Large Mesozoic mammals fed on young dinosaurs

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Mesozoic mammals are commonly portrayed as shrew- or rat-sized animals that were mainly insectivorous, probably nocturnal and lived in the shadow of dinosaurs[1–5]. The largest known Mesozoic mammal represented by substantially complete remains is *Repenomamus robustus*, a triconodont mammal from the Lower Cretaceous of Liaoning, China[6,7]. An adult individual of *R. robustus* was the size of a Virginia opossum. Here we report a new species of the genus, represented by a skeleton with most of the skull and postcranium preserved in articulation. The new species is 50% larger than *R. robustus* in skull length. In addition, stomach contents associated with a skeleton of *R. robustus* reveal remains of a juvenile *Psittacosaurus*, a ceratopsian dinosaur. Our discoveries constitute the first direct evidence that some triconodont mammals were carnivorous and fed on small vertebrates, including young dinosaurs, and also show that Mesozoic mammals had a much greater range of body sizes than previously known. We suggest that Mesozoic mammals occupied diverse niches and that some large mammals probably competed with dinosaurs for food and territory.

The Early Cretaceous Jehol Biota from the Yixian Formation in Liaoning, China, has yielded several mammal species[8]. Two of them, *Repenomamus robustus*[6] and *Gobiconodon zofiae*[9], are from the basal member of the formation that has a radiometric date older than 128 and younger than 139 million years[8,10]. The fossil-bearing tuffs of this member are structureless and have preserved numerous articulated, three-dimensional skeletons of vertebrates, suggesting "a single, catastrophic, mass mortality event"[8] probably induced by volcanic activities. Fossils from the tuffs include frogs, squamates, dinosaurs, mammals[8,11] and the new specimens reported here.

Mammalia Linnaeus, 1758
Triconodonta Osborn, 1888
Repenomamidae Li, Wang, Wang & Li, 2000
Repenomamus Li, Wang, Wang & Li, 2000
Repenomamus giganticus sp. nov.

Etymology. *Giganticus* from Greek *gigantikos*, referring to the large size of the new species among Mesozoic mammals.
Holotype. A partial skull with complete right upper dentition, associated right mandible with complete lower dentition, and articulated postcranium with pes and manus missing, IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V14155 (Figs 1 and 2).
**Locality and horizon.** Liaoning, China, the basal member of Yixian Formation at Lujiatun village (N 41°36.201′; E120°54.793′), Early Cretaceous.
Diagnosis. Dental formula 3.1.2.4/2.1.2.5 (incisors, canine, premolariforms, molariforms in upper/lower jaws), differing from *R. robustus* in being 50% larger in skull length and having proportionally larger incisors, double-rooted upper canine, first upper premolariform much smaller than upper canine, upper molariforms with complete lingual cingulum and partial labial cingulum, shallower pits on the palate for accommodations of lower molari-

forms, proportionally deeper mandibular symphysis, more robust mandible, less widely spaced incisors, canine and premolariforms, and larger cusps c and d on lower molariforms.

The entire body of IVPP V14155 is more than one metre in length (skull, 160 mm; trunk, 522 mm; preserved tail, 364 mm), comparable to that of a large Tasmanian devil[12]. The head–body is 60% longer than that of *R. robustus*. The skull of *R. giganticus* has a stronger sagittal crest, lambdoid crest, and zygomatic arch compared to *R. robustus* (Fig. 1). The stout dentary of *R. giganticus* has an obliquely oriented symphysis, a broad coronoid process and a deep masseteric fossa. The upper and lower incisors are the strongest teeth in the upper and lower tooth rows, respectively. The upper canine is situated at the premaxilla-maxillary suture and is similar in shape to the incisors. The premolariforms are simple with pointed tip. The molariforms have blunt crowns, bear wear facets on cusps, and decrease in size posteriorly.

Judging from its size, the eruption of all cheek teeth and the extensive wear on most teeth, this specimen represents an adult
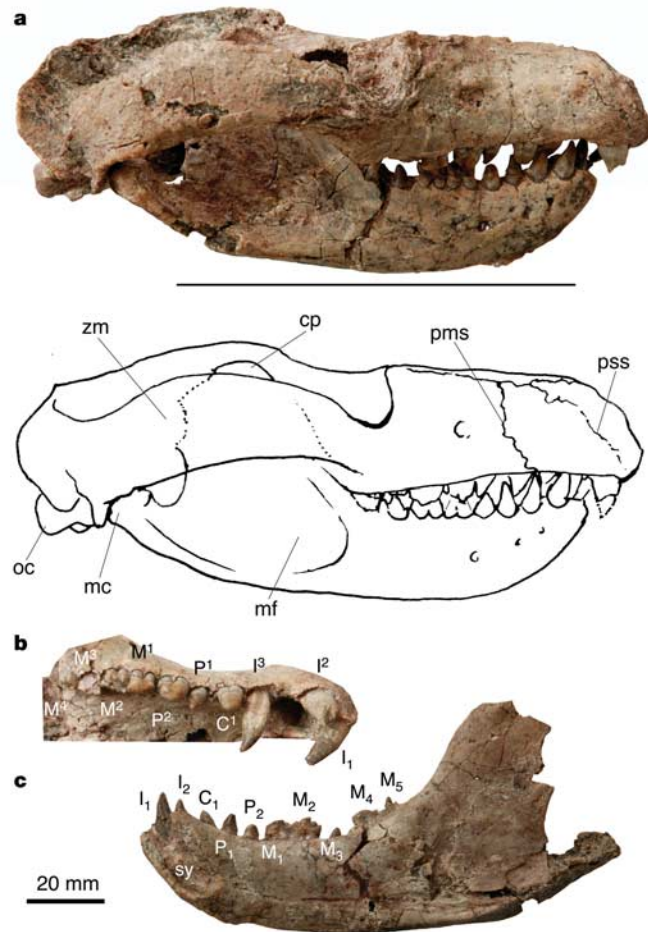
Figure 1 Holotype of *Repenomamus giganticus* (IVPP V14155). **a**, Lateral view of the skull and associated lower jaw. For comparison, the line in (**a**) indicates the skull length of *R. robustus*. **b**, Ventral view of the right upper dentition. **c**, Medial view of the right mandible. cp, coronoid process; mc, mandibular condyle; mf, masseteric fossa; oc, occipital condyle; pms, premaxilla-maxillary suture; pss, premaxilla-septomaxillary suture; sy, symphysis; zm, zygomatic arch; $I^{1–3}$ and $I_{1,2}$, upper and lower incisors; C^1 and C_1, upper and lower canine; $P^{1,2}$ and $P_{1,2}$, upper and lower premolariforms; $M^{1–4}$ and $M_{1–5}$, upper and lower molariforms. Measurements of teeth (length/width in mm): I^1, 6.9/4.3; I^2, 8.0/4.6; I^3, 6.4/4.2; C^1, 6.2/4.2; P^1 (erupting), 5.0/3.7; P^2, 7.0/4.6; M^1, 6.4/4.8; M^2, 6.3/5.7; M^3, 5.8/5.3; M^4, 5.6/4.8; I_1 (erupting), 4.6/4.6; I_2, 5.3/4.3; C_1, 4.6/4.3; P_1, 4.5/4.7; P_2, 4.4 /4.2; M_1, 7.5/4.7; M_2, 8.3/5.0; M_3 (erupting), 8.0/?; M_4, 7.5/4.8; M_5, 6.1/4.2.
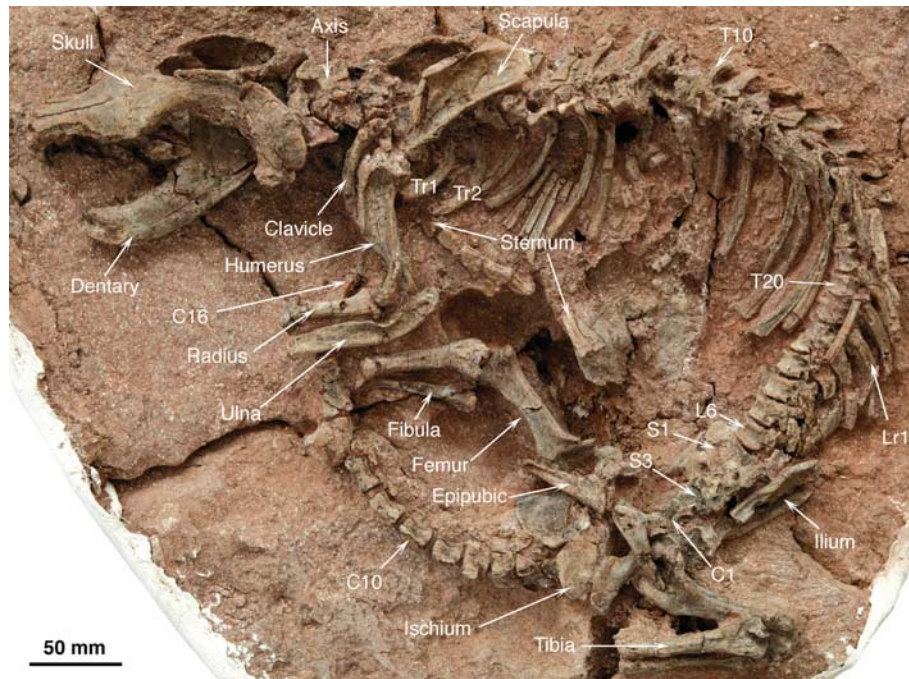
Figure 2 The holotype skeleton of *Repenomamus giganticus* (IVPP V14155). C1, C10, and C16: first, tenth and sixteenth caudal vertebrae; Lr1, first lumbar rib; L6, sixth lumbar vertebra; Tr1 and Tr2: first and second thoracic ribs; S1 and S3: first and third sacral vertebrae; T10 and T20: tenth and twentieth thoracic vertebrae.
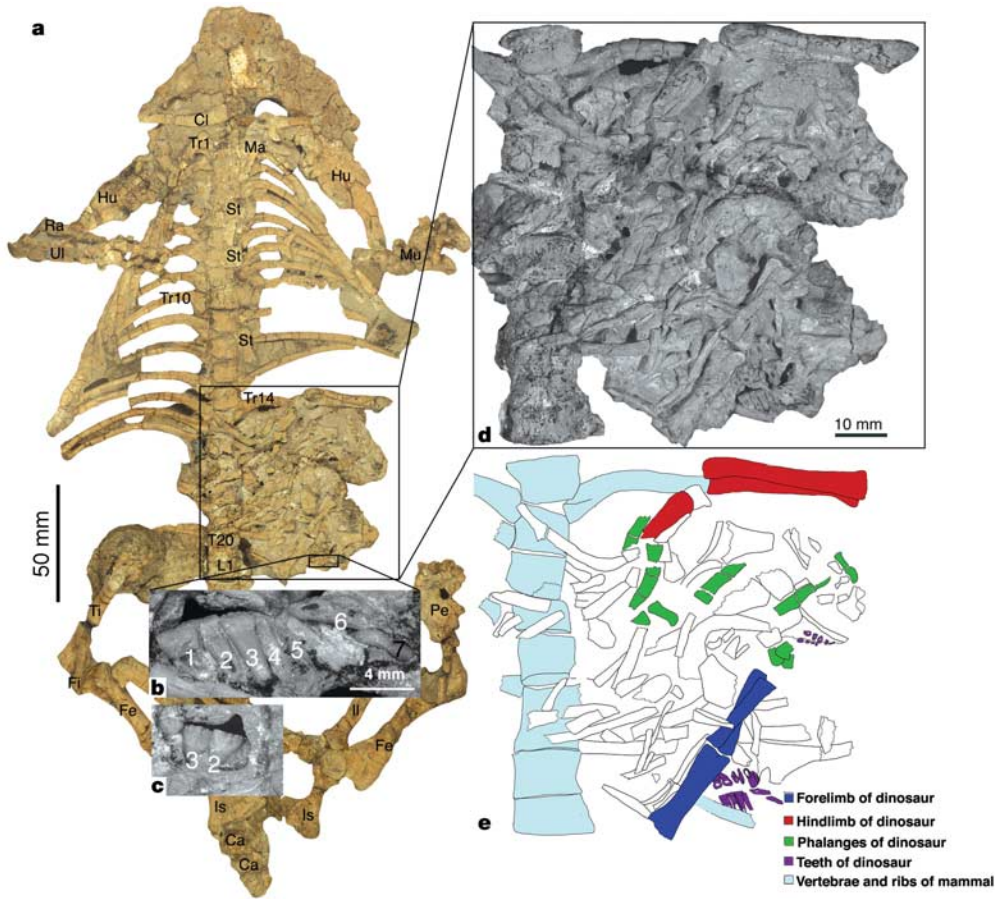
Figure 3 The postcranial skeleton of *R. robustus* (IVPP V13605). **a**, Ventral view of the skeleton and its stomach content. Associated partial skull and lower jaws not illustrated. **b**, Buccal view of lower teeth of the juvenile *Psittacosaurus*. **c**, Lingual view of two lower teeth of the juvenile *Psittacosaurus*. **d**, **e**, Close-up view of the stomach content (**d**) with identified elements highlighted in colour (**e**). Ca, caudal vertebra; Cl, clavicle; Fe, femur; Fi, fibula; Hu, humerus; Il, ilium; Is, ischium; L1, first lumbar vertebra; Ma, manubrium; Mu, manus; Pe, pes; Ra, radius; St, sternum; T20, twentieth thoracic vertebra; Ti, tibia; Tr1, Tr10, Tr14, first, tenth and fourteenth thoracic ribs; Ul, ulna. Measurements of the juvenile *Psittacosaurus* (length in mm): humerus, 21; radius, 18; ulna, 19; tibia, 36; and fibula, 35. See Supplementary Information for more detail.

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individual. However, it is not an old individual because the last lower molariform (M_5) has just erupted, bears no wear and is located at the anterior base of the coronoid process in a position higher than the other cheek teeth (Fig. 1c). When compared to adult specimens of *R. robustus* where all cheek teeth have erupted and are deeply worn[7], V14155 seems to represent a relatively younger individual that has a much larger body size. As in some specimens of *R. robustus*, the third lower molariform (M_3) has partially erupted. The open alveolus indicates that the erupting M_3 probably belongs to a generation younger than other erupted molariforms. The similar sizes of the erupting M_3 and its neighbouring teeth indicate that, as is typical in mammals, a replacement cheek tooth is not significantly larger than its precursor. In addition, the epiphysis and shaft of long bones are fused in IVPP V14155 and

Figure 4 Relationship between basal mammals with attached lower jaws to show their relative sizes (adopted from ref. 7). All jaws are shown on the same scale. *Lambdopsalis, Ornithorhynchus* and *Didelphis* are Cenozoic taxa (jaw shown in outline), others are Mesozoic taxa (jaw shown in solid black). Tritylodontids are a sister group of Mammaliaformes, represented by *Bienotherium* (black jaw) and an undescribed specimen of *Yunanodon* (small white jaw within *Bienotherium* jaw). The lower jaw of *R. giganticus* is shown in black and that of *R. robustus* is inset in white. See Supplementary Information for sources of sizes of lower jaws.
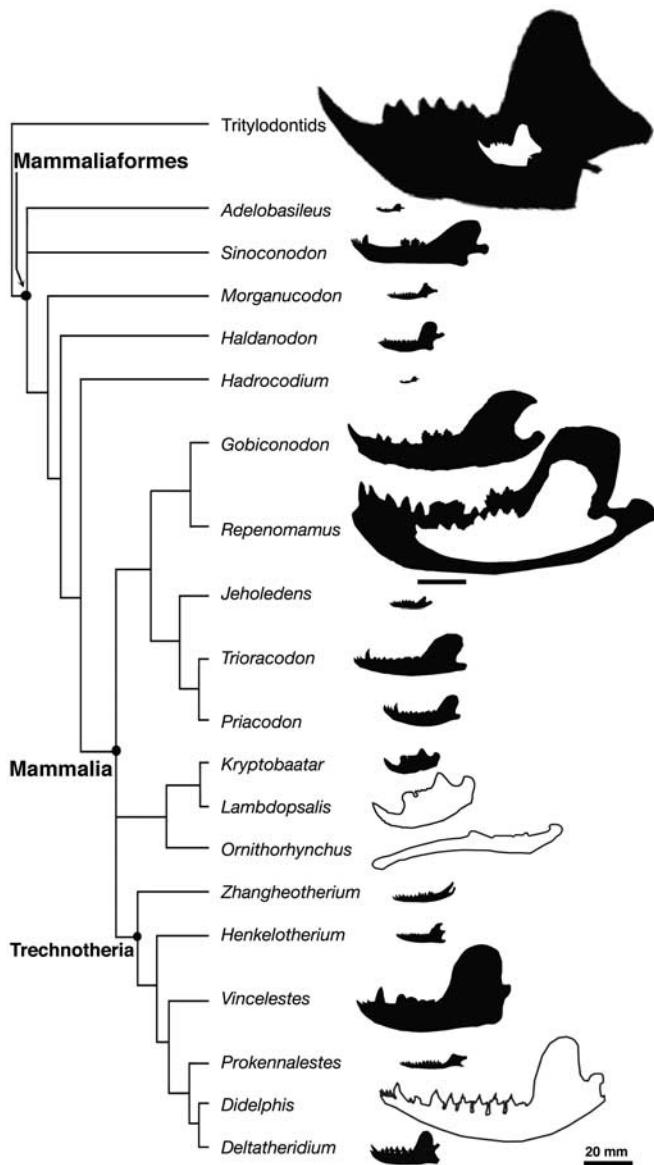
in the *R. robustus* skeleton described below (Fig. 3). These suggest that the growth of *Repenomamus* was determinate, not continual, during ontogeny. In addition to the diagnostic features for the new species, the significant differences in body size and estimated body mass (see below) between V14155 and *R. robustus* exceed those between dimorphic sexes of a species in most extant terrestrial mammals[12,13].

In both species of *Repenomamus*, the lumbar and thoracic vertebrae are well differentiated. The scapula has a large spine and a ventrally faced glenoid fossa. The head of the humerus is semispherical, reflects posterodorsally and twists at an angle of about 25° in relation to the distal end. The femoral head offsets from the shaft dorsomedially and reflects anteriorly. The medial condyle of the distal femur is narrower and deeper than the lateral one, with both pointing posteroventrally. The plantigrade pes and manus of *R. robustus* are short and broad. These features collectively suggest that the limb excursion of *Repenomamus* is more similar to those of non-cursorial therian mammals than to those of monotremes[14]. The large ulnar olecranon and posteroventrally directed femoral condyles allow a semi-erect posture, as in the majority of small- to medium-sized extant therian mammals[15]. *Repenomamus* differs from therian mammals in having a relatively longer trunk and shorter, more robust limbs (see Supplementary Information).

Although most Mesozoic mammals were small, relatively large mammals and close relatives did exist, but these are mostly represented by fragmentary material[16–19]. *Repenomamus* are unquestionably the largest known Mesozoic mammals represented by substantially complete remains. Using empirical regression equations derived from data of extant mammals[20,21], we estimate the body mass to be 12–14 kg for *R. giganticus* and 4–6 kg for *R. robustus* (see Supplementary Information).

An animal the size of *Repenomamus*, equipped with strong and pointed anterior teeth, would probably have been carnivorous. The new skeleton of *R. robustus* (Fig. 3) lends support to this hypothesis. During preparation of the specimen a patch of small bones was revealed within the ribcage, on the ventral sides of the posterior left thoracic ribs and vertebrae, where the stomach is positioned in extant mammals (Fig. 3). Unduplicated dentitions, limb bones and phalanges in the patch confirm that these bones belong to a juvenile individual of *Psittacosaurus*, an herbivorous dinosaur that is common in the Jehol Biota. The serrated teeth in the patched skeleton (Fig. 3) are typical of juvenile *Psittacosaurus*[22] (see also Supplementary Information). The skull and most of the skeleton of the juvenile *Psittacosaurus* are broken, disarticulated and displaced, in contrast to the preservation of the *R. robustus* skeleton, which is essentially in its original anatomical relation. Although fragmentary, the bones of the *Psittacosaurus* are packed in a restricted area. These conditions indicate that the juvenile skeleton of *Psittacosaurus* is the remaining stomach content of the mammal. The head–body length of the juvenile *Psittacosaurus* is estimated to be 140 mm, about one-third of the head–body length of the *R. robustus* (see Supplementary Information). There are at least seven teeth on each jaw quadrant of the juvenile *Psittacosaurus*, of which most are worn. This demonstrates that the *Psittacosaurus* skeleton is not from an embryo. A few long bones are preserved in articulation (Fig. 3), suggesting that the juvenile *Psittacosaurus* was dismembered and swallowed as chunks.

In addition to its stomach content, other features of *Repenomamus* also indicate that it was a carnivore. The dentition of *Repenomamus* is suitable for meat-eating, although invertebrates and vegetable items could also be part of its diet, as is the case for some extant carnivores[23]. The large and pointed incisors and similarly shaped canines and premolariforms form an apparatus for catching, holding and ripping prey. This apparatus is powered by strong jaw musculature, as evidenced by the robust dentary and zygoma, large temporal fossa and deep masseteric fossa. Large pointed anterior teeth accompanied by small posterior teeth

characterize many carnivorous non-mammalian synapsids[24]. The molariform teeth at the back of the dentition of *Repenomamus* are small with blunt crowns; they probably played a minor role in food processing. Although mammals are considered definitive chewers within amniotes[25], the dental morphology and large pieces of prey in the stomach of *Repenomamus* suggest that chewing as a derived feature in mammals was probably not present in *Repenomamus*.

It is not easy to assess whether *Repenomamus* was a predator or scavenger. Scavengers are relatively rare among mammals—among extant carnivorous mammals, only two species of hyenas are habitual scavengers[12,26]. Compared to their hunting cousins, these hyenas have smaller second upper incisors and less jaw muscle leverage, which probably reflect their inability to capture and handle live prey. In contrast, the enlarged incisors and strong jaw muscles of *Repenomamus* are well shaped for catching prey, favouring it as a predator rather than a scavenger.

For fossil mammals, body size is one of the most important factors influencing life history strategy[27]. Early mammals or their close relatives, such as morganocodontids and kuehneotheriids in the Late Triassic to Early Jurassic periods, were small and considered to be nocturnal insectivores[2,3]; the same is true of most later Mesozoic mammals[28] (Fig. 4). The reason for the very small size of Mesozoic mammals is uncertain[5], but it has often been hypothesized that well-established larger (and presumably diurnal) reptilian carnivores and herbivores, particularly dinosaurs, prevented mammals from invading those niches[29]. *Repenomamus* extend significantly the upper limit of body size of Mesozoic mammals (Fig. 4) and are actually larger than several small dinosaurs, particularly dromaeosaurid dinosaurs, from the same fauna[11]. Larger animals can live longer and move faster, but they also need a larger food supply and broader home range[30]. Judging from their body size, *R. giganticus* could feed on larger prey and forage a wider area for food. These large Mesozoic mammals were probably carnivores that competed with dinosaurs for food and territory. □

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The simplicity of metazoan cell lineages

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Developmental processes are thought to be highly complex, but there have been few attempts to measure and compare such complexity across different groups of organisms[1–5]. Here we introduce a measure of biological complexity based on the similarity between developmental and computer programs[6–9]. We define the algorithmic complexity of a cell lineage as the length of the shortest description of the lineage based on its constituent sublineages[9–13]. We then use this measure to estimate the complexity of the embryonic lineages of four metazoan species from two different phyla. We find that these cell lineages are significantly simpler than would be expected by chance. Furthermore, evolutionary simulations show that the complexity of the embryonic lineages surveyed is near that of the simplest lineages evolvable, assuming strong developmental constraints on the spatial positions of cells and stabilizing selection on cell number. We propose that selection for decreased complexity has played a major role in moulding metazoan cell lineages.

Biological systems are obviously complex in both structure and