

Current Biology

***Microraptor* with Ingested Lizard Suggests Non-specialized Digestive Function**

Highlights

- New specimen of *Microraptor* preserves a nearly complete lizard in its stomach
- The lizard is a new species, which we name after the paleoherpetologist WANG Yuan
- *Anchiornis* egested pellets, but *Microraptor* appears to have lacked this ability

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In Brief

O'Connor et al. describe a new specimen of the volant dromaeosaurid *Microraptor* with the nearly complete remains of a new species of lizard preserved in its abdominal cavity. The sum of current data suggests primitive digestive function compared to *Anchiornis* and stem birds. A preliminary food web for the Jehol is reconstructed.



Microraptor with Ingested Lizard Suggests Non-specialized Digestive Function

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SUMMARY

Direct indicators of diet and predator-prey relationships are exceedingly rare in the fossil record [1, 2]. However, it is through such traces that we can best understand trophic interactions in ancient ecosystems [3], confirm dietary inferences derived from skeletal morphologies [4], and clarify behavioral and ecological interpretations [5]. Here, we identify a previously unrecognized lizard species in the abdomen of a specimen of *Microraptor zhaoianus*, a small, volant dromaeosaurid (Paraves) with asymmetrical flight feathers on both its forelimbs and hindlimbs from the Early Cretaceous Jehol Biota [6–8]. The lizard is largely complete and articulated, confirming the current perception of *Microraptor* as an agile opportunistic predator that, like extant reptiles, including raptorial birds, ingested small prey whole and head first [9]. The lizard can be readily distinguished from previously recognized Early Cretaceous species based on its unusual widely spaced and brachydont dentition. Phylogenetic analysis suggests *Indrasaurus wangi* gen. et sp. nov. is a basal scleroglossan closely related to the slightly older *Liushusaurus* [10]. Comparison of ingested remains preserved across Paraves suggests that dromaeosaurids retained the plesiomorphic condition in which ingested prey were fully digested, rather than egested, as has been demonstrated was the case in the probable troodontid *Anchiornis* [11]. This supports a closer relationship between Aves and *Anchiornis* [12, 13] and suggests that flight did not precipitate the evolution of pellet egestion in Paraves and that the evolution of the “modern avian” digestive system in paravians was highly homoplastic [14]. A preliminary Jehol food web is reconstructed from current data.

RESULTS

Systematic Paleontology

Lepidosauria Haeckel 1866 [15]

Squamata Opper 1811 [16]

Indrasaurus wangi gen. et sp. nov.

Holotype Specimen

STM5-32 (Figures 1 and 2), partial articulated skeleton preserved in the stomach of a nearly complete and fully articulated *Microraptor*. Acquired by X-T. Zheng in 2005.

Locality and Horizon

Jianchang, Liaoning, northeastern China. Lower Cretaceous Jiufotang Formation, 120 Ma [17].

Etymology

The generic name refers to a Vedic legend in which the deity Indra was swallowed by the dragon Vritra during their battle. The species name is in honor of Yuan Wang, for his extensive work on the Chinese fossil herpetofauna and dedication to the promotion of Chinese fossils through museum exhibitions.

Diagnosis

Small scleroglossan with the following unique combination of features: maxilla with short premaxillary process and long jugal process; teeth widely spaced in the anterior dentary and maxilla; teeth brachydont and simple, formed by single cusp only slightly taller than wide; and femur at least 30% longer than the humerus (Table S1).

Ontogenetic Stage

Fusion of the neural arches to the centra and the expanded distal end of the humerus suggest the ingested lizard is not a neonate, but skeletal immaturity is suggested by the relatively poor development of the long bone epiphyses. The lizard is considered a juvenile to subadult.

Lizard Description

STM5-32 consists of a nearly complete and fully articulated *Microraptor* skeleton exposed primarily in ventrolateral view with the ingested remains of a lizard in the abdominal cavity; no feathers are preserved (Figure 1). The *Microraptor* skull is badly crushed except for the rostral halves of the dentaries, but we exclude these data because it is extremely likely the crushed skull has been manufactured and or enhanced—the morphology





Figure 1. Photograph of *Microraptor* STM5-32 Preserving the Lizard *Indrasaurus wangi* gen. et sp. nov. in the Abdominal Cavity

Boxed area indicates the area enlarged in Figure 2. See also Figures S1 and S2.

of the dentaries is inconsistent with other *Microraptor* [18, 19]. STM5-32 shows no other signs of tampering. The new specimen is identified as *Microraptor* based on the presence of a manual minor digit third phalanx that is less than half the thickness of the second phalanx of the major digit and the extreme elongation of the middle caudal vertebrae [8] (Figure S1).

The ingested lizard is largely intact and articulated (Figures 1 and 2). Similar to *Microraptor* IVPP V17992 preserving an ingested enantiornithine [9], the lizard occupies a large region of the abdomen with the feet anteriorly located in the cavity. The lizard tail is overlapped by the *Microraptor* sternum with the lizard skull located anterior to the *Microraptor* synsacrum, both overlapped by and overlying the *Microraptor* dorsal ribs. The lizard skull is nearly fully articulated and faces anteriorly. The vertebral column is folded back over the top of the skull, continuing anteriorly, partially covered by the *Microraptor* sternum, emerging from the lateral margin of the right sternal plate of the *Microraptor*, returning under it, re-emerging from under the posterior margin, and continuing posteriorly to terminate its preserved portion anterior to its rostrum (Figure 2). The thoracic ribs are closely preserved with their respective vertebrae. The left forelimb and hindlimb are exposed; the right forelimb may be covered by the skull. The position of the body suggests that the lizard was swallowed head first, consistent with feeding behavior in extant carnivorous lizards and birds.

The lizard skull has been laterally compressed with the right surface exposed (Figures 2 and S2). The premaxilla bears a moderately long nasal process. The maxilla is triangular in lateral view with a short premaxillary process and a long jugal process so that the anterior margin of the maxilla is steep (demarkating a 42.5° angle), whereas the posterior margin is gently sloped. There are two maxillary teeth attached to the ventral surface of the jugal bar. These are conical (single cusp) and widely spaced such that the diastemata exceed the mesodistal length of the individual teeth. The lateral surface of the maxilla is smooth except

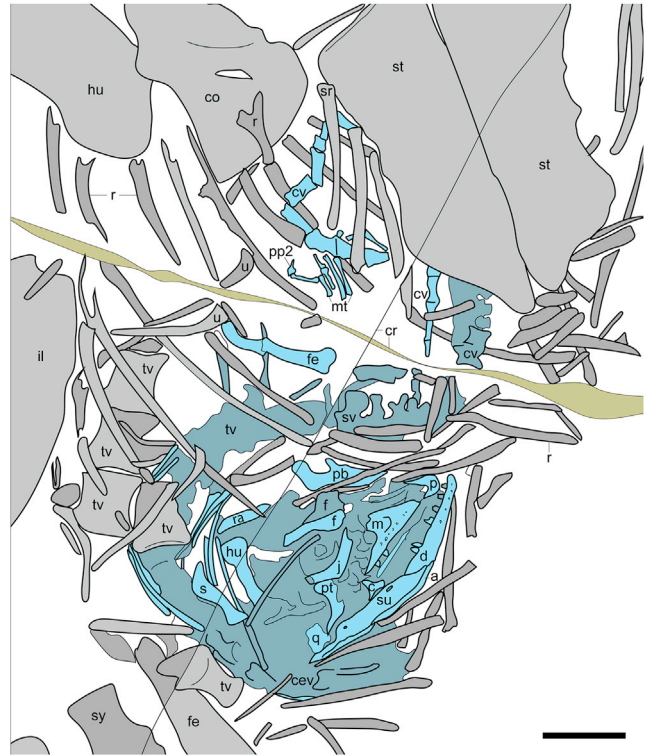


Figure 2. Interpretative Drawing of the Stomach Contents Preserved in *Microraptor* STM5-32

The skeleton of *Microraptor* is marked in gray, and the remains of the lizard *Indrasaurus wangi* gen. et sp. nov. are marked in blue; darker shades indicate poor preservation. a, angular; c, coronoid; cev, cervical vertebrae; co, coracoid; cr, cracks; cv, caudal vertebrae; d, dentary; f, frontal; fe, femur; hu, humerus; il, ilium; j, jugal; m, maxilla; mt, metatarsals; p, premaxilla; pp2, pedal phalanx digit two; pb, pubis; pt, pterygoid; q, quadrate; r, ribs; ra, radius; s, scapula; sr, sternal rib; st, sternum; su, surangular; sv, sacral vertebrae; sy, synsacrum; tv, thoracic vertebrae; u, uncinat process. Scale bar represents 1 cm. See also Figure S2 and Table S1.

where perforated by eight aligned foramina. The dorsal process of the jugal is slightly longer and narrower than the anterior process, which is perforated laterally by several foramina; the posterior process is very reduced. The frontals are paired, but only the right frontal is clearly preserved, expanded at both ends but more so posteriorly and deeply concave along the lateral margin. The pterygoid is preserved in ventral view, bearing four small teeth (Figure S2C). The posterior quadrate ramus is long, tapering, and appears to contact the quadrate. The quadrate is also in articulation with the lower jaw, but no morphological details are preserved. The right lower jaw, in lateral view, preserves the dentary, coronoid, surangular, articular, and angular in full articulation. The dentary is slender and tapers anteriorly, with six teeth preserved (Figure 2). The rostral four teeth are clearly widely spaced as in the maxilla but larger, increasing in size distally. These are all broken, missing their apices. The caudal two preserved teeth are complete and appear to be closely spaced (Figure S2). The crowns are slightly longer than wide, which is fairly brachydont compared to the much narrower and taller crowns of some other Cretaceous lizards (e.g., *Dalinghosaurus*) [20], most closely resembling the teeth of *Dorsetisaurus* [21, 22]. The

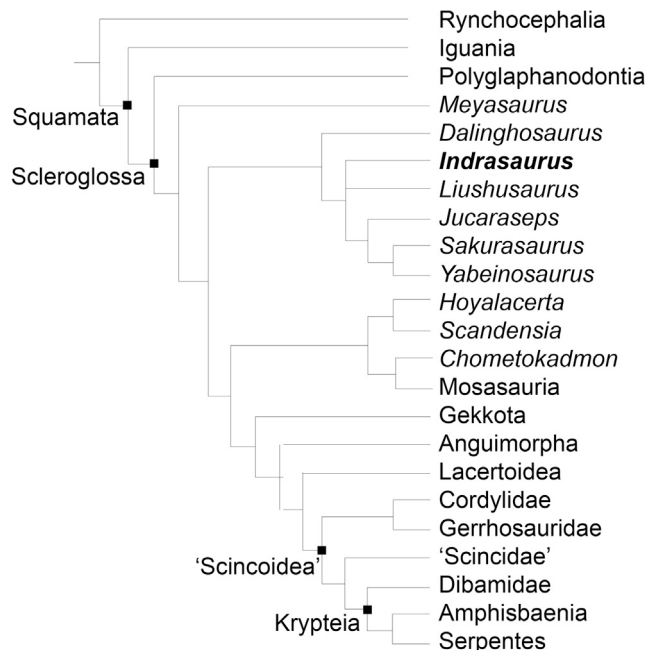


Figure 3. Simplified Results of a Cladistic Analysis Aimed at Squamate Relationships Depicting the Hypothetical Phylogenetic Position of *Indrasaurus wangi* gen. et sp. nov. Relative to Other Included Cretaceous Taxa

I. wangi is resolved as a basal scleroglossan more closely related to other Cretaceous taxa than to extant lineages. The consistency index is 0.177; the retention index is 0.784. See also [Figures S3](#) and [S4](#).

dentary increases in dorsoventral height posteriorly; the lateral surface of the rostral half is marked by five aligned foramina. The dorsal, anteromedial, and posteromedial processes of the coronoid are all well developed, but a labial process is absent. The surangular is slightly longer and more robust than the dentary as in *Liushusaurus* and *Dalinghosaurus* [10, 20]. The anterior and posterior ends are both tapered. The oval anterior surangular foramen is relatively large, dorsally located at the level of the coronoid; the posterior surangular foramen is smaller and more circular, located near level with the anterior margin of the articular facet. The angular underlies the surangular in lateral view. The retroarticular process of the articular tapers posteriorly.

The nearly complete vertebral column consists of at least 19 discernible presacral vertebrae. The anterior-most visible vertebra bears ribs, suggesting the anterior cervical series is obscured by the skull. The ribs are positioned anteroposteriorly along the vertebral column. Two sacral vertebrae can be identified from their neural spines (Figure 2). The middle of the tail is covered by the *Microraptor* sternum and distally incomplete, but based on the curvature of the exposed sections, we estimate it would have been longer than the body (shorter in *Liushusaurus* IVPP V 15508).

The left scapula is preserved in association with the left humerus and radius (Figure 2). The proximal margin of the humerus is rounded, and the distal end is expanded. Near the sacral vertebrae, there is an element tentatively identified as the left pubis. The right femur is elongate relative to the humerus, although not as elongate as in *Dalinghosaurus* [20]. Distal to the femur

part of the right foot is preserved with the phalanges of four digits. The absence of marked pitting and scarring on the bone indicates that *Microraptor* STM5-32 died shortly after consuming the lizard, before significant digestion occurred.

DISCUSSION

Microraptor STM5-32 is an exceptional specimen not only because it preserves direct evidence of trophic interactions within the Jehol Biota but because the lizard consumed by this specimen shortly before its death additionally represents a previously unrecognized species readily distinguished from other known Jehol lizards on the basis of its widely spaced and brachydont dentition. In all other Jehol lizards, the diastemata are small to non-existent (e.g., *Yabeinosaurus*, *Dalinghosaurus*, and *Liushusaurus*), whereas in *Indrasaurus wangi*, the diastemata exceed the width of the individual teeth. Preliminary phylogenetic analysis resolves *Indrasaurus* as a basal scleroglossan closely related to *Liushusaurus* from the older Yixian Formation [10] (Figure 3). This exceptional specimen increases the ecological and species diversity of Jehol squamates and contributes to our understanding of trophic interactions in the Jehol Biota (Figure 4).

This is the fourth specimen of *Microraptor* described with ingested remains preserved in the abdominal cavity, with enantiornithine birds, mammals, and fish previously documented [9, 19, 23]. The probable troodontid *Anchiornis* from the older Late Jurassic Yanliao Biota is roughly the same size as *Microraptor* and is also considered by some researchers to be volant, although it lacks asymmetrical feathers and the feathers on the hindlimb are shorter and more proximally located and thus inconsistent with feathered wings in undoubtedly volant taxa [24, 25]. Recently, one specimen of *Anchiornis* was described with an aggregate of bones belonging to more than one unidentified lizard preserved in the esophagus, interpreted as a gastric pellet prior to egestion [11]. Three additional specimens preserve pellets consisting of fish bones and scales outside the body but in close association with the skeleton, presumably egested shortly before or after death [11]. These data indicate that these two taxa had similar, unspecialized diets consistent with their overall similar skull architecture and skeletal proportions: both taxa are documented feeding on lizards and fish and are considered opportunistic predators. *Microraptor* is additionally documented feeding on mammals and birds, the latter of which are absent in the older Yanliao Biota (Figure 4).

Microraptor and *Anchiornis* are known from similar sample sizes ($n > 200$) [26], and four specimens of each taxon preserve indicators of diet. However, *Microraptor* preserves only stomach contents, whereas *Anchiornis* preserves only gastric pellets. Given the large amount of data available, we suggest this difference has significance and may be indicative of different digestive strategies in these two lineages. This discrepancy suggests that *Microraptor* did not egest gastric pellets, instead passing small bits of bone and indigestible matter, such as fur and feathers, in their excrement, as inferred for non-paravian coelurosaurs based on information from coprolites [27]. This would suggest longer gastric retention time (GRT) in *Microraptor*, consistent with the preservation of stomach contents in several specimens and the absence of such traces in *Anchiornis*. Pellet egestion

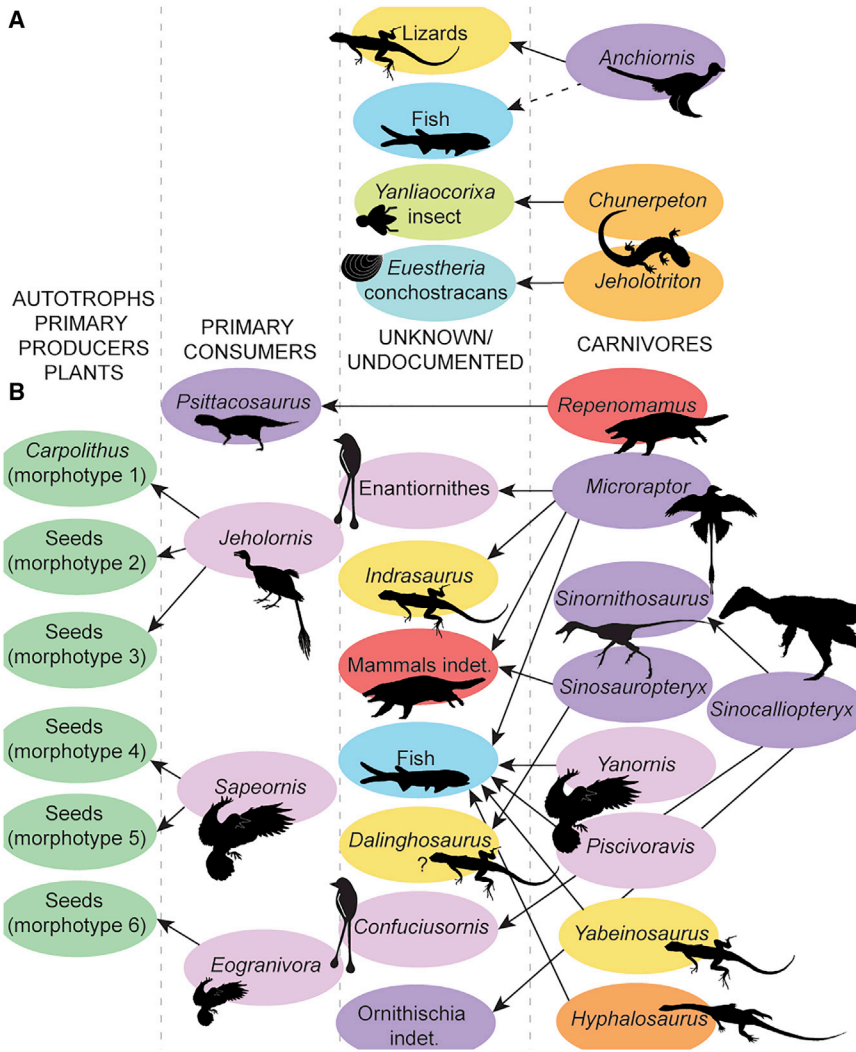


Figure 4. Preliminary Reconstruction of Food Webs in the Yanliao and Jehol Biotas Based on Direct Evidence of Ingested Remains

(A) Four trophic interactions are directly documented in the Yanliao biota.

(B) Currently 20 trophic interactions are directly documented in the Jehol biota.

Direct evidence suggests fish are the most common food source of secondary and tertiary consumers in the Jehol. Purple indicates non-avian dinosaurs; light purple indicates stem birds; red indicates mammals; yellow indicates squamates; light orange indicates salamanders; darker orange indicates choristoderes; blue indicates fish; blue-green indicates conchostracans; light green indicates insects; and darker green indicates plant material (seeds).

presumably reduces GRT and increases digestive efficiency because hard-to-digest remains, such as bones, hair, and feathers, are egested rather than digested [28]. Crocodylians completely digest bone and have documented GRT between several days and 2 weeks, depending on the conditions (temperature and meal size) [29, 30], whereas extant raptors egest pellets within 24 h of meal consumption [31]. Extant crocodylians also egest keratinous remains, but the mechanism is different from that of birds, and pellet formation is at irregular intervals [32–34]; this behavior presumably evolved independently of that in paravians. Bones are documented in the feces of primitive archosauromorphs, which suggests that the digestive strategy of extant crocodylians in which bone is completely decalcified is derived [35] and thus not a good proxy for digestive strategies in non-avian dinosaurs.

The presence of bones in gastric pellets referred to *Anchiornis* indicates a gastric pH greater than two, similar to the condition in owls [36]. In contrast, falconiform pellets contain little to no bone and have a pH less than two [37]. Reports of gastric pH in crocodylians vary from 1.2 to 3 [38, 39]. Although gastric pH overlaps with that of raptorial birds, some of which as mentioned also

completely digest bone [36, 37], the longer GRT in crocodylians [32] is probably due to their more limited gastric motility compared to birds, in which digestion is facilitated by more efficiently mixing foodstuffs with gastric juices [29, 37]. The discovery of four *Microraptor* specimens preserving stomach contents [9, 19, 23] also suggests longer GRT relative to *Anchiornis*, in which no stomach contents are known, although most certainly not as prolonged as in extant crocodylians given that the two-part stomach is inferred to be plesiomorphic to coelurosaurians [2, 11], likely increasing gastric motility in this clade. In raptors that egest pellets consisting of bone or pellets consisting mostly of fur, GRTs are roughly the same, the difference in pellet contents

being related to differences in gastric pH [37]. Without additional information from coprolites belonging to *Microraptor* or a closely related dromaeosaurid, we cannot further narrow down probable GRT in the *Microraptor* lineage.

Intuitively pellet formation can be considered beneficial to volant behavior by reducing the amount of time in which body mass is increased by ingested material [40]. It is not surprising then that the discovery of pellets in *Anchiornis* led to the hypothesis that the evolution of this behavior is flight related [11]. However, the absence of evidence for such behavior in the volant *Microraptor* weakens this hypothesis, especially in light of increasing evidence that *Anchiornis* was not volant [41] as well as the fact that a wide variety of animals have evolved to regurgitate undigestible remains, including non-volant crocodylians and sperm whales [33], in which the effect upon body mass would be negligible. Furthermore, in extant raptors, pellets are not regurgitated until shortly before the next meal [31], indicating that pellet egestion does not necessarily serve to decrease body mass during feeding as much as previously assumed. However, if GRT was relatively prolonged in coelurosaurians lacking the ability to egest pellets, the evolution of this behavior would prevent

hard-to-digest matter from multiple meals from accumulating in the stomach, as it does in extant crocodylians [30], which would presumably have numerous benefits, improving digestive health and function while also rapidly eliminating material with little to no nutritional value, so that it need not pass through the intestines. Although perhaps not directly linked to flight (similarly, many “avian” specializations are documented to have preceded the origin of this clade) [42], the evolution of gastric pellet formation and egestion may have been driven by the necessity for greater digestive efficiency imposed by increased caloric demands related to other physiological changes near the dinosaur-bird transition.

The interpretation that *Microraptor* lacked the ability to egest pellets is contradictory to what one would expect based on the most commonly recovered phylogenetic relationships for *Microraptor* and *Anchiornis* [43], which would suggest that the ability to egest pellets evolved in the common ancestor of *Anchiornis* and *Yanornis* and thus should also be present in *Microraptor* [11]. This may provide indirect support for a close relationship between birds and *Anchiornis* [12, 13]. Alternatively (and not exclusively), this may be further evidence of homoplasy in Paraves [44]. Homoplasy in the evolution of the digestive system is already suggested in stem avians [14], and evidence suggesting this homoplasy extended into non-avians is unsurprising. For example, the crop—an expansion of the esophagus capable of temporarily holding food—is present in the basal pygostylian *Sapeornis* and ornithuromorphs *Eogranivora* and *Yanornis*, all known from the Jehol Biota, but appears to be absent in the phylogenetically intermediate Enantiornithes, which are known from more specimens than *Sapeornis* and the Jehol Ornithuromorpha combined, thus making it unlikely that this absence of evidence is preservational [14]. Furthermore, despite the enormity of the available material (which far exceeds that of all other paravian clades with the exception of the Confuciusornithiformes), there exist no strong data that enantiornithines egested pellets through anti-peristalsis [14], contradicting some previous reports [35]. What has been interpreted as an egested pellet associated with one enantiornithine is better interpreted as a coprolite not belonging to the fossil bird with which it shares a slab based on comparison with gastric pellets and coprolites presumably from a range of taxa documented in numerous deposits of varying age, in which all the gastric pellets lack the ground mass that forms a majority of the purported pellet associated with the enantiornithine, but which occurs in coprolites [11, 14, 45, 46]. These data strongly suggest that evolution of the digestive system among paravians, like their skeletal evolution, was complex and highly homoplastic [44]; “modern avian” features may have evolved (and been lost) multiple times prior to and early during avian evolution, also documented in the evolution of Neornithes [47], indicating that the phenotypic flexibility of the modern avian digestive system dates back at least as far as the Late Jurassic.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
 - Specimen documentation
 - Phylogenetic analysis
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2019.06.020>.

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AUTHOR CONTRIBUTIONS

J.O., X. Zheng, L.D., Z.Z., X. Zhang, X.W., and Y.W. conducted the research. L.D. conducted the phylogenetic analysis. J.O. and L.D. wrote the manuscript. J.O. made the illustrations.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
<i>Microraptor zhaoianus</i> and <i>Indrasaurus wangi</i> STM5-32	This paper	This paper
Software and Algorithms		
TNT	[48]	https://cladistics.org/tnt/
ImageJ	[49]	https://imagej.nih.gov/ij/

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Jingmai O'Connor (jingmai@ivpp.ac.cn; jingmai.oconnor@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The study subject, STM5-32, consists of a nearly complete, fully articulated specimen of *Microraptor zhaoianus* with a partially articulated skeleton of a lizard (*Indrasaurus wangi* gen. et sp. nov.) in the abdominal cavity. The specimen was collected in deposits of the Lower Cretaceous Jiufotang Formation (120 Ma) near Jianchang in Liaoning Province, northeastern China, and was acquired by X-T. Zheng for the Shandong Tianyu Museum of Nature (Pingyi, China) in 2005.

METHOD DETAILS

Specimen documentation

The specimen STM5-32 was studied using a Leica binocular microscope and photographed using Canon EOS 5DS. Measurements were taken from the photographs using Fiji (ImageJ 2.0) [49]. Figures were created using Adobe Photoshop and Illustrator.

Phylogenetic analysis

The new lizard preserved in *Microraptor* STM5-32, *Indrasaurus wangi*, was analyzed using a modified version of the Gauthier et al. [50] data matrix (Data S1). As published this matrix contains very few Early Cretaceous lizards. We therefore added the following well-preserved Early Cretaceous genera to the matrix (unpublished data): the Chinese *Yabeinosaurus* [51, 52], *Dalinghosaurus* [20, 53], and *Liushusaurus* [10], all from the Jehol Biota; the Japanese *Sakurasaurus* [54, 55]; the Early Cretaceous Spanish *Jucaraseps* [56], *Hoyalacerta* [57], *Meyasaurus* [58], and *Scandensia* [59, 60]; and the Early Cretaceous Italian *Chometokadmon* [61]. The modified matrix consists of a total of 203 taxa scored across 610 characters. Only 61 characters could be scored for the new lizard “*Indrasaurus*” (90% missing data). Some characters were treated as ordered following Gauthier et al. [50]. We added the Early Jurassic rhynchocephalian *Gephyrosaurus* to the outgroup, rather than relying only the more derived living taxon, *Sphenodon* (as used by Gauthier et al. [50]).

The data was analyzed using TNT v 1.5 [48] using the New Technology search with Ratchet (20 iterations), and 1000 replicates in the RAM (default parameters for other variables). In the strict consensus tree (Figure S3) there was little resolution between the major clades, which were well resolved within themselves, with Squamata consisted of a polytomy including all newly added Cretaceous taxa and major clades (e.g., Scincomorpha, Anguimorpha). We reran the matrix using implied weighting and molecular constraints, both of which increased resolution. Implied weighting is demonstrated to increase resolution in large datasets with high homoplasy [62], therefore we chose to use these results as a rough estimate of the phylogenetic position of this new taxon. The resultant relationships changed only slightly with varying k values – in all analyses “*Indrasaurus*” is resolved as closely related to other Early Cretaceous taxa. The presented tree represents the results of the data when analyzed with a k value of 12 (Figures 3 and S4). The new taxon forms a clade consisting entirely of Cretaceous taxa including other Jehol lizards (*Liushusaurus*, *Dalinghosaurus*, *Yabeinosaurus*), *Jucaraseps*, and *Sakurasaurus*. On a higher clade level, the resultant relationships are somewhat different from those of Gauthier et al. [50] which is most likely due to the addition of these ten Cretaceous taxa. In general, squamate relationships are currently not very stable between available datasets [50, 63]. The addition of new taxa can greatly change resultant relationships. This is particularly an issue with the addition of incomplete fossil taxa, such as the new specimen studied here.

The results of the analysis with implied weighting k = 12 (Figure S4) are somewhat problematic in that several well-established clades (e.g., Scincoidae and Scincidae) are not recovered although the analysis [presented here] does resolve a partial Scincidae with other taxa typically included in Scincidae instead forming successive outgroups or ingroups (Figure S4). Similar results are

produced using implied weighting with lower k values ($k = 3$). In the strict consensus tree (using *a priori* weights) the analysis recovered the Scincoidea and the Scincidae but with no resolution between Early Cretaceous fossil taxa and major squamate lineages (Figure S3). We also ran the new taxon in the original Gauthier et al. [50] matrix, modified only to include the new taxon; using implied weighting $k = 12$ the new taxon was resolved as a basal most squamate, similar to the results in the *a priori* weighted analysis using the expanded matrix presented here (Figure S3), and clades such as the Scincidae were recovered. This suggests that addition of other Early Cretaceous taxa (e.g., *Meyasaurus*, *Sakurasaurus*) are affecting Scincidae relationships.

Phylogenetic relationships in fossil squamates are difficult to determine with currently available matrices [50]. The Reeder et al. [63] matrix, which is primarily based on the Gauthier et al. [50] dataset but also includes molecular data, analyzed using parsimony, likelihood and Bayesian analysis, recovered topologies also quite different from that of Gauthier et al. [50]. Given the uncertainty regarding squamate relationships at this time, we do not find it unusual that our results add to the current disparity. The purpose of the analysis presented here is not to discuss the relationships between major squamate lineages, but rather to make some hypothesis regarding the position of the new taxon relative to previously described Early Cretaceous taxa. In most analyses of the expanded matrix used here the results resolve most of the ten included Early Cretaceous taxa close together which suggests they may be part of an extinct clade, or at least more closely related to each other than they are to extant species.

DATA AND CODE AVAILABILITY

The holotype specimen of *Indrasaurus wangi* is deposited in the Shandong Tianyu Museum of Nature (Pingyi, China) under the collection number STM5-32.