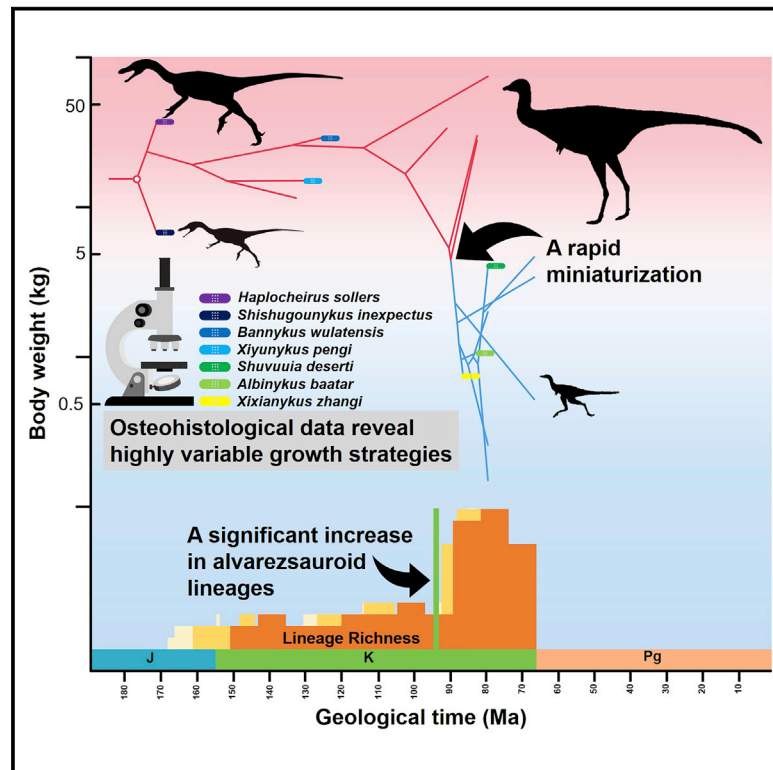


Current Biology

Growth and miniaturization among alvarezsauroid dinosaurs

Graphical abstract



Authors

Zichuan Qin, Qi Zhao,
Jonah N. Choiniere, James M. Clark,
Michael J. Benton, Xing Xu

Correspondence

xu.xing@ivpp.ac.cn

In brief

Qin et al. report their broadly sampled osteohistological analyses and quantitative body size macroevolution reconstruction for a bizarre theropod dinosaur group, the Alvarezsauroidea. Highly variable growth strategies and quick miniaturization are found in alvarezsauroids, possibly associated with a dietary switch to feeding on social insects.

Highlights

- How and why the bizarre alvarezsauroid dinosaurs miniaturized is poorly known
- We reveal a rapid Late Cretaceous alvarezsauroid miniaturization and radiation
- Osteohistological data show highly variable growth strategies among alvarezsauroids
- Alvarezsauroid miniaturization is possibly associated with adaptations to digging



Report

Growth and miniaturization among alvarezsauroid dinosaurs

Zichuan Qin,¹ Qi Zhao,^{2,3} Jonah N. Choiniere,⁴ James M. Clark,⁵ Michael J. Benton,¹ and Xing Xu^{2,3,6,*}¹School of Earth Sciences, Life Sciences Building, University of Bristol, Tyndall Avenue, Bristol BS8 1TQ, UK²Key Laboratory for the Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China³CAS Center of Excellence in Life and Paleoenvironment, Beijing 100044, China⁴Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa⁵Department of Biological Sciences, George Washington University, Washington, DC, USA⁶Lead contact*Correspondence: xu.xing@ivpp.ac.cn<https://doi.org/10.1016/j.cub.2021.06.013>

SUMMARY

Sustained miniaturization, here defined as a drop in body size of at least two orders of magnitude from ancestors to descendants, is a widespread and important phenomenon in animals,^{1–3} but among dinosaurs, miniaturization occurred only rarely, once in the lineage leading to birds and once in the Alvarezsauroidae,^{1,3–5} one of the most bizarre theropod groups.^{1,5–7} Miniaturization and powered flight are intimately linked in avialan theropods,^{3,5,6,8–11} but the causes and patterns of body size reduction are less clear in the non-avian Alvarezsauroidae.^{1,5,6,12,13} Here, we present results from analyses on a comprehensive dataset, which not only includes new data from early-branching alvarezsauroids but also considers the ontogenetic effect based on histological data. Our analyses show that alvarezsauroid body mass underwent rapid miniaturization from around 110 to 85 mya and that there was a phylogenetic radiation of small-sized alvarezsauroids in the Late Cretaceous. Our analyses also indicate that growth strategies were highly variable among alvarezsauroids, with significant differences among extremely small taxa. The suggested alvarezsauroid miniaturization and associated phylogenetic radiation are coincident with the emergence of ants and termites, and combining previous functional morphological data, our study suggests that alvarezsauroid miniaturization might have been driven by ecological changes during the Cretaceous Terrestrial Revolution, more specifically by a shift to the myrmecophilous ecological niche.

RESULTS

Ontogenetic ages and growth rates

Osteohistological analysis (Figure 1) shows that the holotypes of *Shishugouonykus inexpectus*, *Xixiyanikus zhangii*, and *Albinykus baatar* are adults and, thus, that their body masses accurately reflect skeletally mature individuals. This assessment is supported by the presence of an external fundamental system (EFS) (tightly packed growth lines indicative of substantial truncation in growth), as well as by avascular lamellar-zonal bone. The holotypes of *Xiyunykus pengi* and *Bannykus wulatensis* are subadults, lacking an EFS, but have a thinner outer annulus with lower porosity and intense secondary remodeling close to the endosseous surface.¹⁴ The holotype of *Haplocheirus sollers* and a specimen of *Shuvuuia deserti* are juveniles,¹⁵ without any evidence supporting an advanced ontogenetic stage, and the holotype of *Aorun zhaoui* is even younger, being likely a hatchling.¹⁶

The two smallest and most closely related alvarezsauroids in our dataset, *Xixiyanikus zhangii* and *Albinykus baatar*,^{12,17} exhibit markedly different life histories (Figure 2) but very similar body sizes. In bone thin sections, the holotype of *Xixiyanikus zhangii*

shows seven growth marks with at least four more eroded, which indicate an age at death of 11, over three times as old as the holotype of *Albinykus baatar*. But they are both at advanced ontogenetic stages, supported both by osteohistological characters (EFS structure in *Xixiyanikus zhangii* and outer avascular lamellar-zonal bone in *Albinykus baatar*) and a distinct decline in porosity (Figure 2; Table S1). The first annual record of *Albinykus baatar* shows a higher porosity than all other annual records from *Xixiyanikus zhangii*, but the last two records have similar porosity to *Xixiyanikus zhangii*.

When comparing larger and smaller alvarezsauroids, vascular complexity simplifies (circumferential to reticular to longitudinal) and randomness in bone-fiber orientation diminishes (fibrolamellar bone dominates in the form of observed parallel-fibered bone) in smaller forms, as reported in other theropods.¹⁸ In reviewing all specimens, age and size are not correlated. The number of lines of arrested growth (LAGs) found in osteohistological sections depends more on the ontogenetic age than the size of specimens. For example, the largest alvarezsauroid for which we considered osteohistological data, *Haplocheirus sollers*, has four LAGs in femoral slices and complex circumferential vascular canals and fibrolamellar bone, suggesting a young



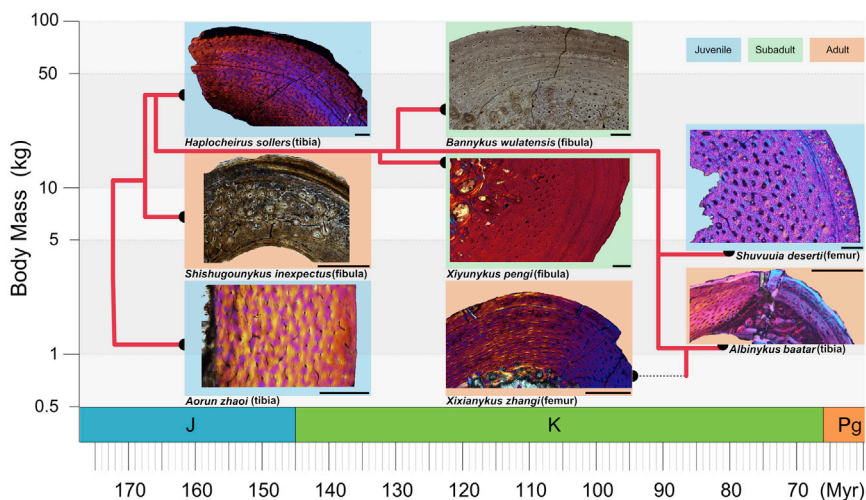


Figure 1. Cladogram of alvarezsauroids showing the osteohistological slices with respect to geological time and body mass

Juvenile specimens are colored as blue, subadult specimens are colored as green, and adult specimens are colored as orange. Scale bars, 500 μm . See also Figures S1 and S2.

ontogenetic stage and rapid growth rate. In contrast, the smallest alvarezsauroids, *Xixianykus zhangii* and *Albinykus baatar*, provide inconsistent counts of growth marks, but both have a simple cortex dominated by longitudinal vascular canals, supporting consistent slow growth rates compared to their large relatives (Figure 2).

Our morphology-based estimates of ontogenetic stages are generally consistent with our osteohistological inferences (Table 1). In cases where the osteohistological and morphological evidence are inconsistent, where possible, we chose the histological age assessment, because the status of the morphological characters could reflect phylogeny (e.g., heterochrony) as much as ontogeny. Correcting mass estimates for ontogenetic stage greatly changes the inferred pattern of body size evolution in alvarezsauroids.

Body size evolution

We use the mass dataset excluding juveniles (details in STAR Methods) to reconstruct body size evolution of alvarezsauroids. During the first 70 Ma of alvarezsauroid evolution (Figure 3A), body masses range between 10 kg and 50 kg with one exception, the 72 kg *Bonapartenykus ultimus*. Alvarezsauroids initially had divergent body masses, with some penecontemporaneous early-branching members weighing less than 10 kg (like *Shishugouonykus inexpectus*) and others weighing nearly 50 kg (like *Haplocheirus sollers*). The inferred ancestral body mass of alvarezsauroids is around 23 kg. From 110 to 85 Ma (Albian to Santonian), mean body size along the alvarezsauroid stem plunged rapidly to a very small mean body mass of <5 kg. Some of these miniaturized alvarezsauroids are in fact among the smallest non-avian dinosaurs known, weighing <0.5 kg (Figure 3A).

Of the evolutionary models we tested (details in STAR Methods), the Ornstein-Uhlenbeck model is preferred, with lowest AICc score of 46.580, an AICc weight of 0.744, and $p = 0.012$ when compared to the next-best-fit model, the Brownian motion model. Our test for rate heterogeneity of body size as a trait on our phylogenetic tree suggested no distinct rate shift (Figure S3). Palaeodiversity time series analysis using our preferred topologies (Figure 3B) shows a low and consistent

diversity range during the early evolution of alvarezsauroids, followed by a tripling of diversity at around 90 Ma, between the Turonian and Coniacian (Figures 3B and S3).

We also tested the same analyses on the unpruned raw mass data and compared results from both datasets. With juvenile specimens included, there was a substantial underestimation of the

ancestral size of Alvarezsauroida (8 kg versus 23 kg for the corrected dataset) but only minor effects on the estimations of late-branching nodes (Figure S4).

DISCUSSION

Our osteohistological data show that some tiny alvarezsauroids (<1 kg) were somatically mature and support their status as among the smallest known non-avian dinosaurs. Differing life histories are found in the closely related, fully adult alvarezsauroids *Xixianykus zhangii* and *Albinykus baatar*.^{12,17} This suggests two different growth paths toward similar tiny body sizes, where *Albinykus baatar* grows faster but with a short lifespan and *Xixianykus zhangii* shows greater longevity but a very slow overall growth rate, even in its juvenile period. Interestingly, giant theropods with similar body sizes but different life-history parameters were also reported recently,¹⁹ suggesting divergent growth strategies might have been widespread among similarly sized theropods. In sum, our osteohistological comparisons among alvarezsauroids suggest that the main factor producing size variance among alvarezsauroids is annual growth rate rather than longevity, and different miniaturized species also grow at different rates.

Assessing the ontogenetic status of alvarezsauroids profoundly affects the reconstructions of body mass on the tree. If the juveniles had not been pruned, the ancestral states reconstruction would have accumulated the underestimates from each branch represented by immature specimens and resulted in a significant underestimation of the size of the common ancestor. In such cases, early-branching taxa would have a disproportionately large effect on reconstruction of the common ancestor and then on assumptions about overall evolution. Therefore, we suggest that an ontogenetic stage check is essential when making a body size dataset, especially in the case of early-branching members of the target group. In cases where some taxa are represented only by very young specimens, like the holotypes of *Aorun zhaoi* and *Haplocheirus sollers*, they should either be removed (eliminate distinct outliers)^{1,5} or their adult body masses could be estimated to reflect a more plausible distribution of sizes across the tree.

Table 1. The absolute age, ontogenetic stages, and adult body mass estimates with 95% confidence intervals (in brackets) of all alvarezsauroid specimens involved in the macroevolution analyses

	Absolute age	Ontogenetic stage	Adult body mass (kg)
<i>Achillesaurus manazzonei</i> (MACN-PV-RN 1116)	–	Subadult-Adult	30.00 ^a
<i>Albinykus baatar</i> (MAE PSS 04–18)	3	Adult	1.07 (0.47–2.42)
<i>Alvarezsaurus calvoi</i> (MUCPV 54)	–	Juvenile	28.00 ^a
<i>Bannykus wulatensis</i> (IVPP V25026)	8	Subadult	29.13 (15.84–53.57)
<i>Bonapartenykus ultimus</i> (MPCA 1290)	–	Adult	71.55 (33.82–151.35)
<i>Ceratonykus oculatus</i> (MGI 100/975)	–	Subadult-Adult	0.26 (0.11–0.65)
<i>Haplocheirus sollers</i> (IVPP V15988)	4	Juvenile	41.00 ^a
<i>Linhenykus monodactylus</i> (IVPP V17608)	–	Subadult-Adult	2.00 (0.87–4.61)
<i>Mononykus olecranus</i> (GIN 107/6)	–	Subadult	4.66 (2.53–8.57)
<i>Nemegtomykus citus</i> (MPC-D 100/203)	–	Adult	3.31 (1.80–6.09)
<i>Parvicursor remotus</i> (PIN 4487/25)	–	Adult	0.15 (0.073–0.32)
<i>Patagonykus puertai</i> (MCF-PVPH 37)	–	Subadult-Adult	33.60 (18.27–61.79)
<i>Qiupanykus zhangji</i> (41HIII-0101)	–	Subadult	0.50 (0.27–0.91)
<i>Shishugounykus inexpectus</i> (IVPP V23567)	9	Adult	6.01 (3.26–11.05)
<i>Shuvuuia deserti</i> (MGI 100/975)	2	Juvenile	3.05 (1.66–5.61)
<i>Tugulusaurus faciles</i> (IVPP V 4025)	–	Subadult-Adult	11.51 (6.26–21.16)
<i>Xixianykus zhangji</i> (XMDFEC V0011)	11	Adult	0.74 (0.30–1.82)
<i>Xiyunykus pengi</i> (IVPP V22783)	9	Subadult	17.26 (9.39–31.74)

See also [Tables S2](#) and [S3](#).

^aEstimates based on growth curve or reference to close relatives

Though there were several early lineages of alvarezsauroids that showed size reduction (e.g., *Shishugounykus* and *Xiyunykus*), substantial body size miniaturization of nearly two orders of magnitude only occurred after around 110 Ma (Aptian) in the late Early Cretaceous ([Figure 3A](#)). Our finding for the timing of alvarezsauroid miniaturization is notably earlier than previous suggestions that this happened in the Late Cretaceous.^{12,20} All the very small (mean body mass of <5 kg) Late Cretaceous alvarezsauroids form a clade, marked by accelerated miniaturization and rapid radiation of species ([Figure 3A](#)). This miniaturization was extremely fast with a tempo extending over three orders of magnitude within 25 Ma from Albian to Santonian and is comparable to the body size doubling of tyrannosauroids within 16 Ma from Turonian and Campanian,²¹ suggesting very strong selective pressure ([Figure 3A](#)). The preference for the Ornstein-Uhlenbeck model of body size evolution, sometimes interpreted as evolutionary attraction to a central or optimal trait value,²² indicates that, among alvarezsauroids, the optimal body mass was very low relative to other theropods.

From a phylogenetic point of view, the size reduction of alvarezsauroids parallels that of paravians that took place earlier and is opposite to the general trends in body-size enlargement in most clades of maniraptorans, including their close relatives, like the therizinosaurians.²³ Previous studies of body-size macroevolution of dinosaurs suggested that only a few dinosaur lineages broke the small body size threshold seen much more commonly among mammals, around 1 kg or less.⁵ In theropod dinosaurs, such a small size is found only in alvarezsauroids, scansoriopterygids, and Pygostylia.^{1,5,8,12} Also, these morphological innovations of Late Cretaceous tiny alvarezsauroids may have new implications on our understanding of

specialization within paravians. Alvarezsauroids had no adaptations for flight or gliding, so characters shared by tiny alvarezsauroids and birds, like the keeled sternum and atypical vertebrae,

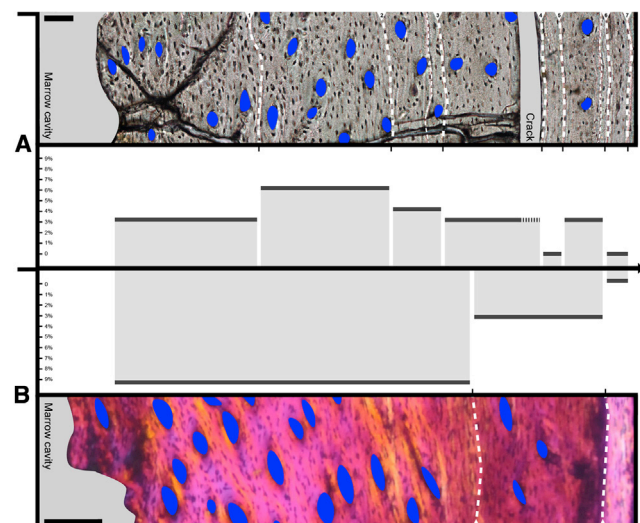


Figure 2. Two osteohistological strips from the inner marrow cavity to the outer periosteal side

Strips from the femoral slice of *Xixianykus zhangji* (interrupted by a crack; A) and the tibial slice of *Albinykus baatar* (B), with osteon canals labeled as blue and the LAGs labeled as white dash line. Histograms showing the porosity (the density of osteon canals) changes through their lifespan are shown. Scale bars, 50 μ m. See also [Figure S1](#) and [Table S1](#).

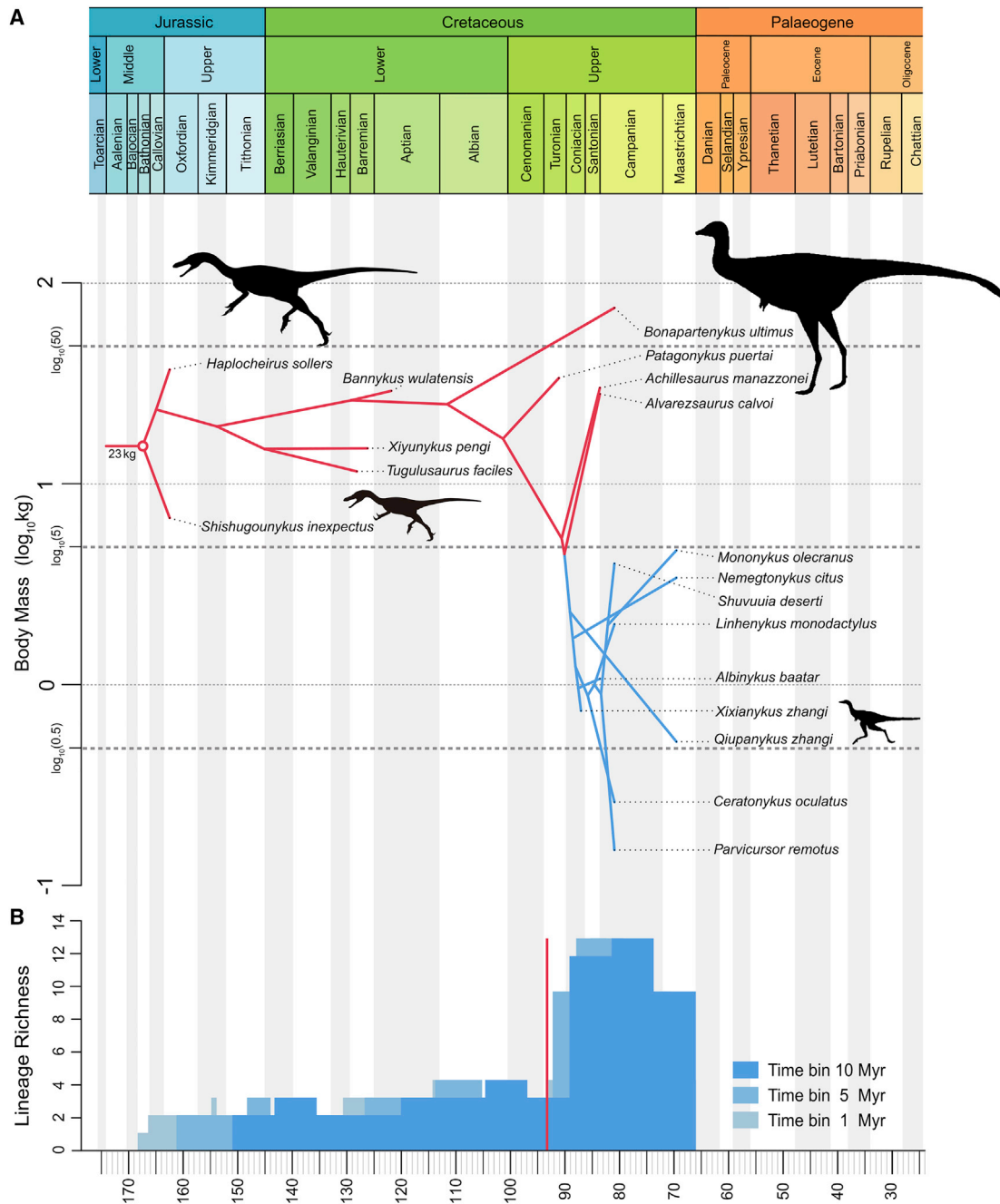


Figure 3. Body mass evolution and explosive diversification of Alvarezsauroidea

(A) Body mass evolution within Alvarezsauroidea, showing a swinging body size range from Jurassic to mid-Cretaceous (colored red) followed by a rapid miniaturization (colored blue).

(B) Phylogenetic lineage richness (resolution from 1 to 10 Ma) against time shows that explosive speciation and diversification occurred after the red line.

See also [Figures S3](#) and [S4](#) and [Table S4](#).

might be related to size reduction or ecological niche shift rather than adaptation to powered flight.

From Early to Late Cretaceous, many clades of dinosaurs show synchronous body size shifts, including tyrannosaurids,^{21,24} neoceratopsians,²⁵ and hadrosaurids.²⁶ These clades all showed size increases of one to two orders of magnitude, whereas alvarezsaurids decreased by comparable amounts.^{5,6,21,24} This sharp

decrease in size may be related to some of the bizarre alvarezsaurid modifications seen only in the Late Cretaceous late-branching species.^{13,14} Though morphological modification of alvarezsaurids started early, in the Late Jurassic,^{13,16,27} some typical features are found only in Late Cretaceous forms, such as the highly modified hand, keeled sternum, and the atypical vertebrae (strongly opisthocoelous cervical centra, opisthocoelous dorsal

centra, and fused sacral centra with ventral knees, commonly seen in tiny members, but also some indication in *Patagonykus* and *Xiyunykus*).^{13,14,28} These highly modified characters indicate a distinctive ecological niche for the Late Cretaceous late-branching alvarezsauroids when compared to other theropod lineages.

Another key point about the mid-Cretaceous miniaturization of alvarezsauroids is that speciation seems to have been promoted at the same time as the distinct size drop. This diversification happened around 90 Ma and was associated with a 3-fold increase in lineage richness (Figure 3B), coincident with the evolution of tiny sizes (<5 kg) of alvarezsauroids. Species-area effects are a source of bias confounding our understanding of Late Cretaceous diversification of various dinosaur groups, and it could be that the increase in Alvarezsauroid lineage richness is driven by differences in sampling, particularly in Asia.²⁹ However, during this increase in preservation and sampling, we report smaller and smaller alvarezsauroids and no medium- to large-sized examples, an observation that is counter to a sampling explanation, where large specimens would be easier to find than smaller ones.

What could have been the specific ecological drivers of the sharp size reduction and speciation of alvarezsauroids? Early studies of alvarezsaurids compared the forelimbs to fossorial mammals,³⁰ even inferring a burrowing habit,³¹ and according to relevant research on living burrowing mammals, a fossorial habit might limit the basal metabolic rate and further lead to a smaller body size.³² But recent functional analyses suggest that the body forms of alvarezsauroids cannot be explained by adaptations for fossorial habits.^{20,28,33,34} Another hypothesis suggests these modifications related to certain dietary preferences (e.g., small, concentrated sources of protein and fat, like insects or nuts). In the other miniaturized theropod lineage, paravians, there is also evidence for a dietary change in the apomorphic teeth of troodontids and tooth reduction in Mesozoic birds.^{35,36} Similar changes also occurred in alvarezsauroids, suggesting the Late Cretaceous forms may have been obligate insectivores, even myrmecophagous.^{17,20,34}

There is further evidence for alvarezsauroid myrmecophagy from the insect fossil record. This shows that true eusocial insects, the termites, began to flourish as part of the Cretaceous Terrestrial Revolution (KTR).³⁷ Morphological specializations of the different termite castes and even large eusocial aggregations of termites were recently reported in mid-Cretaceous Burmese amber, revealing an unanticipated flourishing of eusocial termite societies then.^{38,39} These prosperous termite colonies from the mid- to Late Cretaceous might have made an obligate myrmecophagous ecological niche possible. Earlier macroevolutionary studies of dinosaurs rarely exhibited cases of coevolution and ecological interaction during the KTR. We suggest that at least the two miniaturized theropod lineages, alvarezsauroids and birds,^{35,36} responded to this global environmental change³⁷ with major changes in body form accompanying ecological niche shifts to previously unexplored ecomorphologies. Evidence from phylogenomic reconstruction of insect phylogeny supports these diversifications of eusocial insects during the KTR (details in STAR Methods).

The miniaturization of alvarezsauroids was a complex process with extreme rate variation and perhaps several ecological drivers. Different growth strategies identified by our

osteohistological research suggest that even the miniaturized alvarezsauroids followed multiple paths to achieve small size, perhaps involving different heterochronic mechanisms. This phenomenon was reported in living animals but rarely in fossil organisms.² The coincidence of substantial and rapid size reduction and enhancement of apparent adaptations for digging seen in Late Cretaceous alvarezsauroids may indicate an insectivore feeding habit, but more details from ethological and functional research are needed to provide conclusive evidence to support this hypothesis.

STAR★METHODS

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

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability
- METHOD DETAILS
 - Histological sampling among alvarezsauroids
 - Location and production of thin sections
 - Inferring relative ontogenetic stages
 - Inferring the absolute age
 - Calculation and correction of body mass
 - Phylogenetic body size macroevolutionary analysis
 - Supplementary osteohistology information
 - *Xixianykus zhangi*
 - *Haplocheirus sollers*
 - *Shishugounykus inexpectus*
 - *Aorun zhaoi*
 - *Bannykus wulatensis*
 - *Xiyunykus pengi*
 - *Shuvuuia deserti*
 - *Albinykus baatar*
 - Growth curves and adult size estimation
 - Feeding habits of alvarezsauroids

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.06.013>.

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AUTHOR CONTRIBUTIONS

X.X. and Q.Z. designed the project. X.X., Q.Z., Z.Q., J.N.C., and J.M.C. contributed to the field trips and fossil collecting. Z.Q., Q.Z., and J.N.C. provided histological slices. Z.Q. and Q.Z. performed the histological analyses. Z.Q., J.N.C., and M.J.B. performed and improved the phylogenetic macroevolution analyses. Z.Q., Q.Z., J.N.C., and X.X. wrote the manuscript. All authors reviewed the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Osteohistological slices	This paper	Supplemental information
Morphological ontogenetical indicators	This paper & published literature	Supplemental information (Table S2)
Measurements and size estimation	This paper & compiled from Benson et al. ⁶	Supplemental information (Table S3)
Software and algorithms		
R 3.6.2	https://cran.r-project.org/	N/A
Microsoft Excel	https://www.microsoft.com/en-us/	N/A
Mesquite V 3.03	http://www.mesquiteproject.org/	N/A
ImageJ	https://imagej.nih.gov/ij/index.html/	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Xing Xu (xu.xing@ivpp.ac.cn)

Materials availability

The authors declare that all specimens underwent their osteohistological experiments and their bone slices were housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

Data and code availability

The authors declare that all data generated or analyzed during this study are included in this published article or at the [Supplemental information](#).

METHOD DETAILS

Histological sampling among alvarezsauroids

We collected original osteohistological data from the holotypes of *Haplocheirus sollers* and *Xixianykus zhangii*. We combined these with a reinvestigation, using published data and reassessment of histological slides, of the Chinese alvarezsauroids *Aorun zhaoi*, *Shishugounykus inexpectus*, *Xiyunykus pengi*, and *Bannykus wulatensis*^{13,14,16} and the Mongolian alvarezsauroids *Shuvuuia deserti* and *Albinykus baatar*.^{12,15} The information we collated for this portion of the analysis consists of osteohistological characters associated with ontogeny including Lines of Arrested Growth (LAGs) and porosity of the regions contained between LAGs.

Location and production of thin sections

For adequate histological information and to establish growth curves, thin sections were mainly made from hindlimb load-bearing long bones like the femur and tibia, and we also made some sections from bones which are not load-bearing such as the fibula and pubis. We sampled the femur, tibia and fibula from the holotype of *Shishugounykus inexpectus*, the holotype of *Haplocheirus sollers* and the holotype of *Aorun zhaoi*. We sampled the femur, tibia and metatarsal from the holotype of *Xixianykus zhangii*. We sampled the fibulae of the holotypes of *Xiyunykus pengi* and *Bannykus wulatensis*.¹⁴ We sampled the tibia and femur from the holotype of *Albinykus baatar* and a referred specimen of *Shuvuuia deserti*.^{12,15} Histological thin sections of long bones were made using standard techniques.⁴⁰ Previous studies of dinosaur long-bone histology, as well as general principles of bone growth, indicate that a section taken at the middle of the shaft of a long bone is optimal for obtaining a maximally complete growth record from that bone.^{40,41} Specimens were embedded in resin, and mid-shaft, diaphyseal transverse thin sections were cut using a diamond circular saw fitted with a diamond-tipped wafering blade. One surface of each section was smoothed with a wheel grinder (EXAKT400CS) by rough emery paper (500 grit), and then ground using smoother emery paper (4000 grit) to produce a smooth texture ideal for gluing to a glass slide. The section was then cut to a thickness of about 250 μm with a diamond circular saw before being ground further to the desired final thickness of 50–80 μm , leaving the exposed surface of the section smooth. Each slide was then cleaned in a water-filled ultrasonic cleaner to remove microscopic grit, and finally capped with a glass coverslip. The completed thin sections were studied in normal and polarized light.^{40,41}

Inferring relative ontogenetic stages

We determined the ontogenetic stages of 18 specimens involved in this research using two approaches. In the first approach, we collected observations on previously hypothesized morphological indicators for ontogeny, such as sutures between bones and co-ossification of the neural arch and centrum.⁴² In this approach, the individual's age could be underestimated because some adults retain unfused bones, but it is hard to overestimate the age. This indicates that our body mass estimates are more likely to contain underestimation errors than overestimates. Our second approach used osteohistological indicators, like the appearance of typical structures like the EFS, or a distinct decline of porosity in the outer cortex. When the osteohistological and morphological evidence were not consistent with each other, the histological ontogeny assessments were preferred. More detail on these analyses is available in the [STAR Methods](#).

Inferring the absolute age

The histological sections made it possible to estimate the age in years of each individual at the time of death, based on the typical pattern of formation of LAGs on an annual basis in dinosaur long bones. In sections that showed a small medullary cavity, the number of visible LAGs was taken to correspond approximately to the individual's age in years, although it is unlikely that each LAG was completed exactly on the anniversary of hatching. The number of LAGs can be taken as a minimum bound on age in years, with a possible error of several months. However, in older individuals, we were careful to look for enlargement of the medullary cavity, which introduces a well-understood complication, whereby the enlargement occurs through internal resorption of the bone cortex and this tends to eliminate LAGs beginning with the innermost. To count the LAGs eliminated as a result of this type of erosion, we used the average distance between the most internal LAG and the perimeter of the medullary cavity to roughly represent the minimum average distance between the LAGs eliminated. With other basic measured data of these sections, we could calculate the number of LAGs eroded by estimating the original medullary cavity size and the distance to the new inner bound. Different bones from one individual may show slightly different amounts of LAGs. But because the fossil record of alvarezsauroids is sparse, we did not have a wide choice and different bones (including femur, tibia and fibula) were involved in our histological comparison.

Calculation and correction of body mass

The body mass of each specimen was estimated by an empirical formula based on femoral midshaft circumference, and measurements are also collected from previous published dataset,^{5,43} or measured personally. For specimens lacking femoral midshaft circumference data, we used the regression equation for bipedal dinosaurs to estimate the shaft oval circumference.⁵ The holotype of *Achillesaurus manazzoni* lacks any practicable measurements relating to the femoral midshaft, but it has a very close (slightly shorter) width of the distal tibia compared to the holotype of *Patagonykus*, and we assume its body mass was around 30 kg in our analyses.

Since the ontogenetic stage of every specimen was estimated, we assume that the body mass of specimens in sub-adult to adult stages represents the 'adult mass'. For immature specimens, we used growth curves to estimate the expected 'adult mass' of the specimens under osteohistological approaches, and we referred to data on close relatives for specimens that lack histological checks ([Table S2](#)). These approaches provide us with a general adult body mass dataset of every specimen in our dataset ([Table 1](#)), with three raw body masses corrected ([Table S3](#)).

The methods to establish growth curves mostly came from previous papers on dinosaur growth and lifespan.^{44,45} We used the Developmental Mass Extrapolation scaling principle^{44,45} coupled with the age differences to model growth rates through development. In this process, circumferences of each growth mark were used to estimate the midshaft circumference of each year of growth. The periosteal and LAG circumferences were measured using the software ImageJ.⁴⁶

Phylogenetic body size macroevolutionary analysis

To analyze body size evolution of alvarezsauroids, data were collected from specimens of published alvarezsauroid species (most are holotypes). The phylogenetic framework came from three recently published analyses,^{13,14,47} with the two newly published alvarezsauroids *Shishugouonykus* and *Nemegtomykus* included.

We removed *Aorun zhaoi*, *Kol ghuva* and *Albertonykus borealis* from the phylogenetic analysis, because the holotype of *Aorun zhaoi* is too young to provide a practicable estimation of its 'adult mass', and because the holotypes of *Kol ghuva* and *Albertonykus borealis* are too incomplete to estimate body mass, and the holotype of *Kol ghuva* has very few characters supporting alvarezsauroid affinities. Our macroevolutionary analysis requires fully bifurcating phylogenetic trees, but no available trees matched this requirement. Thus, the relationships of the unresolved part of our tree, including *Linhenykus*, *Mononykus*, *Ceratomykus*, *Parvicursor*, *Shuvuuia*, and *Ceratomykus*, were derived from published phylogenetic results.⁴⁸ Variation in their phylogenetic positions has almost no influence on the results of the analyses.

To establish the ancestral body masses of alvarezsauroids, we used maximum-likelihood approaches to our corrected 'adult mass' database, to explore the evolution of this continuous character. Our "adult mass" database is log-transformed before the following ancestral character state analyses. We calculated the ancestral character states of body mass using the 'ace' function of the 'ape' R package,⁴⁹ with tree branch lengths estimated by the 'DatePhylo' function in the 'strap' R package.⁵⁰ Then, we use the 'contMap' and 'phenogram' functions from the 'phytools' package to map how body mass changed through the phylogeny,⁵¹ plotting as a heatmap and a projection of the phylogenetic tree in a space defined by body mass (on the y axis) and time (on the x axis) respectively. To assess tendencies in body mass evolution, we used the 'fitContinuous' function from the 'geiger' package

to test the model-fitting of our results.⁵² For the commonly used evolutionary models, including Brownian motion,⁵³ Ornstein-Uhlenbeck,²² Early Burst,⁵⁴ and Trend,⁵⁵ we used AICc values to assess the explanatory power of each model given our data. In our estimation of branch lengths for the alvarezsauroid tree, we arbitrarily chose the ‘equal’ method of the ‘strap’ package, which indeed returns a preference for our data fitting an Ornstein-Uhlenbeck model (among the single regime models we tested). However, other branch length calculation methods might return best fits to other models. In a further series of analyses, we applied different approaches to the tempo of miniaturization and lineage richness through time. To investigate alvarezsauroid palaeodiversity, we used the ‘phyloDiv’ function from the ‘paleotree’ package to plot phylogenetic lineage diversity through time,⁵⁶ we used three time-bin resolutions, namely 1 Myr, 5 Myr and 10 Myr. Further, the rate heterogeneity of this trait was also tested by the fit function ‘transformPhylo.ML’ from the ‘motmot’ package.⁵⁷

Supplementary osteohistology information

In this study, we first present osteohistological approaches to two published Chinese alvarezsauroid specimens, including femoral slices from the holotype of *Xixianykus zhangj* and tibial slices from the holotype of *Haplocheirus sollers*, with ontogenetic information.

Xixianykus zhangj

This slice provides concordant evidence for an advanced ontogenetic stage. The Femoral sections have compact primary cortices with the majority of fibrolamellar bone inside and lamellar bone outside (Figures S1A–S1C). LAGs in are well preserved and circumferentially continuous, with some presenting as doublets. The femoral section preserves seven LAGs (Figure S1D). We estimate the number of LAGs eroded by the marrow cavity, using a published method for estimating eroded growth marks on single bones.⁵⁸ In total, we infer that four LAGs were erased, and thus we estimate the age of this individual to be 11 years. Typical of its ontogenetically old age, the femoral sections contain evidence of somatic maturity, such as EFS structures (Figure S1E) with at least five LAGs tightly bunched, and well-developed endosteal bone (Figure S1B).

Haplocheirus sollers

The tibial section cortex is mainly composed of fibrolamellar bone and four distinct LAGs (Figure S1F). The cortex of this section is distributed by similar size longitudinal and circumferential canals from inside to outside without a clear conversion on type of these primary osteons. The bone tissue type also remains as fibrolamellar bone as well (Figures S1G and S1H). Except the innermost interval, intervals between each LAG are similar in width, showing a steady growth of this individual. Lack of typical endosteal lamellae bone or EFS structure also support this conclusion. We therefore infer IVPP V15988 is a juvenile, presumably four years old.

We also collected data on ontogenetic related characters from previously published osteohistological studies, including researches on *Shishugounykus inexpectus*, *Aorun zhaoi*, *Bannykus wulatensis*, *Shuvuuia deserti* and *Albinykus baatar*.^{12,14–17,27} We summarize the relevant osteohistological description here, both from the original literature and our new observations of these bone slices.

Shishugounykus inexpectus

Transverse osteohistological slices were made from the femur, tibia and fibula of IVPP V23567, the holotype of *Shishugounykus inexpectus*,¹³ providing concordant evidence for the advanced ontogenetic stage of this species. The tibial and femoral sections are similar (Figures 3A and 3B, from Qin et al.¹³), with bone cortex separated by five LAGs. There are layers of parallel-fibered tissue at the outermost of both sections. Both femora and tibiae have open, circular medullary cavities with distinct evidence of expansion, around four LAGs were eroded by this expansion. The medullary expansion of the femur is slightly more severe than that of the tibia based on the evidence from the location of the innermost LAGs. The endosteal margins of both bones are internally lined by lamellae, though much thinner compared to the fibula, giving robust evidence of the termination of medullary expansion. The compacta of the fibula can be distinctly divided into three portions from medullary cavity to outer cortex, all support a very advanced ontogenetic stage (Figure 3C, from Qin et al.¹³). The innermost region is occupied by two layers of endosteal lamellae, together with the central Haversian tissue and the outmost EFS structure. All sections from these three bones suggest that this individual is an adult, aged about nine years.

Aorun zhaoi

Transverse osteohistological slices were made from the fibula and tibia of IVPP V15709, the holotype of *Aorun zhaoi*,¹⁶ with both elements supporting a very young ontogenetic stage of this individual (Figure 21, from Choiniere et al.¹⁶). The majority of the diaphyseal cortices of both sections are composed of fibrolamellar matrix with longitudinal, reticular and circumferentially oriented primary vascular canals.¹⁶ Typical indicators of an advanced ontogenetic stage, such as developed secondary osteons or endosteal bone, are absent in every section. Likewise, none of the sections show LAGs or other kinds of growth marks. Based on our new observations on these osteohistological slices, in contrast with its initial description the outermost bone matrix is not typically avascular and does not form an annulus or a LAG. No distinct decrease of porosity exists in the outer cortex, and the vascular canals still open to the periosteum, which suggests continuing growth rather than slowing or an arrest there. Both sections suggest that this individual is a young juvenile, probably less than one year old.

Bannykus wulatensis

A transverse osteohistological slice was made from the fibula of IVPP V25026, the holotype of *Bannykus wulatensis*,¹⁷ providing evidence for a relatively advanced ontogenetic stage (sub-adult) of this individual (Figure 1, from Xu et al.¹⁷). The cortex of the fibula is fibrolamellar bone with predominantly longitudinal vascular canals. Eight LAGs exist in the cortex in total, and the inner two LAGs are distinctly separated from the six outer LAGs. Small primary osteons are scattered in the outer cortex. On the other hand, in a relatively large zone, several generations of secondary osteons are mostly located on the inner side, limited to lie inside cortex. There is no EFS on the outside part of the cortex, but the intervals between the outer five LAGs are narrower than those of the inner LAGs. The lack of an EFS suggests this individual was still growing, but other characters like the reduction in thickness of the outer annulus, lower density of vascular canals in the outer cortex and the intense secondary reworking of the inner cortex suggest that growth would not last much longer. IVPP V25026 was interpreted as a sub-adult when published, which is supported by our additional observations here, and aged about 8 years.

Xiyunykus pengi

A transverse osteohistological slice was made from the fibula of IVPP V22783 (Figure 2, from Xu et al.¹⁷), the holotype of *Xiyunykus pengi*,¹⁷ also from an individual of a relatively advanced ontogenetic stage (sub-adult). The cortex of the slice is fibrolamellar bone with predominantly longitudinal vascular canals. There are nine LAGs in the cortex in total, and the intervals between the outer five LAGs are narrowing. Like the slices of *Bannykus wulatensis*, no EFS structure is observed in this slice. The density of vascular canals in the outer cortex is relatively low, less porous compared to that of IVPP V25026. The inner cortex was reconstructed by several generations of secondary osteons, with several big erosion cavities. All this evidence indicates that the holotype of *Xiyunykus pengi* is histologically older than the holotype of *Bannykus wulatensis* but is still a sub-adult aged around nine years.

Shuvuuia deserti

The osteohistological research of *Shuvuuia deserti* was included in a broad osteohistological comparison among dinosaurs.¹⁵ A femur of *Shuvuuia deserti*, AMNH 100/99, was identified as from an ontogenetically young animal with one LAG and longitudinal vascular canals dominating the cortex (Figure 1, from Erickson et al.¹⁵). The first growth curves were also calculated to describe the lifespan of *Shuvuuia deserti*,¹⁵ which is involved in our comparison.

Albinykus baatar

An osteohistological study of *Albinykus baatar*, IGM 100/3004, was included with the report of its holotype.¹² Thin sections from the tibia showed a fibrolamellar to parallel-fibered cortex with dominated longitudinal vascular canals (Figure S1F, from Nesbitt et al.¹²). Two LAGs were observed, both located peripherally. Though there was no clear EFS, IGM 100/3004 was interpreted as a sub-adult based on the existence of an outermost thin band of avascular cortex (lamellar-zonal bone) and its two growth marks.¹²

Growth curves and adult size estimation

We made growth curves from the of the holotype of *Shishugounykus inexpectus*, IVPP V23567 and the holotype of *Xixianykus zhangii*, XMDFEC V0011.

We estimated the absolute ages and counted LAGs eroded by the medullary cavity for each slice by the interval between preserved LAGs (details in [Method details: Inferring the absolute age](#)). Thus, the correspondence of preserved LAGs and ages are established. 4 LAGs were eroded in IVPP V 23567 and 3 LAGs were eroded in XMDFEC V0011.

Because both bone slices do not cover the whole cross section of femur, we use the CT scanning slices from where the histological slices were made to help us estimating the circumference of LAGs. Each circumference is listed in following tables. Based on the Developmental Mass Extrapolation scaling principle,^{44,45} annual body mass data were estimated by empirical formulas.⁴³

Previous studies suggested the Logistic function with comparable best R² fits, and we also use Logistic function to regress our data.^{44,45} We use the Logistic function from Erickson et al., 2001, showing as $Mass = a/(1+e^{b(Age-c)})+d$, to reconstruct the lifespan of the two alvarezsauroids. For the parameters, the 'a' was estimated by the max body mass, which is fully supported by our bone histological evidence (both are adult). The 'b' was from the slope relationship and 'c' from the age data where the greatest slope occurs. We did not include 'd' in our formula, suggested as min body mass here, because both dinosaurs are tiny but old in ontogeny, and their hatching size are difficult to estimate.

Because the holotype of *Haplocheirus sollers* is at a juvenile stage and its osteohistological slices are from tibia, it is hard to establish a reliable Age-Mass growth curve. But osteohistological exam of this specimen have suggested the death age of this individual is around 5 years old with no clear growth records missed. According to the two growth curves we made, they both provide a 10 –12 years of maturity age, and a consistent exponential growth around 5 years old. Thus, we refer these two growth curves from *Shishugounykus inexpectus* and *Xixianykus zhangii* as two brackets, showing the matured size of an individual is around 2.09 to 1.90 times larger than its size when it as a 5 years old juvenile. The body mass estimated by the measurements from the holotype of *Haplocheirus sollers* is 20.45 kg. So here, we estimated the adult size of *Haplocheirus sollers* range from 38.86 kg to 42.74 kg, and around 41 kg in average.

Hence, the osteohistological information and growth curves help us to make a relatively arcuate estimation of adult mass of *Haplocheirus sollers*, *Shishugounykus inexpectus* and *Xixianykus zhangii*. The holotypes of *Shishugounykus inexpectus* and

Xixianykus zhangii are both adults, so the body mass of their holotype represent their adult mass. Instead, the holotype of *Haplocheirus sollers* is a young juvenile, with a rough estimation of adult mass around 41 kg.

Feeding habits of alvarezsauroids

Previous morphological evidence and functional analyses suggested that the early-branching alvarezsauroids occupied a variety of niches, most likely omnivorous to carnivorous,⁵⁹ whereas the Late Cretaceous forms may have been obligate insectivores, with some suggestions they were myrmecophagous (feeding on termites and ants).^{17,23,34} This hypothesis is supported by morphological characters shared by late-branching members, like the anterior diastema toward the front of the jaws, the reduced and simplified teeth, long and narrow jaws, weak mandibles and reduced jaw articulations.^{17,23,34}

On the other hand, statistical studies of living vertebrates demonstrate that insectivorous predators have a smaller body size threshold than other faunivores (e.g., piscivores and carnivores).⁶⁰ Analyses from mammals with a mainly myrmecophagous diet show a low upper body size threshold, around 11 to 13 kg, with very few exceptions. This is because it is difficult to support a larger body size together with a relatively high metabolism with an obligate myrmecophagous diet.³² While the late-branching alvarezsauroids are widely accepted as cursorial animals, supported by characters from their slender hind limbs,¹⁷ they might also have had relatively high metabolism. Potentially, similar physiological factors might have driven the evolution of small body size in late-branching alvarezsauroids.

In support of a strictly myrmecophagous ecological niche for tiny alvarezsauroids, eusocial behavior, high diversity and considerable biomass of termites and ants are required. According to recent fossil and molecular studies, the eusocial insects are mostly recognized as emerging during the latter half of the Mesozoic.³⁹ The fossil record shows that termites started an early radiation in the Early Cretaceous,^{38,39} and molecular dates for the most recent common ancestor of ants ranges from 115–135 Mya.^{61–63} The time of emergence of eusocial insects corresponds with the miniaturisation recognized by our analyses, supporting our hypothesis of a dietary shift as a specific ecological driver for miniaturization of alvarezsauroids. But we need to address here that our hypothesis is mainly supported by the matching in geological time between the emergence of eusocial insects and miniaturization in alvarezsauroids. Dietary remains are rarely preserved in association with alvarezsauroid fossils. Although records are few and not worldwide, there are some reports about the coexistence of alvarezsauroids and eusocial insect trace fossils in North America.²⁰

Update

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Correction

Growth and miniaturization among alvarezsauroid dinosaurs

Zichuan Qin, Qi Zhao, Jonah N. Choiniere, James M. Clark, Michael J. Benton, and Xing Xu*

*Correspondence: xu.xing@ivpp.ac.cn

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After publication, two errors were discovered in the original paper.

First, we neglected to log-transform body mass information when estimating rate heterogeneity. In the “Phylogenetic body size macroevolutionary analysis” section of the Method details, an additional point is needed in the third paragraph: log-transforming the body size measurements is essential in ancestral reconstruction. We have added a sentence to clarify this point.

In the “Body size evolution” section of the Results, there is an error in the sentence “Our test for rate heterogeneity of body size as a trait on our phylogenetic tree suggested a rate decrease after node 27 (the common ancestor of *Qiupanykus zhangi* and its sister group; colored in blue in Figure 3A; Figure S3).” In the reanalyzed dataset, using log-transformed data, with reasonable AIC thresholds, we return no inference of rate shifts. We have changed this sentence to “Our test for rate heterogeneity of body size as a trait on our phylogenetic tree suggested no distinct rate shift (Figure S3).” The different outputs from log- and non-log-transformed datasets are mainly caused by the very tiny size of late-branching alvarezsauroids. The evolutionary rate did decrease in absolute values, but when considering their tiny body size, the changes are insignificant.

Finally, a sentence in the Discussion, “Upon reaching the inferred optimal small body mass of less than 5 kg (Figure S3; after node 27 in the phylogenetic tree), later alvarezsauroids (including *Qiupanykus* and its sister group) showed relatively little innovation in body size,” should be deleted because there is no strong evidence supporting a rate shift there.

In our macroevolutionary analyses, we ran the ancestral state reconstruction of body mass evolution on both log-transformed (log kg) and original (kg) mass data, but considering the need for log-transformed data, we have replaced Figure S3B based on the log-transformed dataset. The only difference between these two panels is that the mass data are log-transformed.

Second, we selected a branch-length calculation method arbitrarily, and other methods return preferences for different models. In our estimation of branch lengths for the alvarezsauroid tree, we arbitrarily chose the “equal” method of the strap package, which indeed returns a preference for our data fitting an OU model (among the single-regime models we tested). However, other branch-length calculation methods return best fits to other models. For example, using the “mbl” argument to calculate branch lengths using the “palaeotree” package returns a preference for a BM model, among the single-regime models we tested. Because the fit of a given evolutionary model to our data is not robust to arbitrary differences in branch-length calculations, we can no longer robustly support selective pressure for smaller body sizes. However, our qualitative observations about the decrease in alvarezsauroid body mass remain unaffected. Increased samples, use of a variety of branch-length scaling methods, and the evaluation of multi-regime models of evolution on our observations will undoubtedly improve our ability to understand the processes by which alvarezsauroid body mass decreased.

These errors do not negate our observations about patterns of body size evolution among alvarezsauroids. We are grateful to Roger Benson (University of Oxford) for pointing out the issues of concern. The authors apologize for any confusion.



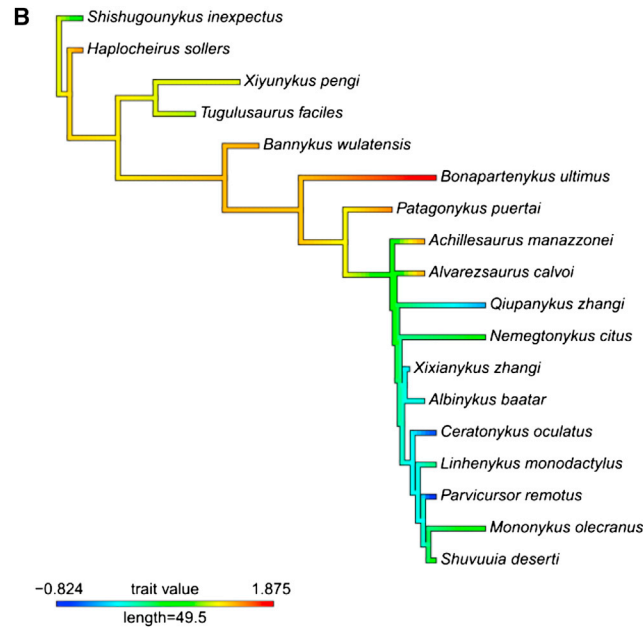


Figure S3B. Alvarezsaurid phylogenetic tree with geological time scale, ancestral state reconstruction of body mass, trait rate heterogeneity and phylogenetic lineage diversity through time. Related to Figure 3. (corrected)

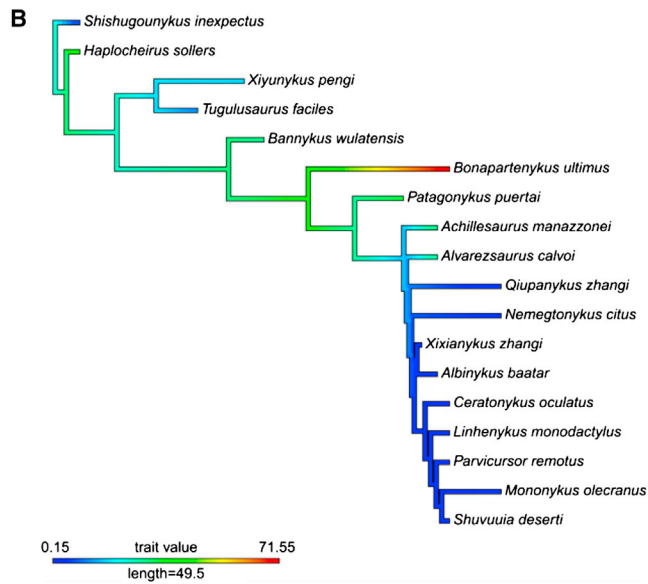


Figure S3B. Alvarezsaurid phylogenetic tree with geological time scale, ancestral state reconstruction of body mass, trait rate heterogeneity and phylogenetic lineage diversity through time. Related to Figure 3. (original)