaur *Microraptor gui* includes preserved gut contents. Previous reports of gut contents and considerations of functional morphology have indicated that *Microraptor* hunted in an arboreal environment. The new specimen demonstrates that this was not strictly the case, and offers unique insights into the ecology of nonavian dinosaurs early in the evolution of flight. The preserved gut contents are composed of teleost fish remains. Several morphological adaptations of *Microraptor* are identified as consistent with a partially piscivorous diet, including dentition with reduced serrations and forward projecting teeth on the anterior of the dentary. The feeding habits of *Microraptor* can now be understood better than that of any other carnivorous nonavian dinosaur, and *Microraptor* appears to have been an opportunistic and generalist feeder, able to exploit the most common prey in both the arboreal and aquatic microhabitats of the Early Cretaceous Jehol ecosystem.

KEY WORDS: Avian evolution, dinosaurs, fossil gut contents, paleontology, paleoecology, piscivory.

Because of its phylogenetic and temporal positions (a basal dromaeosaurid from the Early Cretaceous), the functionally disputed elongate and asymmetric feathers on the hind limbs, and the exquisite details preserved in many specimens, *Microraptor* (Theropoda: Maniraptora; Xu et al. 2000) has become a focal point in the current inquiry into the origin of birds and the evolution of early avian flight. As such, many aspects of the paleobiology of *Microraptor* have been widely speculated on and are the subjects of scientific controversy (see, e.g., the ongoing disputes over the flight/gliding potential of the fore and hind limbs [Padian and Dial 2005; Xu et al. 2005; Zhou and Zhang 2005; Chatterjee and Templin 2007; Alexander et al. 2010; Brougham and Brusatte 2010] and over the climbing specialization of the manual and pedal claws [Senter 2006; Dececchi and Larrson 2011; Gong et al.

2012]). Recently, O'Connor et al. (2011) reported on a specimen of *Microraptor gui* with bones from an enantiornithine bird preserved within the abdominal cavity. These gut contents have been interpreted as evidence that *M. gui* hunted in an arboreal context and, by extrapolation, have been taken as behavioral support for the arboreal-origin (trees-down) theory of avian flight (O'Connor et al. 2011; Gong et al. 2012). Here, we report the discovery of QM (Qijiang Dinosaur National Geological Park Museum) V1002, a new and exceptionally well-preserved specimen of *M. gui* that also includes gut contents within the abdominal cavity. However, the gut contents of QM V1002 are composed entirely of bones from teleost fish, providing the first definitive evidence of piscivory in a maniraptoran and showing that the feeding habits of *M. gui* were more diverse than previously assumed.

Description

QM V1002 comes from the Jehol Group (Jiufotang Formation) of northeastern China. The skeleton is nearly complete and fully articulated (Fig. 1), with the left metatarsals displaced cranially and only the phalanges of the left hind foot, a portion of the right ankle, and the terminal caudal vertebrae missing. The hind limbs are preserved in a prone position with the femora extending laterally from the hips—a posture typical of other articulated *Microraptor* skeletons (Gong et al. 2012). Although some authors regard the *Microraptor* species *M. gui* and *Microraptor zhaoianus* to be synonymous (Turner et al. 2012), QM V1002 is here referred to the species *M. gui* and is distinguishable from *M. zhaoianus* based on the presence of a biceps tubercle near the proximal end of the radius (visible on the left radius, but, because of how the specimen lays, not the right), a strongly curved pubis, metacarpal I and manual phalanx I-1 together much shorter in proximodistal length than metacarpal II, and manual ungual II subequal to manual ungual I in size (manual ungual I of *M. gui* is nearly half the relative size of manual ungual I in *M. zhaoianus*; Xu et al. 2003). QM V1002 represents the largest specimen of *M. gui* yet known (femur length = 109 mm; axial length = 800 mm).

The centra and neural arches of all vertebrae appear to be fused, giving no indication that QM V1002 represents an immature animal. However, the right pubis and ischium have separated from each other and from the ilium, suggesting that the bones of the hip may not have been fully fused. The sternal plates and furcula are articulated and are visible in dorsal view. The sternum is well ossified, although the central suture is discernible. The posterior edge of the sternum has an arrowhead shape. On the left side, five uncinata processes are present in life position and, together, form a single osteological line crossing the anterior-most five ribs.

The skull, visible in right lateral view, is virtually complete but badly crushed, making it difficult to discern the outlines of individual elements. Nevertheless it shows several details of the cranial anatomy not seen in any previously described *Microraptor* specimen. The triangular premaxilla has four teeth. The dorsal (nasal) process of the premaxilla is posteriorly “kinked” at its midpoint giving the muzzle a distinctly squared-off profile (Fig. S1). Only the alveolar margin of the maxilla is preserved, which has nine alveoli, four less than in *Microraptor hanqingi* (Gong et al. 2012). The lateral (orbital) margin of the frontal forms a distinct lip along its entire length. The left frontal is 32-mm long and widest posteriorly. Anteriorly, the frontal expands laterally where it forms a scarf contact with the nasal. The right quadrate is preserved out of position below the mandible. The pterygoid process of the quadrate extends the entire height of the quadrate, unlike *Bambiraptor* in which there is a distinct “neck” between the ventral condyles and the ventral edge of the pterygoid process (Burnham 2004). The lateral condyle and the smaller



Figure 1. Articulated skeleton of *Microraptor gui* (QM V1002). The abdominal mass is highlighted in blue. F, furcula; Int, feathered integument; Mt, metatarsus; Pu, pubis; Q, quadrate; Sk, skull; St, sternum; T, tibia. Scale bar = 10 cm.

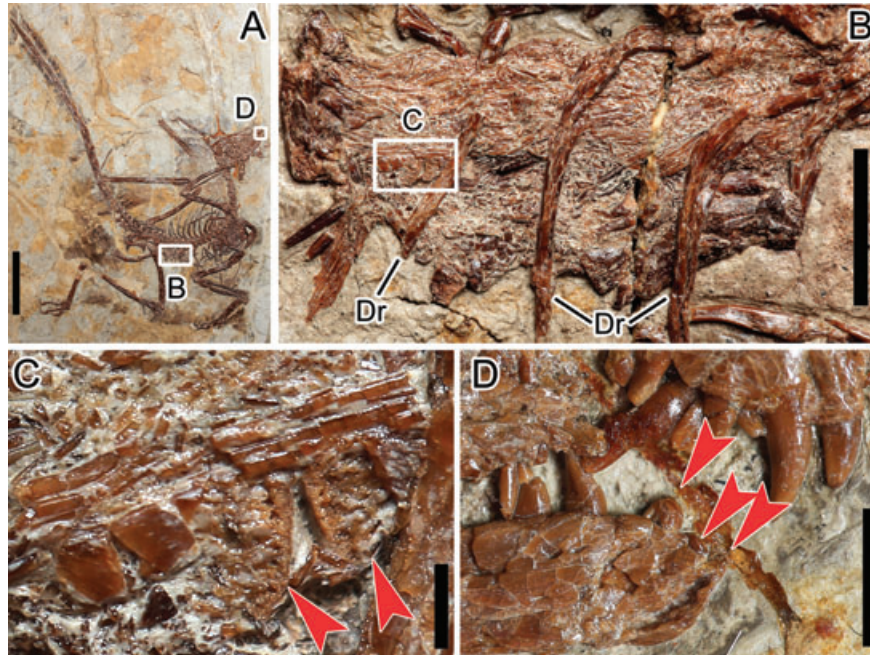


Figure 2. Details of *Microraptor gui* QM V1002. Overview of specimen, scale bar = 10 cm (A). Disarticulated mass of osseous elements within the abdominal cavity. Note the aligned orientation of the fin rays within the mass. Dr, dorsal rib. Scale bar = 1 cm (B). Magnified view of gut contents showing the aligned elongated elements, arrows point to the two fish vertebrae, scale bar = 500 μm (C). Anterior margin of the jaws, arrows point to the first three dentary tooth positions, each with a strong anterior orientation, scale bar = 5 mm (D).

medial condyle are separated from each other by a shallow sulcus. The quadratojugal notch forms an embayment on the ventral half of the quadrate. The dentary is 48-mm long and ventrally bowed as in *M. hanqingi* and *M. zhaoianus* (Gong et al. 2012) and has at least 15 alveoli. The anterior three teeth, although broken, are angled anterodorsally.

As in other *Microraptor* specimens (Xu et al. 2003; Xu and Zhang 2005; O'Connor et al. 2011; Gong et al. 2012; Li et al. 2012), QM V1002 preserves traces of long contour feathers with the rachises originating from the forelimbs, hind limbs, and—in a frond-like arrangement—the posterior portion of the tail. Also preserved are the keratinous sheathes of the manual and pedal unguis. Just anterior to the pelvis and medial to three of the right dorsal ribs, such that it unambiguously lies within the abdominal cavity, is a dense elliptical mass of disarticulated osseous elements (Fig. 2). This mass is interpreted as preserved gut contents and is primarily composed of long (up to 6.7 mm) and thin (0.1–0.3 mm in diameter) fin rays, ribs, and neural/hemal spines of fish. These elongate elements have a shared orientation parallel to the *Microraptor* body axis. Using the partially preserved internal anatomy of the small compsognathid *Scipionyx* (Dal Sasso and Maganuco 2011) as a guide, the position of the mass suggests it was located in the posterior portion of the digestive tract, most probably within or near the jejunum, and the alignment of the elongated elements likely reflects their prior passage through the anterior portion of the tract. Similar evidence of ingested

bones transiting through the intestinal track has been reported in other theropod specimens (Dal Sasso and Maganuco 2011; Xing et al. 2012) and in theropod coprolites (Chin et al. 1998, 2003). However, ingested bone does not travel through the intestines of extant crocodylians (Dal Sasso and Maganuco 2011).

Also visible in the gut content mass are a pair of fish vertebral centra (Fig. 2) and several thin bones with rugose surface textures and evidence of gastric etching, which are tentatively identified as probable fish cranial elements. The absence of ossified scales among the gut contents and the presence of transverse sulci on the lateral surfaces of the centra suggest that the fish bones are those of a teleost. Primitive teleost fossils are abundant throughout the Jehol Group (Lu 1994; Zhou et al. 2003) and have been previously reported within the gut contents of the Jehol bird *Confuciusornis* (Dalsätt et al. 2006) and *Yanornis* (Zhou et al. 2002, 2004).

Discussion

A third species of *Microraptor*, *M. hanqingi*, has recently been proposed (Gong et al. 2012) and was distinguished from *M. gui* based on its larger size, having unfused sternals, and various subtle differences in the pelvis (a robust and less curved pubis with squared distal end, a posteriorly tapering pubic boot, and ischia with a straight posterior edge and a concave ventral edge). *M. hanqingi* was also diagnosed as having fewer caudal vertebrae (Gong et al. 2012); however, a complete caudal series is unknown

for any *M. gui* or *M. hanqingi* specimen, and the validity of this character is, therefore, dubious. QM V1002 is shorter in estimated total body length than the only referred specimen of *M. hanqingi*, but equals *M. hanqingi* in femoral proportions. As such, QM V1002 demonstrates that “larger” size is nondiagnostic of *M. hanqingi*, but simultaneously rules out allometry as an explanation for the differences observed in the pelvis of *M. hanqingi* (although sexual dimorphism and individual variation remain conceivable explanations).

Previous reports of *Microraptor* gut contents include the remains of a small, possibly scansorial, mammal (Larrson et al. 2010) and an enantiornithine bird (O’Connor et al. 2011). In the latter report, O’Connor et al. (2011) interpreted this evidence of presumed predation on flight-capable prey as proof that *M. gui* was an adept hunter in an arboreal environment. The gut contents of QM V1002 now provide equal evidence that *M. gui* was an adept hunter of aquatic prey.

As is always the case with dietary inferences based on preserved gut contents, scavenging (as opposed to active predation) cannot be ruled out—although, in the case of QM V1002, the relatively short spoilage time of fish carrion provides circumstantial evidence against a scavenging interpretation—and caution is always warranted in the extrapolation of behavioral and microhabitat specializations from single instances of gut content preservation. The bird remains described by O’Connor et al. (2011) are indisputably consistent with arboreal feeding habits, but bird remains have since also been documented in the abdominal cavity of another Jehol theropod: the giant compsognathid *Sinocalliopteryx gigas* (Xing et al. 2012). A terrestrial predator, *S. gigas* was over 2.5 m in length, and it demonstrates that an arboreal lifestyle was not a necessity for successfully feeding on Jehol avialians (Xing et al. 2012).

In light of QM V1002, it is apt to examine the morphology of *M. gui* for evidence of piscivorous specializations. As a genus, *Microraptor* is characterized as lacking anterior tooth serrations (Xu et al. 2000). Functionally, the loss of serrations may aide a tooth in spearing, rather than slicing, and serration loss is common among extinct and extant piscivores, including many spinosaurids (Holtz 1998; a group of theropod dinosaurs, which have also been shown through preserved gut contents to be partially piscivorous; Charig and Milner 1986, 1997) and unenlagiines (a group of long-snouted Gondwana dromaeosaurids, for which piscivory has been previously proposed based on morphologic and paleohabitat evidence (Gianechini et al. 2009). The first three teeth in the dentary of QM V1002 are angled anterodorsally and are procumbent (Fig. 2). Although these teeth are broken and the tips are absent, it is clear that, when complete, the anterior-most two would have extended well beyond the anterior margin of the lower jaw. This trait has not been previously recognized in *Microraptor*, but it is also observable in the *Microraptor* specimens IVPP V

12330 and IVPP V 13320. A forward-projecting anterior tooth arrangement is common to piscivorous animals, including many crocodylians, fish, pterosaurs, and some spinosaurs. Whether the hind limbs and talons of *Microraptor* could have been used in fishing is unclear. *Microraptor* lacks an enlarged hallux, which may have made clutching prey with the foot impractical. However, debate remains over the grasping capabilities of the hallux and the possibly opposable digit II (Senter 2006; Gong et al. 2012).

The Jehol Group is interpreted as a forested, freshwater-lake environment (Zhou et al. 2003). Small-bodied fish easily rank as the most abundant vertebrate fossils from the Jehol Group and *Microraptor* is the most common of the nonavian theropods (Zhou et al. 2003). From an ecological perspective, it is not surprising that *Microraptor* was able to exploit the most common potential prey item in its environment.

Taken together, the direct dietary evidence supplied by the exceptional Jehol specimens makes the feeding habits of *Microraptor* the best sampled of any nonavian dinosaur. We join O’Connor et al. (2011) in concluding that *Microraptor* was probably an opportunistic and effective generalist, capable of hunting a variety of prey, and add that *Microraptor* also appears to have been capable of successfully hunting in a variety of microhabitats, and its hunts were evidently not restricted to the trees. Such a diversity of prey and predatory habits is not unusual. Among modern animals, many small felids, mustelids, procyonids, and varanid lizards all commonly feed on fish, scansorial mammals, and birds. Although some of these modern analogs are more aquatically and arboreally adapted than others, they show that a predator/prey relationship does not necessitate similar locomotive habits. Because *Microraptor* is among the oldest and most basal of the known dromaeosaurids (Xu et al. 2000), these conclusions suggest ancestral dromaeosaurids were varied in feeding ecology and hunting style, a generalization that may have contributed to the success and wide geographic distribution achieved by the group in the Late Cretaceous.

ACKNOWLEDGMENTS

The first author wishes to recognize the second author’s equal contribution to this work. The authors thank Y. Zhang for preparing the specimen, L. Fang for assisting with photography, and J. Zhang (IVPP) for his critical comments and suggestions. The authors also thank T. Lenormand for his services as editor and C. Dal Sasso and an anonymous reviewer for their helpful and constructive feedback. This research was supported by the Qijiang District Bureau of Land and Resources and by the National Natural Science Foundation of China (No. 41120124002).

LITERATURE CITED

Alexander, D. E., E. P. Gong, L. D. Martin, D. A. Burnham, and A. R. Falk. 2010. Model tests of gliding with different hindwing configurations in the fourwinged dromaeosaurids *Microraptor gui*. *Proc. Natl. Acad. Sci. USA* 107:2972–2976.

- Brougham, J., and S. L. Brusatte. 2010. Distorted *Microraptor* specimen is not ideal for understanding the origin of avian flight. PNAS 107:E155.
- Burnham, D. A. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the late cretaceous of montana. Pp. 67–111 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright, eds. Feathered dragons, Indiana Univ. Press, Bloomington, IN.
- Charig, A. J., and A. C. Milner. 1986. Baryonyx: a remarkable new theropod dinosaur. Nature 324:359–361.
- . 1997. Baryonyx walkeri: a fish eating dinosaur from the wealden of surrey. Bull. Natural History Museum, Lond. 53:11–70.
- Chatterjee, S., and R. J. Templin. 2007. Biplane wing platform and flight performance of the feathered dinosaur *Microraptor gui*. Proc. Natl. Acad. Sci. USA 104:1576–1580.
- Chin, K., T. T. Tokaryk, G. M. Erickson, and L. C. Calk. 1998. A king-sized theropod coprolite. Nature 393: 680–682.
- Chin, K., D. A. Eberth, M. H. Schweitzer, T. A. Rando, W. J. Sloboda, and J. R. Horner. 2003. Remarkable preservation of undigested muscle-tissue within a late Cretaceous tyrannosaurid coprolite from Alberta, Canada. Palaios 18:286–294.
- Dalsätt, J., Z. Zhou, F. Zhang, and P. G. P. Ericson. 2006. Food remains in *Confuciusornis sanctus* suggest a fish diet. Naturwissenschaften 93: 444–446.
- Dal Sasso, C., and S. Maganuco. 2011. *Scipionyx samniticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy—osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. Mem. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano. XXXVII:1–281.
- Dececchi, T. A., and H. C. E. Larrson. 2011. Assessing arboreal adaptations of bird antecedents: testing the ecological setting of the origin of the avian flight stroke. PLoS One 6:e22292.
- Gianechini, F. A., P. J. Makovicky, and S. Apesteguía. 2009. The teeth of the unenlagiine theropod *Buitreraptor* from the Cretaceous of Patagonia, Argentina, and the unusual dentition of the Gondwanan dromaeosaurids. Acta Palaeontol. Polonica 56:279–290.
- Gong, E. P., L. D. Martin, D. A. Burnham, A. R. Falk, and L. H. Hou. 2012. A new species of *Microraptor* from the Jehol Biota of northeastern China. Palaeoworld 21:81–91.
- Holtz, T. R. Jr. 1998. Spinosaurus as crocodile mimics. Nature 282:1276–1277.
- Larrson, H. C. E., D. W. Hone, T. A. Dececchi, C. Sullivan, and X. Xu. 2010. The winged non-avian dinosaur *Microraptor* fed on mammals: implications for the Jehol Biota ecosystem. J. Vert. Paleont. 30:114A.
- Li, Q., K. Q. Gao, Q. Meng, J. A. Clark, M. D. Shawkey, L. D'Alda, R. Pei, M. Ellison, M. A. Norell, and J. Vinther. 2012. Reconstruction of *microraptor* and the evolution of iridescent plumage. Science 335:1215–1219.
- Lu, L. 1994. A late jurassic acipenseriform from lingyuan, liaoning. Vert. PalAs. 32:134–142.
- O'Connor, J., Z. Zhou, and X. Xu. 2011. Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds. PNAS 108:19662–19665.
- Padian, K., and K. P. Dial. 2005. Could 'four-winged' dinosaurs fly? Nature 438:E3.
- Senter, P. 2006. Comparison of forelimb function between *Deinonychus* and *Bambiraptor* (Theropoda: Dromaeosauridae). J. Vert. Paleont. 26:897–906.
- Turner, A. H., P. J. Makovicky, and M. A. Norell. 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bull. Am. Museum Natural History 371:1–206.
- Xing, L., P. R. Bell, W. S. Persons, IV, S. Ji, T. Miyashita, Q. Ji, and P. J. Currie. 2012. Abdominal contents from two large compsognathids demonstrate feeding on dromaeosaurids and confuciusornithids. PLoS ONE 7:e44012.
- Xu, X., and F. Zhang. 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. Naturwissenschaften 92:173–177.
- Xu, X., Z. Zhou, and X. Wang. 2000. The smallest known non-avian theropod dinosaur. Nature 408:705–708.
- Xu, X., Z. H. Zhou, X. W. Kuang, X. L. Wang, F. C. Zhang, and X. K. Du. 2003. Four-winged dinosaurs from China. Nature 421:335–340.
- Xu, X., Z. Zhou, X. Wang, X. Kuang, F. Zhang, and X. Du. 2005. Xu et al. reply. Nature 438:E3–E4.
- Zhou, Z., and F. Zhang. 2005. Zhang & Zhou reply. Nature 438:E4.
- Zhou, Z., J. A. Clark, and F. Zhang. 2002. *Archaeoraptor's* better half. Nature 420:285.
- Zhou, Z., P. M. Barrett, and J. Hilton. 2003. An exceptionally preserved Lower Cretaceous ecosystem. Nature 421:807–814.
- Zhou, Z., J. Clarke, F. Zhang, and O. Wings. 2004. Gastroliths in *Yanornis*: an indication of the earliest radical diet-switching and gizzard plasticity in the lineage leading to living birds? Naturwissenschaften 91: 571–574.

Associate Editor: C. Farmer

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Articulated skull of *Microraptor gui* (QM V1002).