

## GENERALIST DIET OF *MICRORAPTOR ZHAOIANUS* INCLUDED MAMMALS

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**ABSTRACT**—Gut contents are extremely important for inferring trophic interactions between extinct species. These are, however, very rare in the fossil record and it is not always possible to accurately identify both the carnivore and the consumed organisms. Here we describe the remains of a small fossil mammal foot preserved inside the body cavity of the holotype specimen of the small feathered dinosaur *Microraptor zhaoianus*. This adds to the known diversity of diet for this genus, which also consumed birds, fish, and lizards. Previous interpretations that *Microraptor* was an arboreal hunter of birds and adept hunter of fish are not supported. Although the various known stomach contents would be plausible prey items based on size, there is no clear evidence that any of them were predated rather than scavenged, and *Microraptor* likely did both and foraged in multiple habitats.

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### INTRODUCTION

Determining the diet of non-avian dinosaurs (hereafter, simply ‘dinosaurs’) is problematic owing to the often sparse and non-specific nature of the data available in the fossil record (Hone & Rauhut, 2010). This is because animals that were consumed by carnivores, either partially or completely, were likely to be involved in a process that limits their preservation potential. Individuals that were consumed may have been subjected to extensive oral processing and then the process of digestion, limiting diagnostic potential even if they are preserved as gut contents. Furthermore, any remains that persisted after the primary predation event are often accessible to scavengers, environmental damage and erosion once the carnivore that ingested them is dead. In addition to these factors, consumers often disrupt or remove parts of the remains. This process not only changes the preservation potential of the prey elements but also their association with each other. These factors reduce our ability to accurately recognize either predation or scavenging in the fossil record, as the elements that would show direct evidence of these events are missing, and therefore, evidence of consumption or scavenging is rare or difficult to determine.

Note that here we prefer to speak of ‘carnivore-consumed’ relationships, rather than ‘predator-prey’ relationships, when referring to fossil evidence that particular carnivores fed on particular animals (following Hone & Tanke, 2015). Predator-prey terminology, while commonly used in the scientific literature in reference to fossil carnivore gut contents, does imply a

specific relationship between actors that cannot be easily verified. A jackal may scavenge and consume a caudal vertebra of an elephant, but this would not involve a predation event, and the consumed animal would not be considered prey. Thus evidence of consumption (through bite marks or gut contents) should not immediately be assumed to represent a direct predatory interaction between the two animals. A carnivore-consumed relationship may be established based on failed predation attempts with distinctive marks and evidence of healing (Chin, 2012), though other explanations are also possible (if less likely) even for observations of this kind. Even exceptional fossil associations, such as the ‘fighting dinosaurs’ specimen with skeletons of a *Protoceratops* and *Velociraptor* interlocked (Holtz, 2003) or fragmentary *Deinonychus* individuals collected around a partial *Tenontosaurus* (Roach & Brinkman, 2007) do not definitively indicate a predator-prey relationship between these species. Scavenging can also be determined (or inferred) with appropriate taphonomic data on the state of the consumed specimen (Hone & Watabe, 2010). Nevertheless, predator-prey terminology is appropriate when formulating hypotheses or drawing inferences about the actual predatory behavior of fossil carnivores, and would also be appropriate in principle if a particular carnivore-consumed association in the fossil record could somehow be determined to a very high degree of probability to represent predation as opposed to scavenging.

Evidence pertaining to carnivore-consumed interactions may take such forms as bite traces on bones (e.g., Hone & Tanke, 2015), shed teeth from feeding (e.g., Maxwell & Ostrom, 1995), coprolites (e.g., Chin et al., 1998) or pellets (e.g., Freimuth et al., 2021) containing identifiable bones and, most importantly, gut contents (e.g., Dal Sasso & Maganuco, 2011). Bite traces from carnivorous dinosaurs left on the bones of other animals are

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generally not common (e.g., Jacobsen, 1998; Fiorillo, 1991) and, except on rare occasions (e.g., Currie & Jacobsen, 1995; Hone & Watabe, 2010), it is difficult to be specific about the taxonomic identity of even one of the individuals involved in the interaction (Chin, 2012). Gut contents provide a more reliable source of data (as the consumer is generally identifiable) but are rare (Hone & Rauhut, 2010), and thus every new record is important and can provide much new data.

For small carnivorous theropods, certain confounding issues increase the complexity of determining their possible diets, particularly when it comes to predation. For example, larger predators potentially have a wider range of prey sizes to choose from, since they may predate on large or small prey species (even if this capacity is not always exploited, e.g., Costa, 2009) and younger individuals may prey on different species than adults (Dodson, 1975). For a relatively large prey animal, a carcass may not be completely ingested and the remaining portion may preserve traces such as tooth marks. Thus the larger absolute size, and the higher chance of incomplete consumption, lead to these items having a higher preservation potential than more diminutive prey targeted by small theropods. These factors increase the possibility that evidence of carnivore-consumed interactions will be preserved when the carnivore is large. In contrast, smaller taxa, especially those that are less than 10 kg, are expected to have a diet that is more diverse in terms of prey species than those of larger carnivorous taxa, but more restricted in terms of prey size (Carbone et al., 2007). This is linked to the fact that species diversity is greatest at smaller body sizes (Morse et al., 1985; Kozłowski & Gawelczyk, 2002) and more potential prey species should therefore be available to a small predator, even for a narrow range of potential prey size. The increased likelihood of prey being completely consumed coupled with the more delicate nature of the skeletal remains of smaller predators leads to reduced preservation potential for carnivore-consumed interactions involving carnivores in this size class. Thus for smaller taxa we will likely only get a sense of the range of prey through the filter of preserved stomach contents in exceptional specimens in Lagerstätten conditions. This highly biased sampling will therefore underestimate the true feeding niche breadth of smaller theropods. Furthermore, small carnivores may scavenge carcasses of species that they would be unable to capture as prey, so their total range of consumed species may be substantially greater than their range of prey species.

Even accounting for the hypothesis that theropods would have typically taken primarily juvenile prey (Hone & Rauhut, 2010), large carnivorous theropods would have primarily been feeding upon other dinosaurs, as dinosaurs accounted for most large-bodied terrestrial animals of the Mesozoic. In contrast, small theropods would have had a larger diversity of potential consumed species, including very young dinosaurs, terrestrial arthropods, mollusks, mammals, squamates, amphibians, and other prey within their feeding envelope (O’Gorman & Hone, 2012). This division is tentatively represented in the limited data for gut contents in carnivorous theropods (Table 1) with smaller theropods generally showing a greater variety of exploited clades. By contrast, few large theropods have reported gut contents, though in both cases taphonomic biases are likely at work. Note that spinosaurs are unusual in being large theropods with evidence of a diverse diet, and from relatively few specimens (Hone & Holtz, 2017).

When exceptional data from stomach contents are available, they generally come from a single specimen of a given species. However, in the case of the small Early Cretaceous dromaeosaurid *Microraptor*, there are now four records of stomach contents showing a diversity of consumed vertebrate items in their

diet. Specimens of this genus have been described containing a bird (O’Connor et al., 2011), a fish (Xing et al., 2013), and a lizard (O’Connor et al., 2019).

Here we extend the dietary range of *Microraptor* by describing the foot of a mammal that is preserved within the ribcage of the holotype of *M. zhaoianus* (Xu et al., 2000; Fig. 1) and is regarded as gut contents. This represents only the second case of direct evidence for the consumption of mammals by a theropod dinosaur and provides new information on the diet of the small dromaeosaurids.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, U.S.A.; BMNH, Beijing Museum of Natural History, Beijing, China; IVPP, Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China; MPC, Mongolian Palaeontological Centre, Ulaanbaatar, Mongolia; QM, Qijiang Dinosaur National Geological Park Museum, Qijiang, China; STM, Shandong Tianyu Museum of Nature, Pingyi, China; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

## DESCRIPTION

IVPP V 12330 consists of multiple pieces of the part and counterpart of the articulated, partially preserved holotype of *Microraptor zhaoianus* (Fig. 1A; see Xu et al., 2000 for more details). The specimen, although incomplete, is articulated and shows no evidence of abdominal or thoracic rupture as the ribs are well articulated on both sides. An articulated mammalian right foot is preserved within the thoracic cavity. The foot exhibits the mammalian synapomorphies of having a well-defined trochlea on the astragalus, an elongate tuber calcanei, and no more than three phalanges per digit. The foot overlies the medial surfaces of the left ribs and is overlain by ribs from the right side, demonstrating this foot was contained within an articulated thoracic cavity (Fig. 1B, C). The mammalian foot is preserved in dorsal view and largely articulated. The foot includes all tarsals and metatarsals and most phalanges, including unguals of digits I and probably III. Several small shafts of apparent long bones are present under and adjacent to it, suggesting that other parts of the mammal are also preserved.

The digits are slender, similar to *Eomaia* or *Sinodelphys* (Chen & Luo, 2013), though the phalanges are not as elongate as in these two taxa. The tuber calcanei is relatively robust, as in *Sinodelphys*, but there appears to be a narrow navicular, as in *Eomaia* (Luo et al., 2003). The phalangeal index, defined as the ratio of the sum of the lengths of the non-ungual phalanges to the length of the metatarsal, is less than one (0.93) in the consumed foot, a lower value than in the purported highly arboreal Jehol taxa (Chen & Luo, 2013). Similarly, the length ratio of the proximal phalanx to the metatarsal (0.52) and the inter-phalangeal index (the ratio of distal to proximal non-ungual phalanx length, 0.77) are both similar to the corresponding values in *Aki-dolestes* (0.57, 0.82), which is suggested to be primarily terrestrial (Chen & Luo, 2013). The single well-preserved ungual lacks the trenchant, highly recurved morphology seen in extant climbers (Samuels & Van Valkenburgh, 2008). This combination of a mid-range phalangeal index with only mildly curved claws suggests predominantly terrestrial habits, unlike the highly arboreal *Sinodelphys* or *Eomaia* (Luo et al., 2003; Chen & Luo, 2013; Meng et al., 2017).

The total length of digit I, not including the ungual, is 8.1 mm (metacarpal = 4.2 mm, phalanx 1 = 2.2 mm, phalanx 2 = 1.7 mm). Including the ungual brings the total digit length to about 9 mm, similar to *Sinodelphys*, *Yanoconodon*, and *Eomaia* (Meng et al., 2017). Although differences in phalangeal proportions and likely ecology make it difficult to be confident in assuming similar body mass, using these three taxa as a guide suggests a size range

TABLE 1. Records of ingested bony elements by dinosaurian carnivores. Note that *Scipionyx* had ingested multiple individuals of both fish and lepidosaurians of different taxonomic affinities and sizes but these records are combined here for simplicity. Femur lengths from citing reference or from <sup>#</sup>Dececchi et al. (2020b) and \*Wilson et al. (2016).

Consumer body size	Carnivorous taxon	Consumed taxon	Carnivorous taxon Femur length (mm)	Consumed elements	Reference
Less than 100 kg	<i>Coelophysis</i>	Crocodylomorphs	209 <sup>#</sup>	Partial pelvis and femur	Nesbitt et al., 2006
	<i>Scipionyx</i>	?Lepidosaur	37.3 <sup>#</sup>	Centrum, ulna, parts of hindlimb and pedes	Dal Sasso & Maganuco, 2011
	<i>Scipionyx</i>	Fish	37.3 <sup>#</sup>	Scales and vertebrae	Dal Sasso & Maganuco, 2011
	<i>Sinocalliopteryx</i>	<i>Sinornithosaurus</i> (dromaeosaur)	210 <sup>#</sup>	Hindlimb	Ji et al., 2007
	<i>Sinocalliopteryx</i>	<i>Confusisornis</i> (bird)	est. 290	Numerous bones	Xing et al., 2012
	<i>Compsognathus</i>	<i>Bavarisaurus</i> (squamate)	65.8 <sup>#</sup>	Nearly a complete individual	Ostrom, 1978
	<i>Sinosauropteryx</i>	Lizard	86 <sup>#</sup>	Most of an individual	Currie & Chen, 2001
	<i>Sinosauropteryx</i>	Mammal	108 <sup>#</sup>	Tooth bearing element	Ji & Ji, 1997
	<i>Huaxiagnathus</i>	Unknown	163 <sup>#</sup>	Indeterminate bone	Hwang et al., 2004
	<i>Amblopteryx</i>	Unknown	36.8	Indeterminate bone	Wang et al., 2019
	<i>Anchiornis</i>	Lizards	71	Numerous bones	Zheng et al., 2018
	<i>Anchiornis</i>	Fish	35	Bones and scales	Zheng et al., 2018
	<i>Velociraptor</i>	Azhdarchid pterosaur	194	Indeterminate longbone	Hone et al., 2012
	<i>Microraptor</i>	Enantornithine bird	82.3	Forelimb, both feet	O'Connor et al., 2011
	Greater than 100 kg	<i>Microraptor</i>	Teleost fish	109	Various bones
<i>Microraptor</i>		<i>Indrasaurus</i> (lizard)	est. 75 mm	Nearly a complete individual	O'Connor et al., 2019
<i>Microraptor</i>		Mammal		Pes	Larsson et al., 2010
<i>Baryonyx</i>		<i>Iguanodon</i>	est. 1200*	Not specified	Charig & Milner, 1997
<i>Baryonyx</i>		<i>Lepidotes</i> (fish)	est. 1200*	Scales	Charig & Milner, 1997
<i>Tyrannosaurus</i>		Ornithischian	1321 <sup>#</sup>	Various elements (coprolite)	Chin et al., 1998
<i>Daspletosaurus</i>		Hadrosaur	1030 <sup>#</sup>	Caudal vertebrae and dentary	Varricchio, 2001

between 13–43 g based on mass estimates for more complete contemporaneous mammals (Meng et al., 2017). The mid range estimates for *Eomaia* (digit length 9.1 mm) at 30 g and that of *Yanoconodon* (digit length 7.5mm) at 21 g define a reasonable size bracket for this taxon.

## DISCUSSION

### Ecology of *Microraptor*

The general ecology and behavior of *Microraptor* is uncertain and even controversial and this makes it difficult to make reasonable inferences about its possible behaviors as a predator/carnivore. It has, for example, been suggested to be both nocturnal (Schmitz & Montani, 2011) and diurnal (Li et al., 2012). Although *M. gui* appears to have been capable of gliding flight (Xu et al., 2003), there is also evidence it could have achieved powered flight (Xu et al., 2003; Dececchi et al., 2016, 2020a; Kiat et al. 2020; Pei et al., 2020), and little doubt that the taxon was capable of some form of aerial locomotion. As for habitat, both arboreality (Xu et al., 2000, Birn-Jeffery et al. 2012; Cobb & Sellers, 2020), and terrestriality (Dececchi & Larsson, 2011, Dececchi et al., 2016, 2020b) have been suggested. However, most agree that *Microraptor* could be at least partly scansorial (Xu et al., 2003; Chatterjee & Templin, 2007; O'Connor et al., 2011; Birn-Jeffery et al., 2012; Dyke et al., 2013) and that small maniraptoran theropods in general could climb (Naish, 2000). Maniraptorans, including microraptorines, may not generally have been well suited to moving in small diameter branch environments and no non-avian theropod exhibited skeletal traits associated with arboreality (Dececchi & Larsson, 2011). Only the enigmatic scansoriopterygians are a likely exception (Dececchi et al., 2020c). The diverse range of consumed items found within specimens of *Microraptor* do not help resolve the habitat question, as they range from perching birds to fish.

The sheer number of articulated *Microraptor* specimens, over 300 of which have been recovered from the Jiufotang Formation (Alexander et al., 2010), may be a major reason that such a broad diet is represented. This quantity ensures that more examples of gut contents are currently known for *Microraptor* than for any other dinosaur. Additionally, taxonomic variation within *Microraptor* could at least partially explain the dietary breadth that has been documented for the genus as a whole. Three species have been erected within the genus from collected specimens, and these putative taxa differ in body size and in subtle osteological characters. The proposed anatomical differences may reflect different ontogenetic stages, anagenetic species clines sampled from different temporal horizons within the formation, sympatric species, intraspecific variation, or some combination of these factors. To date, specimens assigned to *M. zhaoianus* have been found with gut contents of a lizard (O'Connor et al., 2019) and now a mammal. *M. gui* specimens have been found with a fish (Xing et al., 2013) and a bird (O'Connor et al., 2011). Even if the two species were distinct in their dietary preferences, each clearly consumed a wide enough range of small vertebrates, at least on occasion, to imply relatively generalist feeding habits.

### Size of Consumed Items

In extant organisms, predators generally exceed the body size of their prey, often by a considerable margin (not including 'grazing' on another organism such as cookie-cutter sharks, *Isistius*, biting out parts of much larger fish) (Cohen et al., 1993; Vézina, 1985). There are exceptions, and some predators (e.g., some members of Mustelidae) may regularly attack, kill, and consume prey considerably larger than themselves (Carbone et al., 1999). Larger mammalian carnivores do tend to take prey that is proportionally larger (Carbone et al., 1999), though

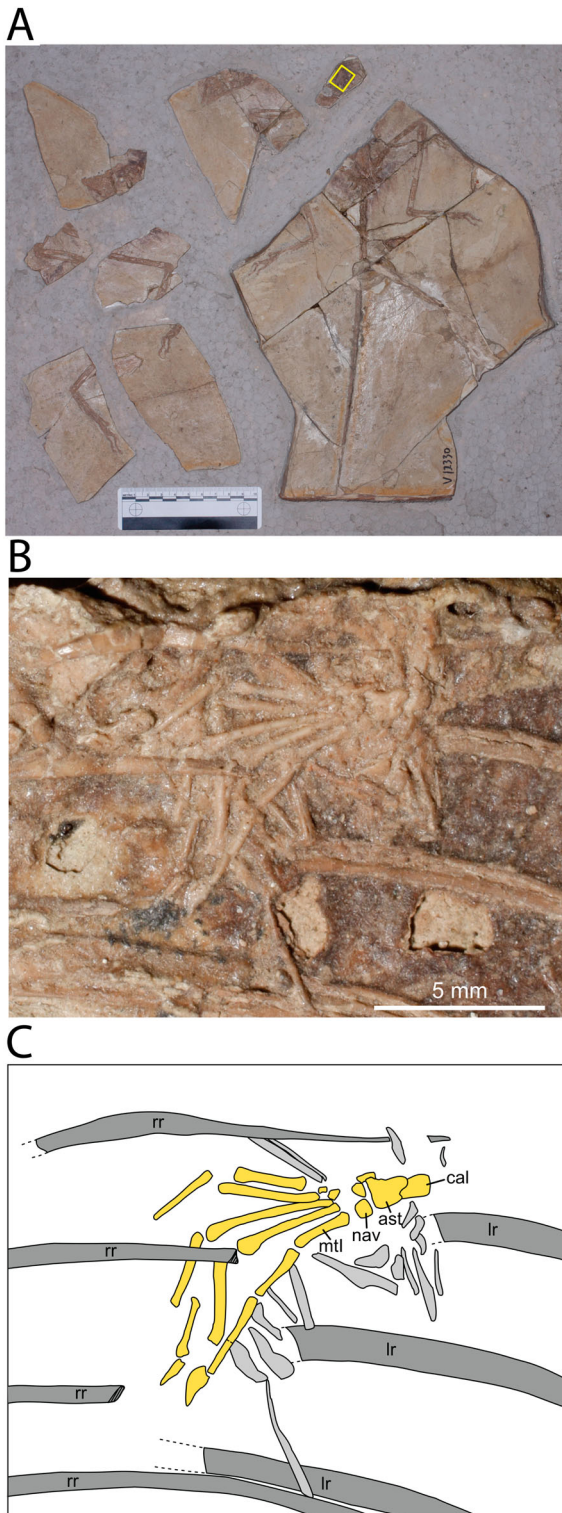


FIGURE 1. Holotype specimen of *Microaptor zhaoianus* (IVPP V 12330) with mammal foot gut contents. **A**, entire specimen. Box inset indicates the location of B and C. **B**, close-up view of mammal foot. **C**, illustration of visible bones: dark gray elements are *Microaptor* ribs, yellow bones are the articulated mammalian foot and light gray are unidentified bones. Note the juxtaposition of the foot over the inside of the left ribs and the overlap of the right ribs over the foot, particularly over digits II and III. **Abbreviations:** *ast*, astragalus; *cal*, calcaneum; *mtl*, metatarsal 1; *nav*, navicular; *lr*, left rib; *rr*, right rib. Scale bar in A equals 100 mm and in B and C equals 5 mm.

potentially still absolutely smaller than the predator. At least some of these carnivorans hunt cooperatively to facilitate capturing prey larger than any individual predator, but collectively the pack is larger in mass (e.g., dhole—*Cuon alpinus*, Woodroffe et al., 2007; painted dogs—*Lycaon pictus*, Radloff & du Toit, 2004). This behavior allows a group to take prey that would be too large for them to subdue alone, at least without extreme risk of injury. However, the general rule that predators exceed the size of their prey holds well, and for mammals at least, smaller carnivores (under 21 kg) typically take prey less than 40% of their own mass (Carbone et al., 1999). Similarly, while some large crocodylians are recorded as attacking and eating large prey, their diet mostly comprises much smaller species (Messel & Vorlicek, 1989).

In the four known examples of *Microaptor* gut contents, the theropod exceeded the size of the consumed items by a considerable margin (Table 2). The consumed bird consisted predominantly of parts of a wing and both feet, and was small (consumed ulna length 10.5 mm compared with 80 mm for the consumer; O'Connor et al., 2011). The lizard was relatively small (consumed femur length 13.4 mm vs 75 mm for the consumer; O'Connor et al., 2019). Similarly, the consumed fish were small based on the size of the preserved vertebrae (Xing et al., 2013). In the new example presented here, the mammal was clearly small (mass estimated to be about 1/10th that of the consumer), and the pes fits within a small portion of the body cavity. These various consumed items would be within the envelope of potential prey items for *Microaptor* if it were assumed to operate as an active predator following the pattern seen in most extant animals, and inferred for carnivorous theropods generally (Hone & Rauhut, 2010).

#### Jaw Mechanics of Dromaeosaurids

Assessing the size range of prey for an individual *Microaptor* must also include details of cranial morphology. The relatively short and deep jaw proportions of *Microaptor* (Xing et al., 2013:fig. S1) are consistent with the inference that this taxon fulfilled its dietary needs in part through predation on small vertebrates, rather than preying exclusively on even smaller invertebrates. In general, predators with slender, elongate jaws tend to target small, agile prey, whereas taxa with shorter, more robust jaws are more likely to attack larger prey. This relationship has been postulated for non-avian theropods (Powers et al., 2020) and exists in extant taxa as divergent as crocodylians (Walmsley et al., 2013) and canids (Slater et al., 2009), although seemingly not in felids (Sakamoto et al., 2010). A simple but powerful mechanical explanation for the connection between jaw length and preferred prey type arises from lever mechanics and beam theory, as applied to the tetrapod jaw apparatus (Ostrom, 1964; Bock, 1966; Thomason, 1991; Preuschoft & Witzel, 2002; Therrien, 2005; Therrien et al., 2005, 2021). The bite force that can be applied to prey by a given tooth in a predator's mouth is inversely proportional to the distance between the jaw joint and the position of the tooth in question. Conversely, the speed with which the tooth can move along a circular arc to engage the prey is directly proportional to that same distance. Longer jaws also permit greater reach. Jaws that are robustly constructed, in the sense of being dorsoventrally deep and/or mediolaterally thick, are better able to withstand stress than more gracile jaws. Although the stress regime experienced by the jaws is partly determined by the presence or absence of specific feeding behaviors, such as bone cracking in some carnivorous mammals (Therrien, 2005), the size of a given prey animal in proportion to that of the predator is presumably another important factor, given

TABLE 2. Estimated body masses of *Microraptor* specimens and characteristics of their gut contents. *Microraptor* specimen masses are based on femoral length per Christiansen and Fariña (2004). Prey size masses are estimated for a complete individual, not only the body portion preserved. Bird mass based on the estimate in O'Connor et al. (2011). Fish mass based on osseous mass of fish in QM V1002 being of similar dimensions (minimally 3.5 × 1.6 cm) as the regurgitate in *Anchiornis* specimen STM0-224, which was estimated at 93 g by Friemuth et al. (2021). Mass of squamate *Indrasaurus* estimated from SVL using Meri (2010); SVL estimated based on closely related and similar sized (femur length 83% of that of *Indrasaurus*) specimen of *Liushusaurus* (Evans & Wang 2010).

Specimen	<i>Microraptor</i> femur length (mm)	<i>Microraptor</i> mass (g)	Prey	Prey size of complete individual (g)	Prey % of predator mass
IVPP V13972A	82.3	760	enantiornithine bird	60–70	8–9%
QM V1002	109	1890	teleost fish	90	5%
STM5-32	75	570	scleroglossan squamate	6–12	1–2%
IVPP V 12330	49.8	150	mammal	21–30	14–21%

the general relationship between jaw proportions and prey size noted above.

The relationship between jaw proportions and prey size is tightly associated, given the functional demands of feeding on prey of different sizes. Assuming a predator can get close enough for a biting attack to be possible, proportionally large prey should be easy to engage with the jaws, because their bodies present a large target area. However, such prey are also likely to require one or more forceful bites to capture, because the amount of tissue that must be penetrated in order to inflict lethal or at least crippling damage is comparatively great. Short, deep jaws are optimized for force production. Relatively small prey, by contrast, offer a smaller target area and hence should be more elusive and difficult to seize, but should require less bite force to dispatch. Capture of small prey should therefore require long, shallow jaws optimized for reach and rapidity of jaw closure. Among extant carnivorans, species that take larger prey do indeed tend to be capable of generating greater bite forces (Christiansen & Wroe, 2007).

Powers et al. (2020) provided a useful foundation for evaluating jaw proportions in dromaeosaurids by carrying out a principal components analysis of maxillary shape in Eudromaeosauria. All the taxa in the analysis fell into one of three visually apparent clusters occupying different positions along PC 1. The highest-scoring taxa on PC 1 were the North American forms *Deinonychus* and *Atrociraptor*, characterized by short, deep maxillae with near-identical length/height ratios of about 1.7 (calculated from supplementary data in Powers et al., 2020). The North American taxa *Saurornitholestes*, *Bambiraptor*, and *Acheroraptor*, together with the Asian taxon *Achillobator*, had intermediate maxillary length/height ratios of about 2.0 (based on *Saurornitholestes langstoni* UALVP 55700 and *Bambiraptor feinbergi* AMNH FARB 30556, as other maxillae in this grouping were damaged; note that ratios for left and right maxillae were averaged when both maxillae were available). Finally, the lowest-scoring taxa on PC 1 were the Late Cretaceous Asian velociraptorines *Linheraptor*, *Tsaagan*, and *Velociraptor*, characterized by comparatively long and shallow maxillae with length/height ratios ranging from 2.4 in *Linheraptor exquisitus* IVPP V 16923 to 3.4 in *Velociraptor* sp. MPC-D 100/982. Powers et al. (2020) suggested that *Velociraptor*, *Linheraptor*, and *Tsaagan* were best suited on the basis of their snout proportions to predation on prey much smaller than themselves, whereas *Atrociraptor* and *Deinonychus* were best suited to attacking relatively large prey. *Achillobator*, *Acheroraptor*, *Bambiraptor*, and *Saurornitholestes* were potentially intermediate between these extremes, and perhaps more generalist in their feeding habits (Powers et al., 2020).

In many *Microraptor* specimens, including IVPP V 12330, the proportions of the maxilla cannot be reliably measured because

both maxillae are absent, unexposed, damaged, or difficult to fully demarcate from adjacent bones. However, the length/height ratio of the maxilla is 2.2 in *Microraptor* sp. BMNH PH881 (measured from Pei et al., 2014:fig. 3) and 2.0 in *Microraptor* sp. IVPP V 13475, values close to those obtained for taxa in the “potentially intermediate” eudromaeosaurian cluster of Powers et al. (2020). Furthermore, the snout of *Microraptor* is overall shorter in proportion to its height than those of *Velociraptor* (Barsbold & Osmólska, 1999), *Tsaagan* (Norell et al., 2006), and *Linheraptor* (Xu et al., 2010), and more comparable in shape to that of *Saurornitholestes* (Currie & Evans, 2020). The fairly short, deep rostrum of *Microraptor* would therefore have been suitable for feeding on prey that were relatively easy to seize but required a forceful bite to injure. In a tiny dromaeosaurid with a body mass well under 1 kg, such snout proportions are consistent with small vertebrate prey forming at least a substantial part of the diet. By contrast, a dromaeosaurid of the same size that preyed exclusively on even smaller insects might be expected to have longer, shallower jaws.

### Predation versus Scavenging in *Microraptor*

The consumed mammal is interpreted as predominantly occupying terrestrial habitats based on its limited claw curvature. Although it is tempting to infer that the mammal was consumed in a predation event in a terrestrial setting by a terrestrial theropod, this is not known. It is also possible that the mammal was a scissor climbing in the trees or other elevated surfaces when it was seized by the theropod, or that it was found dead and was scavenged rather than preyed upon. Thus the inferred ecology of the mammal can provide only weak evidence regarding the ecology of the consumer.

There is evidence for both predation (Fowler et al., 2011) and scavenging (Hone et al., 2010) in dromaeosaurids, and most carnivorous animals are at least facultative scavengers taking advantage of opportunities that may arise when foraging. Scavenging itself as a behavior is underappreciated and more common than often realized (DeVault et al., 2003), and should not be dismissed as a rare behavior or an activity only usually engaged in by specialists. In some ecosystems the majority of mortality may not be through predation, and scavengers can also consume and remove whole organisms (DeVault et al., 2003). Therefore, gut contents in vertebrate carnivores should not be assumed to be the result of predation, even if a whole animal has been consumed.

Although the evidence is limited, the consumption of a mammal foot could potentially be attributed to scavenging given its size and that it is a distal part of a limb. Dromaeosaurids do appear to have been capable of swallowing relatively large items (Hone et al., 2012), but the various items consumed by

*Microraptor* are generally small. The mammalian pes and possibly other elements are collectively small and, although the *Microraptor* specimen is incomplete, these are the only consumed elements. Apparently the animal would have had the capacity to consume other elements, but no evidence exists that it did. Most animals show stereotyped patterns of consuming carcasses (when not swallowed whole or in large parts), beginning with major parts of muscle mass and viscera and ending with areas with little or no muscle (Blumenschine, 1986). These low-muscle areas would therefore be the parts most often available for consumption by scavengers once the more muscled areas had been removed. The pes is a part of the body that would contain relatively little nutrition, and would be among the last parts of a carcass to be consumed. This suggests that the pes was ingested during late-stage carcass consumption, and potentially in a scavenging event.

The suggestion of O'Connor et al. (2011) that *Microraptor gui* actively hunted birds in an arboreal setting, based on the presence of a partial wing and both feet of an enantiornithine bird as gut contents, is problematic. The argument that this was predation rather than scavenging was based on the articulated nature of the consumed bird parts. While a predation scenario is certainly possible, we do not see why a recently dead bird could not have simply been consumed in parts, which would be scavenging. The articulated condition of the bird remains perhaps says more about the ability of small dromaeosaurids to process and break up food items than about the distinction between scavenging and predation. Indeed, the ingestion of parts of the avian skeleton which would yield little in the way of muscles or viscera (e.g., radius and ulna, pes) could be used to argue that this was also a scavenging event based on typical patterns of carcass consumption (Blumenschine, 1986). Furthermore, even perching birds may spend a considerable amount of time on the ground foraging and may be predated upon by fully terrestrial carnivores, potentially including theropods (Xing et al., 2012). For example, striped hyenas (*Crocuta crocuta*; Leakey et al., 1999), cheetahs (*Acinonyx jubatus*; Farhadinia et al., 2012), and red foxes (*Vulpes vulpes*; Larivière & Pasitschniak-Arts, 1996) are known to capture and feed on flying birds. Foxes will take birds that are sitting on nests and will climb trees on occasion (Larivière & Pasitschniak-Arts, 1996). Therefore, although it is possible that *M. gui* hunted arboreal birds in the trees, we do not agree that this is supported simply by the presence of a partially ingested bird.

Similarly, Xing et al. (2013) considered *Microraptor* adept at hunting aquatic prey based on the presence of preserved fish gut contents, but noted they could not rule out scavenging. It is difficult to picture this taxon as adept at hunting both birds in trees and fish in water, foraging modes that would potentially require very different specializations. Some extant birds, such as the bald eagle *Haliaeetus leucocephalus*, do capture birds and fish and so hunt very different prey in different settings (Collins et al., 2010), but this requires a level of flight capability that was clearly not present in *Microraptor*. Regardless of how appealing it is to interpret the presence of a certain prey item as a strong indicator of specific ecological traits in the consumer, there is no clear evidence to support the conclusion that *Microraptor* actively hunted rather than scavenged fish, let alone hunted them proficiently. As the gut contents for *Microraptor* recovered to date represent a wide variety of vertebrates, with three of four being non-aquatic, it is difficult to reconcile these data with the hypothesis that this genus would be in some way well adapted to catching aquatic prey. In short, the presence of multiple different consumed species at least weakens any case for a preferential diet of, for example, fish or birds, and without further

support from functional or other data, these hypotheses of specialization are weak.

The variety of vertebrates known to be consumed by *Microraptor* is far greater than for most theropod taxa. However, this type of broad feeding niche may in fact have been typical for theropods, but rarely documented in the fossil record because few if any specimens with preserved gut contents are known for most taxa. Diet in theropods likely varied not just interspecifically, but intraspecifically among individuals, as well as potentially across regions, seasons, and ontogenetic stages (as recently shown in *Deinonychus*; Frederickson et al., 2020). Preservation may also bias our interpretations further. For example, arthropods or other invertebrates may have made up the majority of the diet but would have had low preservation potential compared with consumed vertebrates because of the lack of durable skeletal structures in many (e.g., see Nielsen et al., 2018). The remains of insects and arachnids sufficient to diagnose them to family level have been recovered from pellets of some small extant owls (Mrykalo et al., 2009), though, suggesting the possibility they could be recovered in theropods. As yet the only pellets found in association with a theropod are for *Anchiornis* (Zheng et al., 2018), most recently recovered as a basally branching avialan (Pei et al., 2020). Recently, Freimuth et al. (2021) described pellets bearing the remains of mammals and tentatively referred them to *Troodon*. Thus despite multiple examples of gut contents, it is difficult to reach firm conclusions about diet. Even carnivores that are well-adapted to scavenging large terrestrial mammals, like hyenas, eat small fish, fruits, and seeds (Leakey et al., 1999), and such items may not show up in the gut contents. Additional data from studies such as enamel microwear and stable isotopes may provide a clearer picture of what a typical diet was for *Microraptor*.

## CONCLUSIONS

The type specimen of *Microraptor zhaoianus* provides clear evidence that this species consumed mammals, at least on occasion, and is a rare example of a fossil that documents interaction between a theropod and Mesozoic mammal. On the wider subject of the carnivorous ecology of *Microraptor*, all that we can say with confidence is that this dromaeosaurid was probably a generalist carnivore that mostly ate small vertebrates. In this regard *Microraptor* was probably no different from many other small, carnivorous theropods. Although gut contents are known disproportionately from exceptionally preserved specimens of theropods, it is notable that in addition to *Microraptor*, *Scipionyx*, *Sinocalliopteryx*, and *Anchiornis* (Table 1) all show evidence of a highly varied diet including multiple vertebrate groups from gut contents alone. In the case of *Velociraptor*, there is evidence to suggest consumption of both small ceratopsians and pterosaurs (Hone et al., 2010, 2012). As discussed above, the diversity of prey species available to small carnivores is much wider than that for larger taxa, and it is likely that many smaller theropods were generalists and took a wide range of prey in addition to opportunistic scavenging. It is certainly even possible that in addition to vertebrates and arthropods, some small carnivorous theropods may have consumed plant matter on occasion since gut contents are informative, but not exclusive indicators of diet.

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