Diverse diets in small theropods - the Cretaceous feathered dinosaur *Microraptor zhaoianus* ate 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 *Microrapator* 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.

Keywords: Dinosauria, Theropoda, Paraves, predator-prey

Introduction:

Determining the diet of non-avialan 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 the term ‘carnivore-consumed’ over ‘predator-prey’ (following Hone & Tanke, 2015). The latter, while commonly used in the scientific literature in reference to 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 predator-prey relationship may be established based on failed predation attempts with distinctive marks and evidence of healing (Chin, 1997), 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 and 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).

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 and 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 and Maganuco, 2011). Bite traces from carnivorous dinosaurs left on the bones of other animals are generally not common (e.g. Jacobsen, 1998; Fiorillo, 1991) and, except in rare occasions (e.g., Currie & Jacobsen, 1995; Hone & Watabe, 2010), it is difficult to be specific about the taxonomic identity of at least one of the two species 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 taxa 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). In addition, as much of this prey choice is relatively larger in larger theropods (i.e. the size of the consumed is a higher proportion of the consumer's mass), 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 the 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; Kozlowski & 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 what preserved stomach contents in exceptional specimens in lagerstatten conditions. This highly biased sampling will therefore underestimate the true feeding niche breadth of smaller theropods.

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, in addition to very young dinosaurs, small theropods would have had terrestrial arthropods, molluscs, mammals, squamates, amphibians, and other prey within their 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).

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.

Carnivorous taxon	**Consumed taxon**	**Consumed elements**	**Reference**
Coelophysis	Crocodylomorphs	Partial pelvis and femur	Nesbitt et al., 2006
Scipionyx	?Lepidosaurs	Centrum, ulna, parts of hindlimb and pedes	Dal Sasso & Maganuco, 2011
Scipionyx	Fishes	Scales and vertebrae	Dal Sasso & Maganuco, 2011
Baryonyx	*Iguanodon*	Not specified	Charig & Milner, 1997
Baryonyx	*Lepidotes* (fish)	Scales	Charig & Milner, 1997
Tyrannosaurus	Ornithischian	Various elements (coprolite)	Chin et al., 1998
Daspletosaurus	Hadrosaur	Caudal vertebrae and dentary	Varricchio, 2001
Sinocalliopteryx	*Sinornithosaurus* (dromaeosaur)	Hindlimb	Ji et al., 2007
Sinocalliopteryx	*Confuscisornis* (bird)	Numerous bones	Xing et al., 2012
Compsognathus	*Bavarisaurus* (squamate)	Nearly a complete individual	Ostrom, 1978
Sinosauropteryx	Lizard	Most of an individual	Currie & Chen, 2001
Sinosauropteryx	Mammal	Tooth bearing element	Ji & Ji, 1997
Huaxiagnathus	Unknown	Indeterminate bone	Hwang et al., 2004
Ambopteryx	Unknown	Indeterminate bone	Wang et al., 2019
Anchiornis	Lizards	Numerous bones	Zheng et al., 2018
Anchiornis	Fish	Bones and scales	Zheng et al., 2018

Velociraptor	Azhdarchid pterosaur	Indeterminate longbone	Hone et al., 2012
Microraptor	Enantornithine bird	Forelimb, both feet	O'Connor et al., 2011
Microraptor	Teleost fish	Various bones	Xing et al. 2013
Microraptor	*Indrasaurus* (lizard)	Nearly a complete individual	O'Connor et al., 2019
Microraptor	Mammal	Pes	Larsson et al., 2010 / this study

It is difficult to provide any kind of accurate division here between 'large' and 'small' theropods. Clearly, there is a continuum from the smallest carnivorous members of this group and the largest, which spans at least three orders of magnitude in body mass. Additionally, ecosystems throughout the Mesozoic are not directly comparable from locality to locality and time to time, making general statements about feeding ecologies impossible. It is reasonable to consider in the context of prey availability that those animals that had a mass in the hundreds or thousands of kilograms are relatively large and those under say 10 kg are relatively small, but a detailed analysis of the separation between the two is beyond the scope of this study. Extant terrestrial mammalian carnivore feeding ecologies can be divided at around 20 kg based on prey type and size (Carbone et al., 2007), yet this is unlikely to be a universal value that should be assumed to hold for non-avialan theropods due to their phenotypic differences from mammals, and to differences in community composition between modern and Mesozoic times. There is still likely to be some general rules and some kind of size-based discontinuity in ecology in theropod communities, though if it was similar to modern mammals, or even if it remained constant across the changing climates, clades and biotas that non-avialan theropods occupied over their ~160 million years, is debatable and well beyond the scope of this work.

Even 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 numerous records of stomach contents showing a diverse 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 – Figure 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.

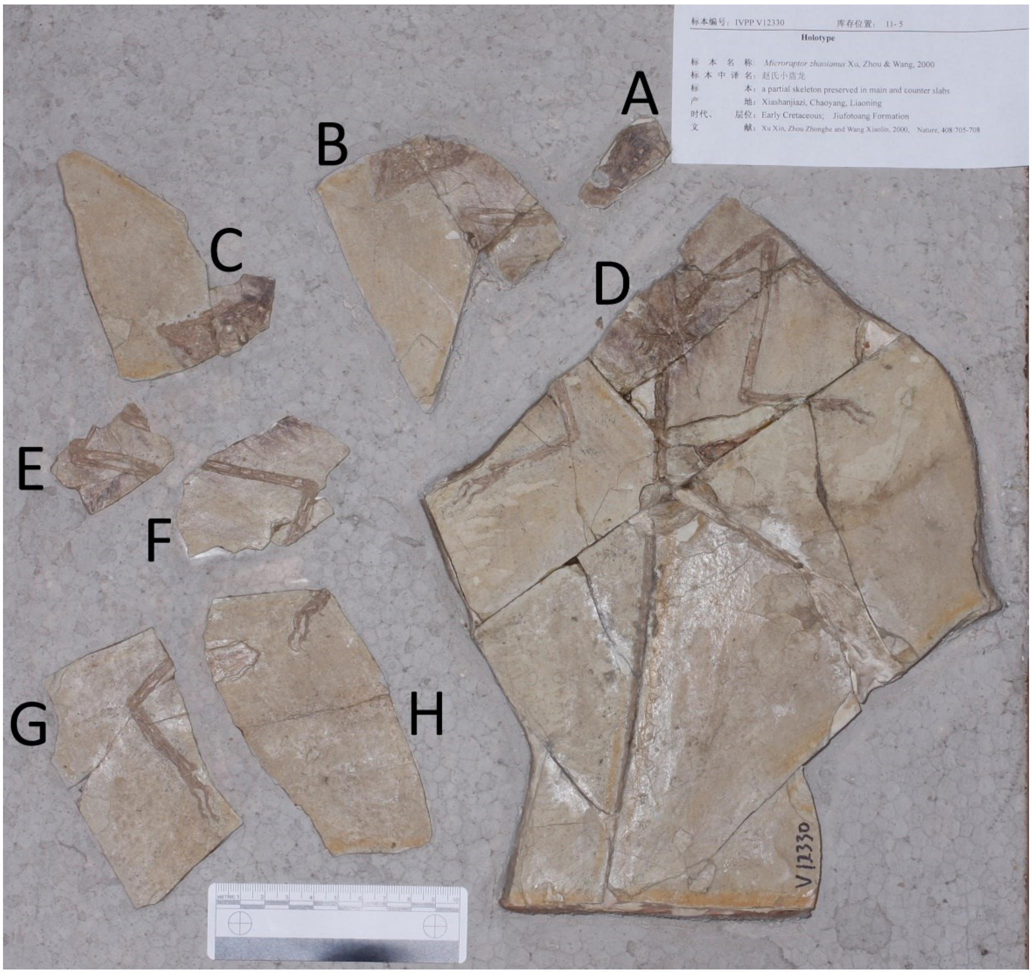

Figure 1. Holotype specimen of *Microraptor zhaoianus* (IVPP V 12330). A, chest containing the mammal foot; B, partial skull and right forelimb; C, partial skull; D, pelvis, legs and tail; E, counterpart forelimb; F, G, H, counterparts for the hindlimbs. Scale bar is 100 mm.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, USA; BMNHC, Beijing Museum of Natural History, Beijing, China; IVPP, Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China. MPC, Mongolia Palaeontological Centre, Ulaan Bator, Mongolia; QM, Qijiang Dinosaur National Geological Park Museum, Qijiang, China; STM, Shandong Tianyu Museum of Nature, Pingyi, China; UALVP, University of Alberta, Laboratory of Vertebrate Palaeontology, 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* (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 overlies ribs from the left side and is overlain by ribs from the right side (Figure 2). The mammalian foot is preserved in dorsal view and largely articulated. It includes all tarsals and metatarsals and most phalanges, including unguals of digits I and probably III. Several small, shafts of apparent longbones are present under and adjacent to it, suggesting that other parts of the mammal are also preserved (Figure 3).

Figure 2. Two alternate views (A and B) of the mammal pes preserved with *M. zhaoianus* under different lighting conditions. Scale bar for both images is 5 mm.

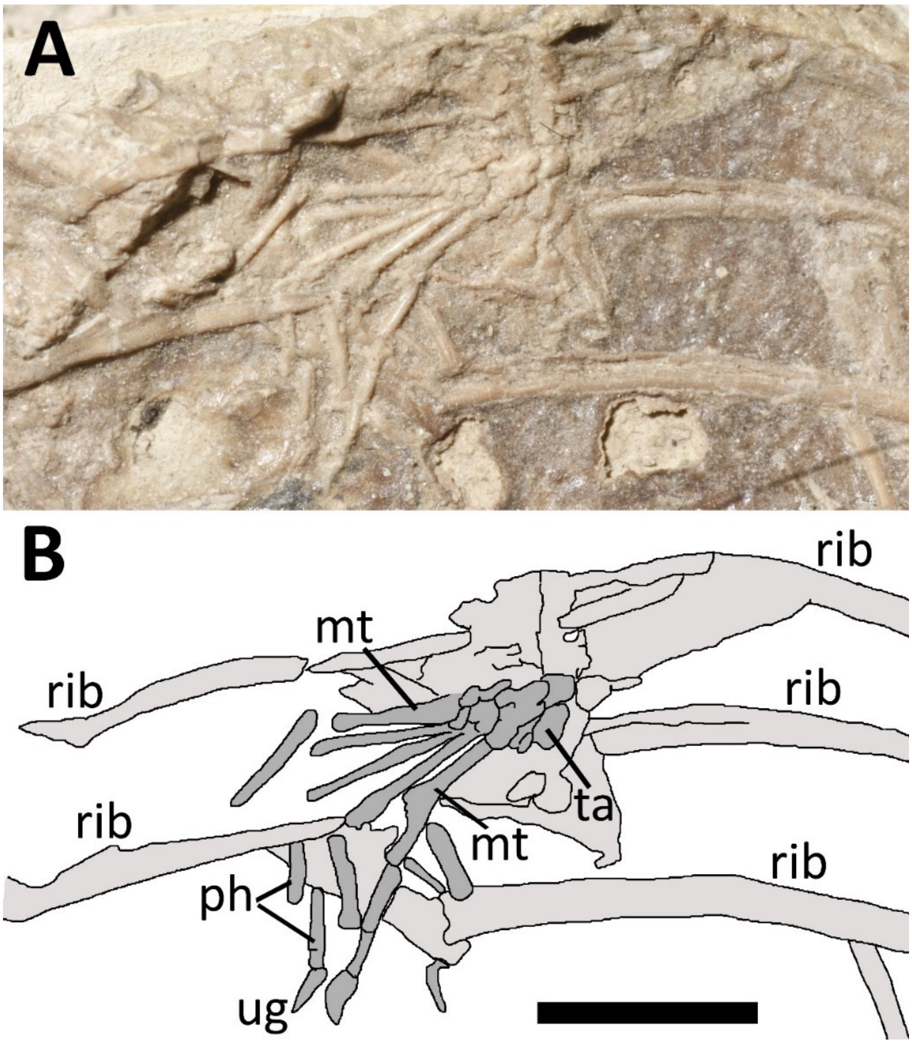

Figure 3. (A) Close up of the mammalian pes with (B) interpretative line drawing. Dark grey shaded elements are mammalian, pale grey elements are *Microraptor* or of indeterminate origin. Abbreviations are as follows: ph, phalanges; mt, metatarsals; rib, *Microraptor* ribs; ta, tarsals; un, unguals. For clarity, not all elements are labelled. Scale bar is 5 mm.

The digits are slender, similar to *Eomaia* or *Sinodelphys* (Chen and Luo 2013), though the phalanges are not as elongate as in these two taxa. 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 and Luo 2013). The inter-phalangeal index (the ratio of distal to proximal non-ungual phalanx length) is similar to that seen in *Akidolestes,* which is suggested to be primarily terrestrial in habit (Chen and Luo 2013). The single well-preserved ungual lacks the trenchant, highly recurved morphology seen in extant climbers (Samuels and Vanvalkenburgh, 2008). This combination of a mid-range phalangeal index with only mildly curved claws suggests a predominantly terrestrial habit, unlike the highly arboreal *Sinodelphys* or *Eomaia* (Luo et al., 2003; Chen and Luo, 2013; Meng et al., 2017) (Figure xxx).

The total length of the digit, not including the ungual, is 8.1 mm. Including the ungual brings the total digit length to about 9 mm, similar to *Sinodelphys*, *Yancodon* 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 between 13-43 g based on mass estimates for more complete contemporaneous mammals (Meng et al., 2019). The mid range estimates for *Eomaia* (digit length 9.1 mm) at 30 g and that of *Yancodon* (digit length 7.5mm) at 21 g define a reasonable size bracket for this taxon.

Discussion:

Ecology of Microraptor

The ecology and behavior of *Microraptor* is uncertain and even controversial and has, for example, been suggested to be both nocturnal (Schmitz & Montani, 2011) and diurnal (Li et al., 2012). Although *M. gui* appears to be capable of gliding flight (Xu et al., 2003), there is also evidence for powered flight (Xu et al., 2003; Dyke et al., 2013; Alexander et al., 2010; Dececchi et al., 2016, 2020a; Hartman et al., 2019; 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 and Larsson, 2011, Dececchi et al., 2016) have been suggested. However, most agree that *Microraptor* could be at least partly scansorial and that small maniraptoran theropods in general could climb (Naish, 2000). They may not generally be well suited to moving in small diameter branch environments (Dececchi and Larsson, 2011), but the enigmatic scansoriopterygians are a likely exception, and perhaps also the first arboreal theropods (Dececchi et al. 2020b). The diverse range of prey items found within specimens of *Microraptor* do not help solve the habitat riddle, as they range from perching birds to fish.

The sheer number of curated *Microraptor* specimens, over 300 of which have been recovered from the Jiufotang Formation (Alexander et al. 2010), may provide some insight into its broad diet. 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 specimens collected, differing in body size and in subtle osteological characters. The 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).

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 cookiecutter sharks biting out parts of much larger fish) (Cohen et al., 1993; Vézina, 1985). There are inevitably exceptions, and some predators (e.g., some mustelids) 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 potentially still smaller than the predator. At least some of these carnivorans hunt cooperatively to facilitate capturing prey larger than each individual, 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 behaviour allows individuals 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 crocodilians are recorded as attacking and eating large prey, their diet mostly comprises much smaller species (Messel and Vorlicek, 1989).

In the four known examples of *Microraptor* 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 to 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 sits with a small portion of the body cavity. These various consumed items would be within the envelope of potential prey items for *Microraptor* 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 and Rauhut, 2010).

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 x 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 *Indrasausrus* 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 and Wang 2010).

Specimen	***Microraptor*** **femur length mm**	***Microraptor*** **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%

Jaw mechanics of dromaeosaurids

The craniomandibular morphology of *Microraptor* is consistent with the inference that this taxon's diet was made up at least in part of small vertebrates, rather than only small invertebrates. The jaw proportions of faunivores are clearly linked to their feeding strategy, in that taxa 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-avialan theropods (Powers et al., 2020) and exists in extant taxa as divergent as crocodilians (Walmsley et al., 2010) 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 and Witzel, 2002; Therrien, 2005; Therrien et al., 2005, 2021). For a predator with a given configuration of the jaw-closing musculature, the temporal part of the skull, and the posterior part of the mandible, the bite force that can be applied to prey by a given tooth in the anteriormost part of the mouth is inversely proportional to the length of the jaws, or more precisely to the distance between the jaw joint and the position of the tooth in question. Conversely, the speed with which upper and lower teeth in that position can come together along a circular arc to engage the prey is directly proportional to that same anteroposterior distance, for a given angular velocity of jaw closure, and 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 behaviours, 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 another important factor. Other things being equal, proportionally large prey should be easy to engage with the jaws but are likely to require one or more forceful bites to kill, whereas proportionally small prey should require less bite force to dispatch but are likely to be more elusive and difficult to seize.

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). An intermediate cluster contained the North American taxa *Saurornitholestes*, *Bambiraptor* and *Acheroraptor* together with the Asian taxon *Achillobator*, with 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 cluster 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 vertebrates much smaller than themselves, whereas *Atrociraptor* and *Deinonychus* were best suited to attacking relatively large prey. *Achillobator*, *Acheroraptor*, *Bambiraptor* and *Saurornitholestes* were intermediate between these extremes, and perhaps more generalist in their feeding habits.

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. BMNHC 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 "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 and Osmólska, 1999), *Tsaagan* (Norell et al., 2006) and *Linheraptor* (Xu et al., 2010), and more comparable in shape to that of *Saurornitholestes* (Currie and 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 vertebrates forming a substantial part of the diet at least, whereas an exclusively insectivorous dromaeosaurid of the same size might be expected to have longer, shallower jaws more like those of *Velociraptor*.

Predation vs 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 scansor 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., 2010b) in dromaeosaurs, and most carnivorous animals are at least facultative scavengers taking advantage of opportunities that may arise when foraging. Scavenging itself as a behaviour is underappreciated and more common than often realised (De Vault et al., 2003), and should not be dismissed as a rare behaviour or an activity only usually engaged in by specialists. The majority of mortality in some ecosystems may not be through predation, but scavengers can nevertheless consume and remove whole organisms (De Vault et al., 2003). Gut contents in vertebrate carnivores should not therefore be assumed to be the result of predation.

Although the evidence is limited, the consumption of a mammal foot could potentially be attributed to scavenging. Dromaeosaurs do appear to be capable of swallowing relatively large items (Hone et al., 2012), but the various items consumed by *Microraptor* are generally small. The mammalian pes and possible 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 did not do so. 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 with the more muscled areas already 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 bird wing as gut contents is problematic on both major points. No evidence was provided that the relationship was genuinely one of a predator-prey interaction and that that the bird was actively killed and consumed, rather than scavenged. 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). Secondly, 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 (*Acionyx 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 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 require very different specializations. 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, the lack of clear evidence to support hunting over scavenging makes it impossible to support the conclusion that *Microraptor* actively hunted fish, let alone did so proficiently. As the majority of 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, there is no strong support for attributing any of these consumption events by various *Microraptor* specimens to predation or scavenging specifically, let alone a discernible overall pattern. The variety of consumed vertebrates known to be consumed by *Microraptor* is far greater than for most theropod taxa. However, this may in fact be more typical for theropods but is rarely documented in the fossil record because few if any specimens with preserved for 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 be very unlikely to preserve. The remains of insects and arachnids sufficient to diagnose them to family levels 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 theropod pellets found in association with a theropod are for the troodontid *Anchiornis* (Zheng et al., 2018), so perhaps dromaeosaurs still had a more plesiomorphically thorough digestion and less chances of preserving any traces that were not bones or teeth. 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:

This specimen does provide clear evidence that *Microraptor* consumed mammals, at least on occasion and this is a rarely documented interaction between a theropod and Mesozoic mammal. At a wider level, on the subject of the carnivorous ecology of *Microraptor,* all that we can say with confidence is that was probably a generalist predator and at least an occasional scavenger that mostly ate small vertebrates. In this regard 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 and even consuming food items like fruit.

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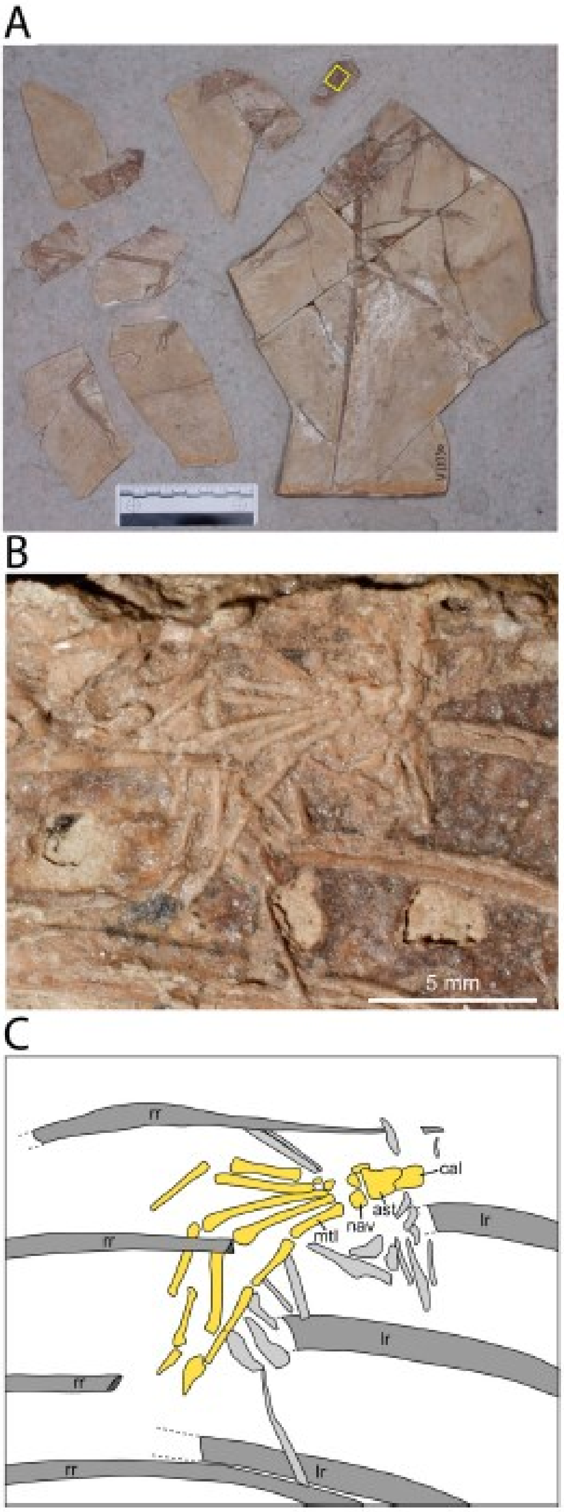
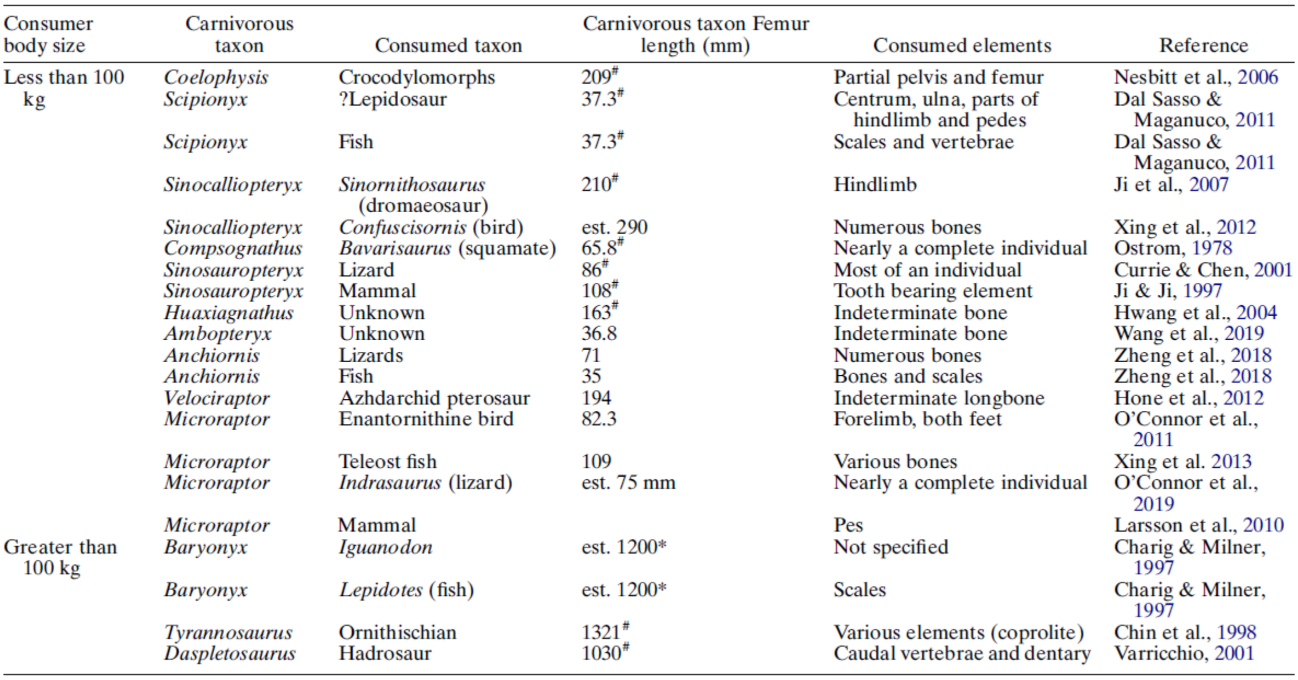


FIGURE 1. Holotype specimen of *Microraptor zhaoianus* (IVPP V 12330) with mammal foot gut contents. A, entire specimen. Box inset indicates the location of B and C. B, close-up view of mammal foot. C, illustration of visible bones: dark gray elements are *Microraptor* ribs, yellow bones are the articulated mammalian foot and

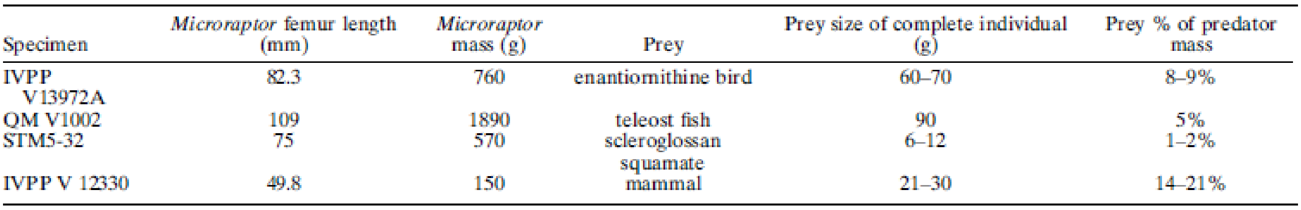
light gray are unidentified bones. Note the juxtaposition of the foot over the inside of the left ribs and the overlap of the right ribs over the foot, particularly over digits II and III. Abbreviations: ast, astragalus; cal, calcaneum; mtI, metatarsal 1; nav, navicular; lr, left rib; rr, right rib. Scale bar in A equals 100 mm and in B and C equals 5 mm.

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 #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	*Coelophysis*	Crocodylomorphs	209#	Partial pelvis and femur	Nesbitt et al., 2006
	Scipionyx	?Lepidosaur	37.3#	Centrum, ulna, parts of hindlimb and pedes	Dal Sasso & Maganuco, 2011
	Scipionyx	Fish	37.3#	Scales and vertebrae	Dal Sasso & Maganuco, 2011
	Sinocalliopteryx	*Sinornithosaurus* (dromaeosaur)	210#	Hindlimb	Ji et al., 2007
	Sinocalliopteryx	*Confuscisornis* (bird)	est. 290	Numerous bones	Xing et al., 2012
	Compsognathus	*Bavarisaurus* (squamate)	65.8#	Nearly a complete individual	Ostrom, 1978
	Sinosauropteryx	Lizard	86#	Most of an individual	Currie & Chen, 2001
	Sinosauropteryx	Mammal	108#	Tooth bearing element	Ji & Ji, 1997
	Huaxiagnathus	Unknown	163#	Indeterminate bone	Hwang et al., 2004
	Ambopteryx	Unknown	36.8	Indeterminate bone	Wang et al., 2019
	Anchiornis	Lizards	71	Numerous bones	Zheng et al., 2018
	Anchiornis	Fish	35	Bones and scales	Zheng et al., 2018
	Velociraptor	Azhdarchid pterosaur	194	Indeterminate longbone	Hone et al., 2012
	Microraptor	Enantornithine bird	82.3	Forelimb, both feet	O'Connor et al., 2011
	Microraptor	Teleost fish	109	Various bones	Xing et al. 2013
	Microraptor	*Indrasaurus* (lizard)	est. 75 mm	Nearly a complete individual	O'Connor et al., 2019
	Microraptor	Mammal		Pes	Larsson et al., 2010
Greater than 100 kg	*Baryonyx*	*Iguanodon*	est. 1200*	Not specified	Charig & Milner, 1997
	Baryonyx	*Lepidotes* (fish)	est. 1200*	Scales	Charig & Milner, 1997
	Tyrannosaurus	Ornithischian	1321#	Various elements (coprolite)	Chin et al., 1998
	Daspletosaurus	Hadrosaur	1030#	Caudal vertebrae and dentary	Varricchio, 2001

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 inQMV1002 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	*Microraptor* femur length (mm)	*Microraptor* 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%