Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds

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Preserved indicators of diet are extremely rare in the fossil record; even more so is unequivocal direct evidence for predator–prey relationships. Here, we report on a unique specimen of the small nonavian theropod *Microraptor gui* from the Early Cretaceous Jehol biota, China, which has the remains of an adult enantiornithine bird preserved in its abdomen, most likely not scavenged, but captured and consumed by the dinosaur. We provide direct evidence for the dietary preferences of *Microraptor* and a nonavian dinosaur feeding on a bird. Further, because Jehol enantiornithines were distinctly arboreal, in contrast to their cursorial ornithurine counterparts, this fossil suggests that *Microraptor* hunted in trees thereby supporting inferences that this taxon was also an arborealist, and provides further support for the arboreality of basal dromaeosaurids.

flight | paleoecology

Since its discovery, *Microraptor gui*, a four-winged dromaeosaurid (Theropoda: Maniraptora) from the Early Cretaceous Jiufotang Formation in northeastern China (1), has been the subject of intense research, speculation, and debate. However, because research on this small dinosaur has primarily focused on its unusual flight surfaces and their likely capabilities (2–4), little is known about other aspects of *Microraptor's* biology. Here, we report on the discovery of a dinosaur (*Microraptor gui*) with a bird preserved in its abdomen, and discuss the implications of this direct predator–prey association.

Such direct fossil examples of trophic relationships are extremely rare in the fossil record. Stomach contents—although considerably rarer than indirect inferences from bite marks (5–7), coprolites (8, 9), and other trace indicators—are the only certain ways to infer fossil diets (10, 11): in this case, little doubt can remain about the identity of the predator (*Microraptor*) and its prey (enantiornithine bird).

Description

The specimen, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V17972, can be referred to the small dromaeosaurid *Microraptor gui* based on its large size (relative to *Microraptor zhaoianus*), the proportions of its manual digits, curvature of the pubis, and slight bowing of the tibia (1). Using the length of the tibia as a proxy for size, the specimen IVPP V17972 is 10% larger than the holotype of *M. gui* (Table S1). Although largely complete and fully articulated in lateral view, IVPP V17972 is nevertheless poorly preserved, split between two slabs (A and B), with few clear morphological details (Fig. 1 and Fig. S1). Integument is preserved only along the dorsal and ventral margins of the skull (absent along the rostrum) and neck, and along the dorsal body margin. A cluster of partially articulated enantiornithine bird bones are also preserved primarily on slab A, within the abdomen of the specimen, neatly delimitated by an articulated rib cage (Fig. 2). These bird bones are exposed laterally on slab A (overlying the left thoracic ribs) and are overlapped by the right thoracic ribs in slab B, which shows that they are within the dinosaur and do not overly it.

The vertebral column of this specimen is complete except for its proximal and distal ends; pleurocoels are absent from the thoracic vertebrae, as in dromaeosaurids and basal birds. Poor preservation prevents clear observation of sutures; however, there does not appear to be any separation between the neural arches and vertebral centra, or any other indicators that the specimen is a juvenile. The number of caudal vertebrae cannot be estimated, but the elongate distal caudals are tightly bounded by elongated zygapophyses, as in other dromaeosaurids. The rib cage is nearly completely preserved; both right and left sides are visible ventrally closed by the articulated gastral basket. Five pairs of uncinate processes are present on slab B; these are long and unfused, each crossing two ribs. The cranioventral view of the furcula exaggerates the interclavicular angle; the scapulocoracoids are poorly preserved and the sternum is absent. The reduced first phalanx of the minor digit (characteristic of *Microraptor*) is not visible on either slab; however, the relative proportions of the major and minor metacarpals and digits themselves are nevertheless diagnostic. The ischium is short and distally expanded; the pubis is strongly concave dorsocaudally. The tibia is long and slightly bowed; proximally it bears a small, cranioproximally projecting cnemial crest. The third metatarsal is the longest, followed by metatarsals IV and II. All of the pedal unguals are large and recurved, with elongate horny sheaths.

Inside the rib cage of the theropod, bird remains consist of an articulated left humerus and antebrachium and both feet (Fig. 2). We have observed no tooth marks on these bones. These remains can be referred to Enantiornithes because of a proximally fused tarsometatarsus with reduced metatarsal IV, an enlarged trochlea on metatarsal II, and large, recurved pedal claws (12). The absence of an intercotylar eminence and intermetatarsal fusion of the tarsometatarsus, and the relatively wide radial shaft, also suggest enantiornithine affinity. The surface of the bone is well preserved on parts of the humerus and antebrachium; the periosteal surface is smooth, indicating it was fully ossified (13), and also suggesting that digestion had not progressed far. Enantiornithine ontogeny is protracted compared with modern birds (14), and compound bones fuse very late (15). Although the specimen is small, the fused proximal end of the tarsometatarsus suggests the animal was an adult, or very near so, at time of death.

The only element that preserves any diagnostic morphology is the tarsometatarsus. Both feet are preserved in the proximal region of the abdomen; the left tarsometatarsus is better preserved and nearly fully articulated, although represented primarily as an impression. The proximal end is preserved as bone; the distal tarsals cannot be differentiated, suggesting they are fused to the metatarsals, although no intermetatarsal fusion is present. Metatarsal III is the longest, followed by IV and then II,

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Fig. 1. Photograph (*A*) and line drawing (*B*) of IVPP V17972A. Anatomical abbreviations: ald, alular digit; cav, caudal vertebrae; cev, cervical vertebrae; den, dentary; fe, femur; fur, furcula; hum, humerus; hy, hyoid bones; ili, ilium; int, integument; isc, ischium; mad, major digit; mid, minor digit; mt, metatarsals; pb, pubis; rad, radius; tb, tibia; thv, thoracic vertebrae; ul, ulna.

which are subequal. Metatarsal IV is the thinnest, as in other enantiornithines, and all three metatarsals are located in the same plane along their entire lengths, lacking the plantar displacement of metatarsal III that characterizes the more advanced ornithurine birds. The trochlea of metatarsal II is the widest; the trochlea of metatarsal IV is reduced. The pedal phalanges are all elongate and delicate; digit II is more robust than the other digits. The claws are all large and recurved (as opposed to the short, uncurved claws present in the cursorial ornithurine birds) with deep lateral grooves. Although the individual is too incomplete to assign to a specific taxon, we tentatively assign the specimen to Cathayornithiformes, the most prevalent enantiornithine group in the Jehol, based on size and the relative trochleal position of the tarsometatarsus (16).

Discussion

The Jehol biota is well known for its exceptional preservation of complete skeletons, some preserving feathers, hair, wing membranes, skin, and even microscopic feather melanosomes (17, 18). A few exceptional specimens have already begun to reveal predator–prey relationships within the biota: the first feathered dinosaur *Sinosauropteryx* often preserves the remains of mammals and lizards in the stomach cavity (10), a specimen of the mammal *Repenomamus* preserves the remains of a baby *Psittacosaurus* dinosaur (19), the basal ornithurine bird *Yanornis* preserves fish remains in the stomach of one specimen (20), and a specimen of the giant compsognathid *Sinocalliopteryx* was reported to have an incomplete dromaeosaurid leg preserved inside its abdominal cavity (21). This report of a dinosaur feeding on birds is unique.

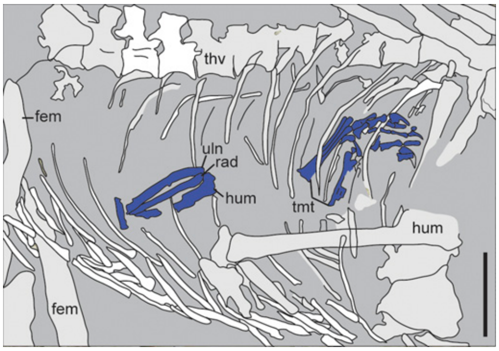

Fig. 2. Detail line drawing of stomach contents preserved in IVPP V17972A. Anatomical abbreviation not listed in Fig. 1: tmt, tarsometatarsus. (Scale bar, 10 mm.)

Dietary inferences regarding extinct taxa help us understand ancient food webs, species interactions, and the evolution of predator–prey relationships. Diet can also reveal the habitat preferences and behaviors of an animal. Although most nonavian theropods are commonly inferred to be carnivorous (but see some recent studies on the diet of coelurosaurian theropods suggesting herbivory is the ancestral condition for coelurosaurs) (22), direct evidence is limited and reconstructions are typically based on tooth and other morphologies (e.g., the raptorial second pedal digit in dromaeosaurids) and comparable faunal elements (i.e., likely prey items based on size) (22–25). Healed bite marks (25), tooth marks (7), associated teeth (24), and coprolites (8) lend further evidence; however, these methods leave uncertainties regarding the taxonomic identity of involved species. With the exception of direct preservation of predator and prey interaction, identifiable digestive remains are the most unequivocal way to infer diet, allowing both the predator and prey to be precisely recognized with no question of their relationship.

Microraptor specimen IVPP V17972 preserves a largely undigested partial skeleton of an enantiornithine bird in its stomach cavity; this indicates that the diet of *Microraptor* included enantiornithine birds. However, we do not suggest that *Microraptor*'s diet was limited to, or even dominated by, these birds; like most predators, *Microraptor* was likely opportunistic, feeding on similarly sized animals from a variety of clades represented in the Jehol biota. This hypothesis is supported by the report of a small mammal bone associated with the holotype of *M. gui*, interpreted as stomach contents (26). What is preserved of the ingested enantiornithine skeleton is still in articulation with the feet located in the proximal end of the stomach, suggesting that the meal was not scavenged, but captured and swallowed nearly whole and proximal end first, as in most living predatory birds. Extant predatory birds take prey in a wide range of sizes, from small insects to animals larger than themselves (27, 28). The mass of *Microraptor* is estimated to be 1500 g (29); the enantiornithine, roughly estimated to be 60–70 g (30), would easily have been consumed by the much larger dromaeosaurid.

Unlike other birds known from the Jehol, all known enantiornithines possess pedal morphologies suggesting they were adapted for arboreal environments rather than for foraging on the ground or in aquatic environments (31, 32). This understanding is supported by pedal proportions, which have been shown in modern birds to be indicative of ecology (33 34), as well as in the morphology of the foot, which is better adapted for perching than walking, with large recurved claws and a hallux that is positioned low on the tarsometatarsus. Although digit III cannot be measured in this specimen (nor can digit IV completely), the penultimate phalanx in digits II and IV are longer than the proximal phalanges, consistent with arboreal habitats (32, 33). The Spanish enantiornithine *Eoalulavis* was preserved with aquatic crustaceans, which were identified as digestive remains (35); however, there is neither strong evidence to support that the remains are in fact inside the specimen, nor any morphological information to support any ecological inferences based on this association. The predation of an arboreal enantiornithine suggests *Microraptor* hunted in an arboreal environment (Fig. 3). The fact the enantiornithine was an adult also suggests that *Microraptor* was capable of active hunting and was a fairly agile predator.

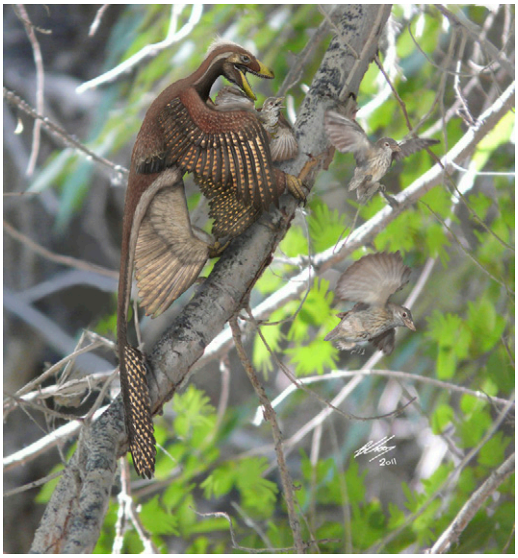

Fig. 3. Reconstruction of the life habits of *M. gui*.

Although given their small size and large numbers, it is assumed that enantiornithines formed at least part of the diet for an array of different carnivorous and potentially omnivorous taxa, this specimen provides direct evidence that enantiornithines were prey in the Jehol biota. Elsewhere, one specimen of an ichthyosaur, a marine reptile whose diet typically consists of cephalopods, from Australia preserves among its stomach contents a single enantiornithine tibiotarsus; given the incompleteness of the enantiornithine and the typical habits of these birds, this occurrence is interpreted as the result of scavenging (36). A pellet from the Lower Cretaceous of Spain preserves four juvenile individuals representing three different species of enantiornithine bird (37); the responsible predator is unknown, but the diversity of juveniles in the pellet suggests prey selection for vulnerable individuals and does not imply the need for well-developed predatory capabilities. Interestingly, these articulated individuals are also incomplete in the Spanish pellet, although age and taxonomic diversity of the sample suggests these young were also likely captured and could have been ingested largely whole; it goes beyond this study to explore the taphonomic basis for this.

The origin of avian flight is heavily debated by paleontologists; although the ecology of purportedly closely related taxa has long been used to argue between either a ground-up (cursorial) or trees-down (arboreal) origin for avian flight, more recent research has focused on the kinematics of the flight stroke itself and suggests that earlier arguments represent a false dichotomy (38, 39). The ontogenetic transitional wing (OTW) hypothesis for flight suggested by Dial et al. (39) suggests that the wing stroke evolved early and was present in protowings, used for controlling descent and flap-running over obstacles. These two plausible functions, however, suggest different primary ecologies: one suggests an arboreal lifestyle, and the other suggests a cursorial lifestyle. Although the arboreal and cursorial hypotheses for the origin of flight, as they have been argued over the past century and a half, may no longer be supported by kinematic models, it is still important to understand the ecological setting in which flight evolved.

Flight is typically inferred to have evolved in an arboreal environment and thus with gravity (fitting the controlled descent function proposed by the OTW hypothesis); however, the known nonavian theropod fossil record has until recently been comprised of cursorial taxa, and thus a cursorial origin (OTW flap-running) was envisioned for avian flight. More recently, small maniraptoran theropods inferred to be arboreal have been discovered in northeastern China (40), providing renewed support for the evolution of flight in an arboreal context (1). The ecology of these taxa, however, soon became a strong point of contention; the most important and by far most controversial of these taxa is *M. gui*, with its feathered forelimbs and hindlimbs. The two-dimensional preservation of this taxon makes it difficult to assess the function and range of movement available to the hindlimbs, and, like *Archaeopteryx*, there is no consensus regarding the ecology of this taxon. This new specimen indicates that *M. gui* fed on arboreal birds, lending further support to interpretations that *M. gui* was spending a substantial amount of time in the trees.

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