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Body size and evolutionary rate analyses reveal complex evolutionary history of Alvarezsauria

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Abstract

Some of the smallest examples of dinosaurian body size are from alvarezsaurians, an enigmatic group of maniraptoran coelurosaurians with a peculiar combination of anatomical features unique among theropods. Despite the large number of alvarezsaurian species described worldwide and the increased understanding this has provided, the body-size macroevolution of alvarezsaurians has received little attention. Here we reconstruct and analyse directional trends of alvarezsaurian body-size evolution through an integrated analysis of body mass, ontogenetic age, and morphological rate data enabled by a comprehensively revised phylogeny. Our analyses identify four periods of high morphological rate evolution (Bathonian–Callovian, Hauterivian–early Berriasian, early Cenomanian, and late Cenomanian–Turonian) that we link to the key effects of animal body-size changes for the first time, including morphological novelty, structural reduction and simplification, elevated homoplasy, and behavioral changes associated with miniaturization. In doing so, this study provides a holistic example of miniaturization in a Mesozoic vertebrate group that offers a framework for other detailed studies of animal body-size evolution, including in more disparate groups.

Introduction

Alvarezsauria includes a series of enigmatic maniraptoran theropods known from the Upper Jurassic and Cretaceous of Asia as well as the Cretaceous of South America, North America, and Europe (Fig. 1). These dinosaurs exhibit a distinctive skeletal bauplan comprising a gracile skull with large rounded orbits, small ziphodont or pachydont teeth and lacking a postorbital-jugal contact, as well as a postcranial skeleton characterized by having very short forelimbs with robust thumbs, long and slender hind limbs, and hyper-elongated tails with procoelous caudal vertebrae (Suzuki et al., 2002; Xu et al., 2013; Choiniere et al., 2014b; Gianechini et al., 2020; Meso et al., 2021b, 2022; Agnolín et al., 2022). These characteristics have been the source of a variety of palaeobiological inferences throughout the study history of the group (Senter, 2005; Longrich and Currie, 2009; Choiniere et al., 2014b, 2021; Fowler et al., 2020; Meso et al., 2021b; Qin et al., 2023).

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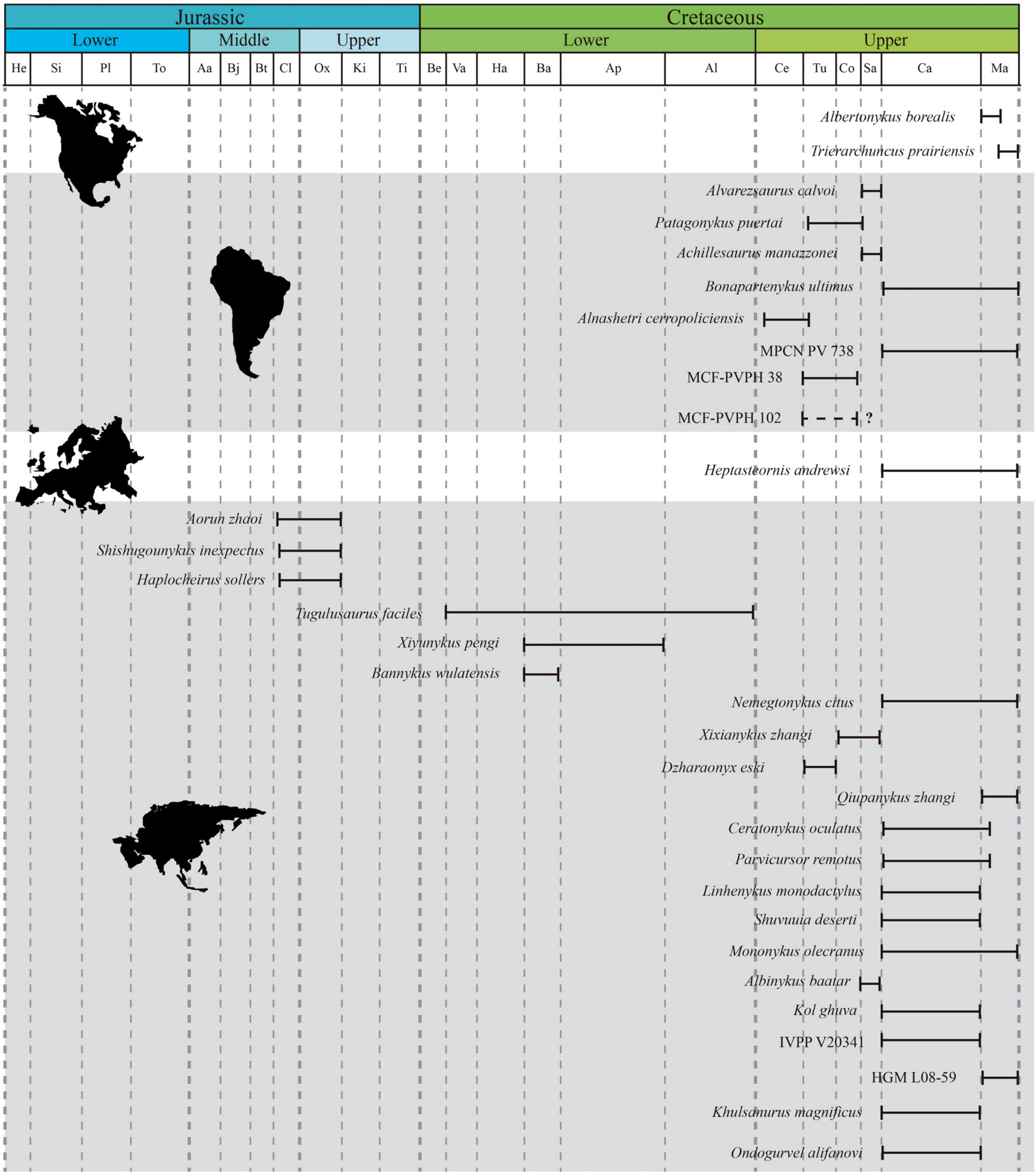

Fig. 1. The stratigraphic range of all known specimens of Alvarezsauria. He, Hettangian; Si, Sinemurian; Pl, Pliensbachian; To, Toarcian; Aa, Aalenian; Bj, Bajocian; Bt, Bathonian; Cl, Callovian; Ox, Oxfordian; Ki, Kimmeridgian; Ti, Titonian; Be, Berriasian; Va, Valanginian; Ha, Hauterivian; Ba, Barremian; Ap, Aptian; Al, Albian; Ce, Cenomanian; Tu, Turonian; Co, Coniacian; Sa, Santonian; Ca, Campanian; Ma, Maastrichtian.

Body size plays an important role in all attributes of life, imposing limitations on the shape, physiology, behavior, and ecology of organisms (Vizcaíno et al., 2016). With dinosaur body sizes ranging orders of magnitude, from 15 g in certain living birds to 90+ tons in some sauropods, dinosaurs are an exemplar of the correlation between body size, phenotype and life attributes from humble beginnings as a ~10–30 kg ancestor some 230 Myr ago (Carrano, 2006; Benson et al., 2018). Quantitative studies of theropod body size have identified miniaturization—evolution towards smaller body sizes from a larger ancestor—most famously along the dinosaur–bird lineage, as well as multiple instances of directional trends of increased body size involving several clades (Carrano, 2006; Zanno and Makovicky, 2013; Lee et al., 2014; Benson et al., 2018). Outside theropods, there are numerous examples of miniaturization across extinct and extant vertebrates and invertebrates (Pearson, 1948; Hanken and Wake, 1993; Lee et al., 2014; Puttick et al., 2014), but theropod examples have rarely been documented outside birds (Turner et al., 2007; Choiniere et al., 2010; Benson et al., 2018; Qin et al., 2021), the exceptions being deinonychosaurians and alvarezsaurians (Turner et al., 2007; Choiniere et al., 2010; Qin et al., 2021). While a focus on Cope's rule of body size increase over time has characterized many theropod body-size macroevolutionary analyses, recent studies have concluded that there is no evidence for directional evolution in body mass (Zanno and Makovicky, 2013; Lee et al., 2014).

Choiniere et al. (2010) were the first to suggest a pattern of miniaturization within Alvarezsauria after the discovery of the early diverging Late Jurassic alvarezsaurian *Haplocheirus*. Subsequently, Qin et al. (2019) found that all alvarezsaurians possessed body masses <50 kg, representing one of the theropod clades with the smallest body sizes outside of birds. They suggested that early diverging alvarezsaurians maintained relatively large body sizes for ~50 Myr, and that miniaturization was restricted to the Late Cretaceous (Qin et al., 2019). Their data also suggested that size variation was greater in early diverging taxa compared to later-diverging ones, even after considering ontogenetic variability in body-mass estimation (Qin et al., 2019). Soon after, Qin et al. (2021) revised their dataset of alvarezsaurian body masses (= Alvarezsauroidea sensu Qin et al., 2021), and concluded that during the first 70 Myr of their evolutionary history, their body mass ranged from 10 to 75 kg. Qin et al. (2021) proposed an Albian–Santonian miniaturization event that drastically reduced later-diverging alvarezsaurid body masses to <5 kg and related it to an ecological niche shift involving myrmecophagy and the emergence of ants and termites during the Cretaceous Terrestrial Revolution (Qin et al., 2021). Their results were suggested to be the best fit for the directional Ornstein–Uhlenbeck model of trait evolution (Qin et al., 2021), whereby continuous body-size characteristics tend to evolve towards one direction and depend on selective pressures such as directional selection (see Butler and King, 2004). More recently, Makovicky et al. (2024) identified a second trend in body-size reduction in the early diverging lineage leading to the early Late Cretaceous *Alnashetri* from South America. In terms of the assembly of the highly specialized alvarezsaurian skeleton, previous studies suggest that the pattern, pace, and timing of its evolution occurred modularly, with processes being independent and happening at different times (Xu et al., 2018).

Unfortunately, a long-standing problem in alvarezsaurian studies has been the limited agreement in the internal phylogenetic relationships of the clade. This prevailing phylogenetic uncertainty necessarily translates downstream to uncertainty in patterns of alvarezsaurian body-size evolution and associated morphological change. The main objective of this study is to improve our understanding of alvarezsaurian phylogeny and to use the more robust framework it provides to reconstruct body-size patterns and potentially related morphological rate changes to clarify the mode and tempo of alvarezsaurian evolution. In doing so, this study offers a valuable reference for researchers interested in studying the body size and morphological evolution of terrestrial vertebrates, especially during the Mesozoic.

Material and methods

Institutional abbreviations

NHMUK, Natural History Museum, London, United Kingdom; IGM, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN-PV-RN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCF-PVPH, Museo "Carmen Funes", Plaza Huincul, Neuquén, Argentina; MPCA-PV, Museo Provincial "Carlos Ameghino", Cipolletti, Río Negro, Argentina; MPC, Institute of Palaeontology of Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MPC, Mongolian Paleontological Center, Ulaanbaatar, Mongolia; MPCN-PV, Museo Patagónico de Ciencias Naturales "Juan Carlos Salgado", General Roca, Río Negro, Argentina; MUCPv, Museo de la Universidad del Comahue, Centro Paleontológico "Lago Barreales", Neuquén, Argentina; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZIN PH, Paleoherpetological collection, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Body mass and length estimates

Reliable body-mass estimates are essential to assess directional trends within Alvarezsauria, as this is the most important variable related to body size, and hence, related to ecological and physical parameters such as fecundity, population density, diversity and metabolic rate, among others (Kleiber, 1947; Damuth, 1981a, 1981b; Gillooly et al., 2001, 2002; Christiansen and Fariña, 2004; McClain and Boyer, 2009). During the last few decades, different methods have been proposed for estimating body mass. However, all of these methods rely on virtually complete skeletons (see Christiansen and Fariña, 2004 and references therein). Given that most Patagonian alvarezsaurids are known from fragmentary specimens, mainly composed of appendicular elements, we chose to use a method proposed by Christiansen and Fariña (2004), an approach that through bivariate and multivariate regressions (NB, see Supporting Information S1: "1. Applied equations") yields high correlation coefficients ($r > 0.975$ and $r > 0.990$) and low standard errors (Christiansen and Fariña, 2004).

Based on the bone elements preserved in each analysed specimen, eight of the 39 equations (see Supporting Information S1: "1. Applied equations" and "2. Abbreviations") described in Christiansen and Fariña (2004) were suitable for our analysis. It should be noted that the analysed dataset covers all alvarezsaurians known to date, except for those taxa where it was not possible to estimate a body mass directly from appendicular bones. In the last case, an approximate body mass could be estimated by comparing the preserved bones. The variables used to estimate body mass, as well as the calculations obtained, are detailed in Supporting Information S1: "3. Body mass-Alvarezsauria". For comparison, the body mass also was calculated for each specimen using the formula developed by Campione et al. (2014), which is based on the circumference of the diaphysis of the stylopodial elements (see Supporting Information S1: "4. Body mass Campione et al"). Estimation of body length follows Therrien and Henderson (2006) (see Supporting Information S1: "5. Body length-Alvarezsauria").

Ontogenetic stage assessment

Building on Qin et al. (2021), our assessment of the ontogenetic stages of the analysed specimens was made using two approaches. First, we took into account morphological characters related to the general skeletal maturity of an individual (e.g. neurocentral sutures) (Carrano et al., 2005; Qin et al., 2019). Secondly, we used osteohistological ages provided by Qin et al. (2021) but excluded the recovered ages of *Aorun zhaoi*, *Shuvuuia deserti,* and *Haplocheirus sollers* because they represent skeletally immature specimens. In contrast to Qin et al. (2021), we consider *Alvarezsaurus calvoi* to be a subadult specimen rather than a juvenile specimen based on the fusion observed between the caudal centra and their corresponding neural arches. We decided not to correct our body-mass estimations for the immaturity of the juvenile specimens (*contra* Qin et al., 2021) because different growth strategies have been observed within Alvarezsauria (Qin et al., 2019; D'Emic et al., 2023) and these are not yet sufficiently known in the juvenile specimens (*Aorun zhaoi*, *Shuvuuia deserti,* and *Haplocheirus sollers*). In this sense, the body mass of immature specimens was considered "unknown" and excluded from the analyses. Nevertheless, we recognize that alvarezsaur diversity within the same formation may be skewed by individuals at different ontogenetic stages (e.g. Makovicky et al., 2012). For example, *Achillesaurus* is considered a synonym of *Alvarezsaurus*, and *Nemegtonykus* is a synonym of *Mononykus.* As a result, we conducted a new analysis excluding *Achillesaurus* and *Nemegtonykus*, using the body mass of the former for *Alvarezsaurus* and that of the latter for *Mononykus.*

Taxonomic nomenclature and phylogenetic analysis

We use a stem-based definition of Alvarezsauria (Agnolín et al., 2012), defining the group as the most inclusive clade in which taxa share a more recent common ancestor with *Alvarezsaurus calvoi* than with either *Passer domesticus* or *Ornithomimus velox*. Alvarezsauridae Bonaparte, 1991 was defined as the least inclusive clade containing *Alvarezsaurus calvoi*, *Mononykus olecranus,* and their most recent common ancestor (Novas, 1996). Parvicursorinae Karhu and Rautian (1996) sensu Xu et al. (2013) and Mononykini are defined as stem-based clades: Parvicursorinae as the most inclusive clade including *Parvicursor remotus* but not *Patagonykus puertai*, and Mononykini as the clade including taxa more related to *Mononykus* than to *Parvicursor*, *Patagonykus* and *Alvarezsaurus* (Agnolín et al., 2012).

Here we use a modified version of the data matrix presented by Xu et al. (2018) and subsequent papers (Qin et al., 2019; Averianov and Lopatin, 2021, 2022a, 2022b; Averianov and Sues, 2021). Our analysis includes virtually all known alvarezsaurian material (except for specimens that have not yet been described such as LACM 153311 and 41HIII-0104; Salgado et al., 2009; Pittman et al., 2015; Lü et al., 2018). We have added 48 new characters to the dataset of Xu et al. (2018) (see Supporting Information S2: 1. Characters and 2. Data matrix), removed character 431 because of the ambiguous delimitation of its character states, modified the definition of character 619 (see Supporting Information S2: 1. Characters), and modified 363 character scorings given by Xu et al. (2018) (see Supporting Information S2: 3. Modifications). The following characters were treated as ordered: 47, 74, 82, 99, 118, 124, 131, 151, 180, 184, 222, 228, 229, 235, 238, 239, 265, 266, 274, 275, 282, 283, 287, 311, 312, 321, 329, 332, 334, 335, 348, 351, 358, 380, 381, 384, 386, 389, 395, 429, 430, 434, 436, 441, 443, 445, 466, 468, 479, 505, 506, 519, 521, 558, 579, 586 and 603 (see Supporting Information S2: 4. Characters ordered). The resulting matrix is composed of 122 taxa and 643 characters (Supporting Information S3). The dataset was assembled in WinClada v.1.00.08 (Nixon, 2002) and analysed in TNT v.1.5 (Goloboff and Catalano, 2016). The search strategy used a combination of the tree-search algorithms including Wagner trees, TBR branch swapping, and sectorial searches until 100 hits of the same minimum tree length (command "xmult = hits 100"). The resultant trees were then subjected to a final round of TBR branch swapping (command "bb") to ensure a thorough sampling of tree space. We also implemented the IterPCR procedure of Pol and Escapa (2009), which generates a reduced consensus without wildcards. At last, the robustness of each node was obtained from the scripts bremsupre-d.run (script currently under development by D. Pol and beta version attached; see Supporting Information S3) and pcrjak.run (Pol and Goloboff, 2020) (see Supporting Information S3), which aim at identifying taxa that decrease the support values because they are unstable in jackknife searches or suboptimal searches.

In order to test whether the erroneous inclusion of distinct semaphorins of the same species in our database biases the alvarezsaurian topology, we chose to carry out a second analysis excluding *Aorun*, *Haplocheirus*, *Achillesaurus*, *Shuvuuia,* and *Nemegtonykus.*

Body-size macroevolutionary analysis

Calculated body-mass estimates were used to trace body-size evolution across the Alvarezsauria clade. Because the construction of our phylogenetic matrix has been focused on resolving the interrelationships of Alvarezsauria, we used the reduced strict consensus from our analysis for the clade Alvarezsauria. For this clade, ancestral body masses were reconstructed for each of their internal nodes using a maximum-likelihood estimation based on our body-mass dataset of subadult and adult individuals (see Supporting Information S1). These ancestral body masses were calculated using the *ace* function of the R software package "ape" (Cuesta et al., 2022), with the lengths of the tree branches estimated using the *DatePhylo* function of the R package "strap" (Wills, 1999). Subsequently, the *contMap* and *phenogram* functions of the "phytools" package of R were used to map the change in body mass across the phylogeny (Revell, 2012). To evaluate trends in the evolution of body mass, the *fitContinuous* function was used from the "geiger" package of R (Harmon et al., 2008). We used traditional models such as Brownian motion, Ornstein–Uhlenbeck, Early Burst, and Trend (Felsenstein, 1973; Butler and King, 2004; Harmon et al., 2010; Hunt and Carrano, 2010), which use corrected Aikake information criterion (AICc) values to examine each model and evaluate which one fits the data best. In order to investigate the diversity of the clade over time, we used the *phyloDiv* function of the "paleotree" package of R (Bapst, 2012). Because a fully resolved tree is needed for this function to execute, the “multi2di” function of the “ape” package of R was used to resolve a single trichotomy present in the Alvarezsaurian tree in a later-diverging group of Parvicursorinae (see Supporting Information S3: Script for macroevolution with DatePhylo). Likewise, a second analysis was conducted using body-mass data transformed logarithmically.

Third and fourth analyses were conducted using the Cal3 and minimum branch length (MBL) methods to calibrate the branches of our reduced consensus tree to avoid any potential bias and provide more data supporting our hypotheses. For the Cal3 method, speciation rates of 0.1 and 0.3 were used, whereas extinction rates were set at 0.05 and 0.2, with the molecular clock rate omitted (see Bapst, 2012). For the MBL method, the minimum branch length (in Myr) was adjusted to 0.5 (see Supportingy Information S3: Script for macroevolution with Cal3 and MBL).

The reduced consensus tree excludes a high percentage of Parvicursorinae species, so the effect of excluding these pruned taxa was addressed. To achieve this purpose, macroevolutionary analyses were carried out on a subset of the most parsimonious trees, considering those that are topologically most different to better sample the diversity of trees (see Supporting Information S3: Trees Used).

Evolutionary rates

Evolutionary rates of morphological change were evaluated based on a parsimony analysis of the character dataset. This was implemented in the script evolrates.run, following the details given in Pol et al. (2024). For this analysis, trees were calibrated against geological time using the oldest age of the first appearance of each terminal taxon, and branches that have zero temporal length were assigned a minimum duration of 1 Myr. The script runs under TNT for trees in memory and uses the parsimony optimization of characters to determine the number of changes along branches of the trees. The rate of morphological change is obtained by dividing the number of changes by the temporal duration of each branch (Pol et al., 2024).

Results

Phylogenetic analysis

The phylogenetic analysis resulted in 999 999 most parsimonious trees (MPTs) of 3395 steps, a consistency index (CI) of 0.220, and a retention index (RI) of 0.590. The strict consensus of these trees reveals a large maniraptoriform polytomy (Fig. S4: Supporting Information S4). The IterPCR procedure identified nine unstable taxa: *Heptasteornis*, *Albertonykus*, *Nemegtonykus*, *Trierarchuncus*, *Stokesosaurus*, *Segnosaurus*, *Gigantoraptor*, *Unenlagia* + *Neuquenraptor*, and *Sinornithoides*. The reduced consensus produced a well-resolved phylogeny that includes a novel topology for Alvarezsauria (Figs S2 and S3: Supporting Information S4). The implementation of the support analyses that account for unstable taxa (pcrjak; Pol and Goloboff, 2020 and the “bremsupred” script) identified well-supported nodes within Alvarezsauria that allows the evolution of the group to be assessed based on a robust framework (Fig. 2).

Alvarezsauria (see Supporting Information S3 for the alvarezsaurians nomenclature history) is included in Maniraptoriformes (Fig. S2; Supporting Information S4), as in previous studies. Numerous characters unambiguously support this hypothesis: a very slender and rod-like jugal (59:1); a tapered quadratojugal process of the squamosal (106:0); a contact between palatine and ectopterygoid (121:1); hollowed basipterygoid processes (133:1); exits of CN X-XII that are flush with respect to the surface of the exoccipital (146:0); a triangular and significantly enlarged forebrain (165:1); the presence of a prootic pneumatic recess (167:1); subparallel dorsal and ventral edges of the dentary (197:0); a straight posterior end of the splenial (217:0); the absence of serrations on premaxillary teeth (225:1); maxillary and dentary teeth lacking mesial (anterior) carina (231:1); cervical neural spines of moderate height (i.e. shorter than the neural arch height) (275:1); a coracoid with a shallow ventral blade and an elongated posterior process (358:1); a shaft diameter of phalanx I-1 that is greater than the shaft diameter of the radius (433:1); a straight or gently curved ventral edge of the anterior ala of the ilium (450:0); an absence of the vertical ridge of the iliadic blade above the acetabulum (466:0); either stout or absent femoral medial epicondyle (medial distal crest, expanded medial lamella) (526:0); a medial proximal condyle of the tibia that is arcuate and posteriorly angular in proximal view (538:1); absent or weakly developed trough on the lateral surface of the proximal fibula (i.e. the surface is instead convex) (547:1); anterior portion of the proximal fibula in proximal view is subequal to the posterior portion in mediolateral width (549:0); and a lack of a horizontal groove across the anterior surface of the astragalar condyles (564:0). Support analyses ignoring unstable taxa indicate that this clade is well-supported, as evidenced by Bremer support values of 3 and jackknife frequencies of 80%.

In contrast to recent studies, we recover Alvarezsauria as the earliest-diverging clade of maniraptoriforms (Fig. S2: Supporting Information S4) rather than Ornithomimosauria as the earliest-diverging branch of this large clade. Eight characters support the grouping of Ornithomimosauria with later-diverging maniraptorans: 86:1, 151:0, 183:0, 266:2, 274:1, 303:0, 395:0, 597:1. However, the support for this novel interrelationship is low, with Bremer support values of 1 and jackknife frequencies <50% (even when the position of unstable taxa are ignored). This indicates that there is currently poor support for understanding the interrelationships of early diverging branches of Maniraptoriformes.

Eight synapomorphies support the monophyly of Alvarezsauria: an internal tuberosity that is separated from the humeral head by a distinct notch, and that often projects proximally above the humeral head (386:1); an internal tuberosity of the humerus that is triangular-shaped (and usually rounded) in anterior

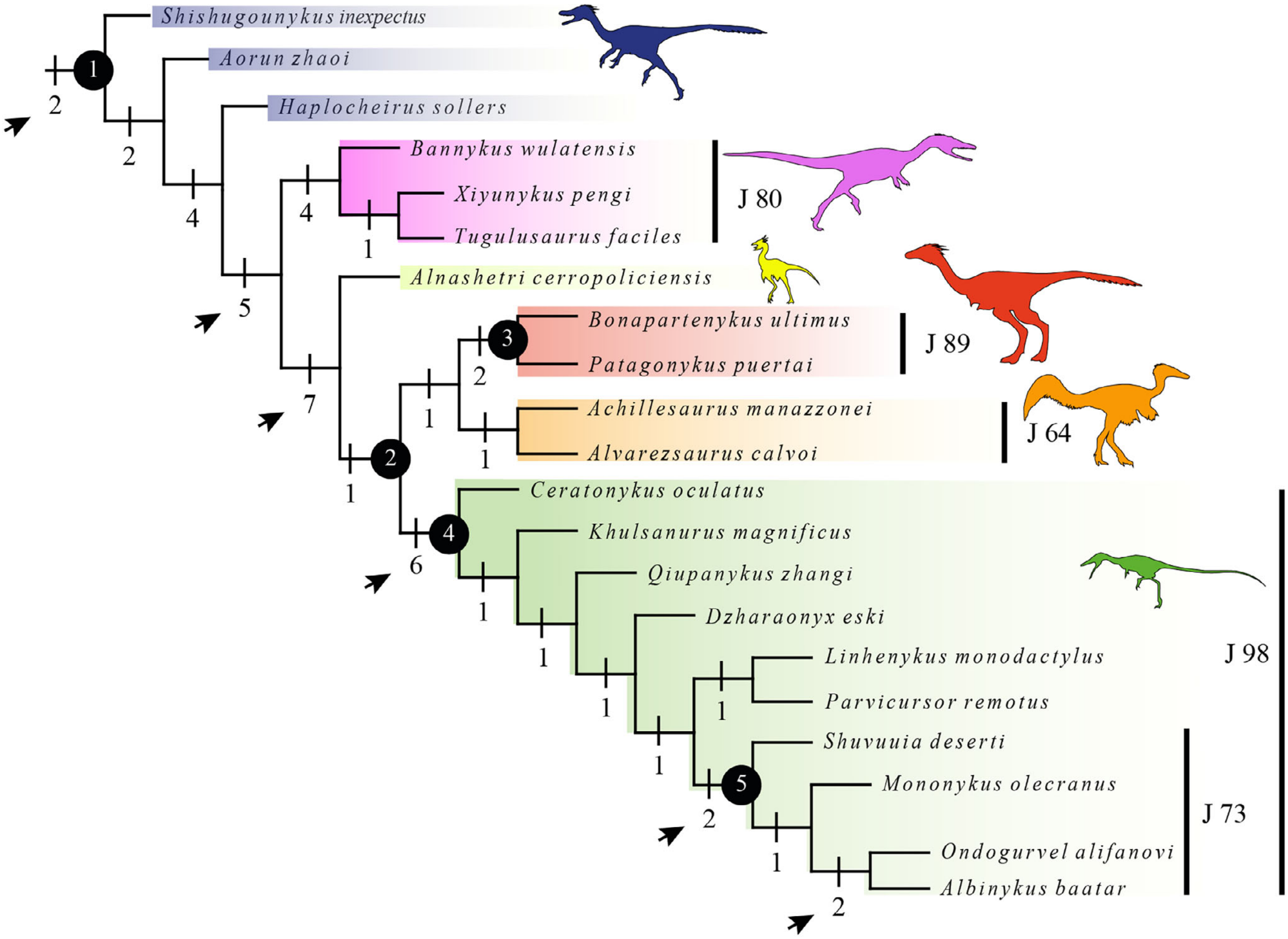

Fig. 2. Detail of Alvarezsauria interrelationships from the reduced consensus (3348 steps, consistency index = 0.223, retention index = 0.597) with *Heptasteornis*, *Albertonykus*, *Nemegtonykus*, *Trierarchuncus*, *Xixianykus*, *Kol*, *Stokesosaurus*, *Segnosaurus Gigantoraptor*, *Unenlagia* + *Neuquenraptor*, and *Sinornithoides* excluded posteriori to increase topographical resolution. Numbers represent Bremer support values and jackknife frequencies for each node, and the arrows highlight the nodes where an increase in Bremer support values is observed when *Kol* and *Xixianykus* are excluded posteriori. The range of blues represents the forms of the Upper Jurassic, the range of pink represents the forms of the Lower Cretaceous, the range of reds represents the forms of the Upper Cretaceous of Patagonia, and the range of greens represents the Parvicursorinae.

view (387:1); distal condyles of Mc I without collateral ligament fossae (418:1); digit I bearing a large ungual, much larger than the unguals of other digits (439:1); manual ungual I-2 showing partially enclosed proximal ends of the lateral grooves in ventral view (445:1); a distinctly projected lateral condyle of the femur that projects further than its medial counterpart, which in turn exhibits a flattened distal surface (531:1); ascending process of the astragalus with a step-like ridge running proximodistally rather than obliquely (545:2); and transversely expanded fossae in the proximal half of the ventral surface of manual unguals (638:1). The support for this clade is moderate even when the position of unstable taxa is ignored, with Bremer support values of 2 and jackknife frequencies of 70%. The moderate support for this node may be related to the number of plesiomorphic features exhibited by some of the early diverging alvarezsaurians, which led early studies to consider some of them (*Aorun* and *Tugulusaurus*) as early diverging maniraptoriforms (Rauhut and Xu, 2005; Choiniere et al., 2014a). In this sense, our analysis agrees with that of Xu et al. (2018) in the placement of *Aorun* and *Tugulusaurus* as early alvarezsaurians (*contra* Salgado et al., 2009; Hartman et al., 2019; Lee et al., 2019).

The three Jurassic alvarezsaurians are retrieved at the base of the clade. *Shishugounykus* is retrieved as the earliest-diverging branch of Alvarezsauria (Fig. 2), sister to remaining *Aorun* plus later-diverging alvarezsaurians (*contra* Xu et al., 2018; Lee et al., 2019; Qin et al., 2019; Averianov and Lopatin, 2021, 2022a, 2022b; Averianov and Sues, 2021). The later-diverging placement of *Aorun* is supported by four synapomorphies (325:1, 431:1, 441:1, 631:1) and support values are rather low (with jackknife frequencies <50%). *Haplocheirus* is depicted at the next branching event, in agreement with previous studies. The closer relationship of *Haplocheirus* with Cretaceous alvarezsaurians is better supported with Bremer support values reaching 4 and jackknife frequencies just >50% (see Supporting Information S5). All Cretaceous alvarezsaurians are clustered in a monophyletic group that is robustly supported, with Bremer support values of 5 and jackknife frequencies of 86% (when unstable taxa are ignored; see Supporting Information S5).

Our analysis recovers a novel clade made up of *Tugulusaurus* + *Xiyunykus*, with *Bannykus* as their sister-taxon (Fig. 2). The sister-relationship between *Tugulusaurus* and *Xiyunykus* has been retrieved in previous studies (e.g. Xu et al., 2018) and is supported by only one character—the presence of a narrow ascending process of the astragalus, which covers only the lateral half of the anterior surface of the tibia (560:1). By contrast, the clade formed by these three alvarezsaurians from the Early Cretaceous of China is novel and well-diagnosed by 10 synapomorphies: a posterior opening of the basisphenoid recess divided into two small, circular foramina (140:1); an expanded external surface of the coracoid ventral to the glenoid fossa and along the dorsal margin of the posteroventral blade (this expansion forms a triangular subglenoid fossa bounded laterally by the coracoidal tuber) (360:1); an acromion whose margin is continuous with the scapular blade (369:0); an internal tuberosity of the humerus that while hypertrophied is not individualized from the humeral head (386:2); a transverse width of distal humerus that is >2.7 times the width of the shaft (389:0); a proximomedial tab on the proximal end of metacarpal I (NB we use traditional nomenclature with digits I, II and III, following the concept of Lateral Digit Reduction) projecting well-beyond the proximal articular surface (415:1); the proximal placement of the flexor tubercles of the manual unguals (441:0); a femoral head that is anteromedially directed (516:0); an ascending process that is higher than the body of the astragalus (558:1); and straight-shaped penultimate manual phalanges (631:0). The support of this clade also is high, with Bremer support values reaching 4 and jackknife frequencies of 80% when unstable taxa are ignored (see Supplemental Data).

Alnashetri is recovered outside Alvarezsauridae (Fig. 2), a proposal that is earlier-diverging than previous phylogenetic analyses based on the holotype (e.g. Makovicky et al., 2012; Gianechini et al., 2018), and later-diverging than in a recent study of this taxon based on a new specimen (Makovicky et al., 2024). Several morphologies support the close affinities of this taxon with alvarezsaurids: a poorly developed basisphenoid recess (137:0); a prominent antitrochanter (473:1); a lesser trochanter that is separated from the greater trochanter by a small groove (519:1); the absence of an ascending process of the astragalus bearing a distinct 'step' that runs obliquely over the anterior surface of the distal tibia (545:0); an astragalus and calcaneum bearing distinct condyles (555:1); a metatarsal IV that is markedly longer than metatarsal II (584:1); deep and proximally extensive extensor ligament pits on the dorsal surface of the phalanges of pedal digit IV (588:1); a deep ventrodistal (flexor) fossa of manual phalanx 1-I (605:1); and keel-shaped flexor process of the manual unguals (641:1). This node is remarkably well-supported when unstable taxa are ignored with a Bremer support value of 7 and jackknife frequencies >90%.

Alvarezsauridae is very well-resolved in our analysis, with a different topology (Fig. 2) than recent analyses based on the Xu et al. (2018) data matrix (e.g. Lee et al., 2019; Qin et al., 2019; Averianov and Lopatin, 2021, 2022a, 2022b; Averianov and Sues, 2021) and with some differences to those based on the TWiG dataset (e.g. Gianechini et al., 2018). The synapomorphies recovered for this clade include: absence of neural spines in the distal caudals (332:1); distal carpals fused to metacarpals (i.e. a carpometacarpus) (409:1); weak curvature of the ventral surface on manual ungual I (442:1); the presence of paired flexor processes on the proximal ventral surface of phalanx I-1 (these processes have a 25–45% dorsoventral extension with respect to the dorsoventral height of phalanx I-1) (603:1); a longitudinal furrow on the lateral and medial sides of manual non-ungual phalanges (634:1); and a height-to-width ratio of the proximal surface of the manual unguals that is <3/2 (636:0). The support of this clade, as well as of the internal nodes involving the lineages recorded in South America, has low values, even when unstable and incomplete taxa such as *Achillesaurus* are ignored.

Our analyses recover two clades within Alvarezsauridae: a clade of Patagonian taxa including Patagonykinae (i.e. *Patagonykus* + *Bonapartenykus*) and a novel unnamed clade (*Alvarezsaurus* + *Achillesaurus*) and a second later-diverging clade representing the Parvicursorinae (Fig. 2). The first clade (i.e. Patagonykinae + [*Alvarezsaurus* + *Achillesaurus*]) is supported by the presence of lateral depressions in the anterior caudal centra (323:1), a scapular blade that is continuous with the margin of the acromion (369:0), and a small tab present proximally on the flexor surface of metatarsal II (574:0). In turn, Patagonykinae is supported by a well-developed spinopostzygapophyseal lamina of the dorsal vertebrae that ends abruptly on the dorsal surface of the postzygapophysis (302:1); a lateral ridge extending along the lateral margin of the coracoid (363:1); a ventral half of the lateral surface of the coracoid that is rugose and heavily textured (364:1); and a ventral portion of the coracoid that is directed ventromedially forming an obtuse angle with the dorsal portion of the bone (365:1). The sister-relationship between *Achillesaurus* + *Alvarezsaurus* is supported by two characters: a lesser trochanter that is separated from the greater trochanter by a deep cleft (519:0), and the presence of a horizontal groove across the anterior surface of the astragalar condyles (565:1). As noted above, these clades are poorly supported and alternative hypotheses depicting Patagonykinae as earlier-diverging or later-diverging than *Alvarezsaurus* are only marginally suboptimal.

The late-diverging Parvicursorinae is recovered as a monophyletic group with a resolved topology, in contrast to a series of recent studies (e.g. Alifanov and Barsbold, 2009; Choiniere et al., 2010, 2014a; Pittman et al., 2015; Cau et al., 2017; Gianechini et al., 2018; Lü et al., 2018; Lee et al., 2019; Qin et al., 2019; Averianov and Lopatin, 2021, 2022b; Averianov and Sues, 2021). This clade is supported by eight synapomorphies: absence of pleurocoels in cervical vertebrae (258:0); triangular or rounded shape of the internal tuberosity of the humerus in anterior view (387:0); absent or reduced, and laterally facing, fibular facet of the astragalus (557:1); broad ascending process of the astragalus covering most of the anterior surface of the distal tibia (559:1); presence of a notch on the medial edge of the ascending process of the astragalus (560:1); a caudally or medially flange projecting posteromedial from the shaft of metatarsal II (577:1); metatarsal III not reaching the proximal end of the metatarsus (579:2); and penultimate manual phalanges with a straight shaft (631:0). Our recovered topology of Mononykini also is different to that of previous studies (e.g. Agnolín et al., 2012; Xu et al., 2018; Lee et al., 2019; Qin et al., 2019; Averianov and Lopatin, 2021, 2022a, 2022b; Averianov and Sues, 2021). This later-diverging clade is supported by the presence of a straight shaft of metacarpal II (420:0); subequal width of the shafts of metacarpal III and metacarpal II (422:0); tapered distal end of ischium (505:2); and a femoral popliteal fossa that is distally closed off by condylar contact (527:1). This group also is highly supported when unstable and fragmentary taxa are ignored, which coincides with the fact that multiple previous studies have retrieved this group as monophyletic (e.g. Agnolín et al., 2012).

The results obtained from the second analysis are essentially similar to those of the primary analysis, except for the position of *Kol ghuva*, which is recovered as an earlier diverging Parvicursorinae. This positioning may be to the consequence of the large number of missing data entries, which places it in an earlier diverging position when *Shuvuuia*, a taxon with which it shares many Mononykini characters, is excluded. Additionally, this analysis reveals a greater number of unstable taxa (see Fig. S4: Supporting Information S4). This suggests that the lack of resolution in the original polytomy is not solely caused by the inclusion of distinct possible semaphoronts of the same species. Instead, it may indicate that the instability of certain taxa is inherent to the dataset, or that ambiguous or shared features hinder a clear resolution of the phylogenetic relationships, irrespective of the exclusion of semaphoronts. This is evident in part from the topological position of *Aorun* and *Haplocheirus* within the first analysis. Although these two taxa represent juvenile individuals, they are positioned as later-diverging alvarezsaurians than *Shishugounykus*, a taxon that, ontogenetically, represents a skeletally mature individual.

Body-mass and body-length estimates

Body-mass and body-length estimates for the earliest-diverging alvarezsaurians were 16.96 kg and 2.41 m for *Haplocheirus sollers* (Choiniere et al., 2010), 4.02 kg and 1.68 m for *Aorun zhaoi* (Choiniere et al., 2014a), and 9.03 kg and 2.06 m for *Shishugounykus inexpectus* (Qin et al., 2019); all from the Oxfordian Shishugou Formation (Junggar Basin, Xinjiang, China). For the remaining, early diverging alvarezsaurians, the body mass and body length of *Bannykus wulatensis* (Xu et al., 2018), from the Aptian Bayingobi (Bayan Gobi) Formation (Gobi Desert, Nei Mongol, China), were estimated at 29.55 kg and 2.77 m; whereas for *Xiyunykus pengi* (Xu et al., 2018) and *Tugulusaurus faciles* (Dong, 1973; Rauhut and Xu, 2005) from the upper section of the Barremian–Aptian Tugulu Group (Junggar Basin, Xinjiang, China), these estimates were 15.42 kg and 2.36 m, and 17.14 kg and 2.42 m respectively (Fig. 3; Supporting Information S1: 3. Body mass-Alvarezsauria and 5. Body length-Alvarezsauria).

Body-size and body-length estimates for Asian alvarezsaurids are in the ranges 0.38–10.8 kg and 0.79–2.16 m (see Supporting Information S1: 3. Body mass-Alvarezsauria and 5. Body length-Alvarezsauria). The oldest known alvarezsaurid from Asia, *Dzharaonyx eski* (Averianov and Sues, 2021) (Turonian Bissekty Formation, Uzbekistan), has an estimated body mass of 1.75 kg (NBthis value was estimated from ZIN PH 2634/16 and 2444/16 because they represent the most somatically mature specimens; Averianov and Sues, 2017, 2021). Among the partial skeletons that have been recovered from China, *Xixianykus zhangi* (Xu et al., 2010) (Coniacian–Santonian Majicun Formation of Henan) and *Linhenykus monodactylus* (Xu et al., 2011, 2013) (Campanian Wulansuhai Formation of Nei Mongol) have comparable body mass estimates (0.48 kg). A slightly higher value of 0.58 kg is recovered for *Qiupanykus zhangi* (Lü et al., 2018) (upper Maastrichtian Qiupa Formation of Henan) (Fig. 3;

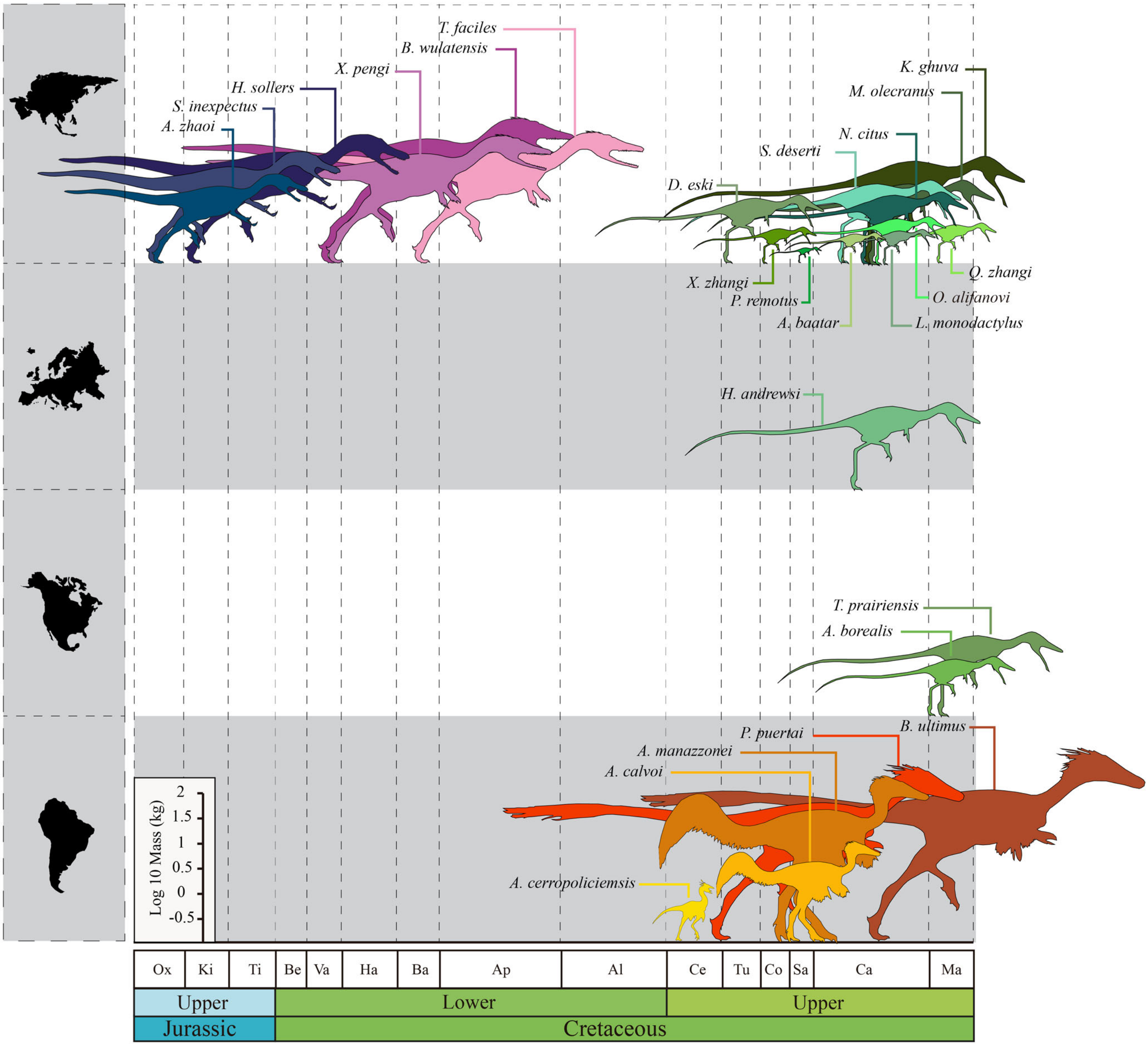

Fig. 3. Relative body sizes of Alvarezsauria calibrated with the geological age of known alvarezsaurian taxa and showing their continental distribution. Silhouettes calibrated with body mass. The range of blues represents the forms of the Upper Jurassic, the range of pink represents the forms of the Lower Cretaceous, the range of reds represents the forms of the Upper Cretaceous of Patagonia, and the range of greens represents the Parvicursorinae.

Supporting Information S1: 3. Body mass-Alvarezsauria). In regards to the exceptionally-preserved alvarezsaurids from the Upper Cretaceous of Mongolia, *Shuvuuia deserti* (Chiappe et al., 1998) and *Kol ghuva* (Turner et al., 2009)—from the upper Campanian Djadokhta Formation—had body masses estimated to be 2.33 and 10.8 kg, respectively, and the values for the coeval *Mononykus olecranus* (Perle et al., 1993, 1994) and *Nemegtonykus citus* (Lee et al., 2019) (both from the upper Campanian-lower Maastrichtian Nemegt Formation) were 4.23 and 2.44 kg, respectively (Fig. 3; Supporting Information S1: 3. Body mass-Alvarezsauria). Four alvarezsaurids are known from the lower Maastrichtian Barun Goyot Formation: *Parvicursor remotus* (Karhu and Rautian, 1996) (body mass estimate 0.20 kg), *Ceratonykus oculatus* (Alifanov and Barsbold, 2009) (1.70 kg), *Khulsanurus magnificus* (Averianov and Lopatin, 2022a) (1.80 kg) and *Ondogurvel alifanovi* (Averianov and Lopatin, 2022b) (2.70 kg). Finally, the Campanian Javkhlant Formation has preserved the small alvarezsaurid *Albinykus baatar* (Nesbitt et al., 2011), whose body mass was calculated as 0.38 kg (Fig. 3; Supporting Information S1: 3. Body mass-Alvarezsauria).

The South American alvarezaurian record comprises entirely taxa from the Upper Cretaceous of Patagonia, Argentina. *Alnashetri cerropoliciensis* from the Cenomanian, Candeleros Formation (Makovicky et al., 2012, 2016) is currently the only non-alvarezsaurid alvarezsaurian from South America with a body mass and body length estimated to be 2.41 kg and 1.48 m, respectively. For *Patagonykus puertai* from the middle Turonian–later Coniacian, Portezuelo Formation (Novas, 1996, 1997) these estimates were 58.17 kg and 3.29 m. Estimates of 4.34 kg and 1.72 m for *Alvarezsaurus calvoi* (Bonaparte, 1991) and 40.84 kg and 3.01 m for the alvarezsaurid *Achillesaurus manazzonei* (Martinelli and Vera, 2007) represent the taxa recovered from the Santonian Bajo de La Carpa Formation. Patagonykine alvarezsaurids *Bonaparenykus ultimus* (Agnolín et al., 2012) and MPCN-PV 738.1 (Meso, 2022), from the middle Campanian–lower Maastrichtian Allen Formation, had body-mass estimates of 43.75 and 59.88 kg, respectively, and body-length estimates of 3.06 and 3.31 m, respectively (Fig. 3; Supporting Information S1: 3. Body mass-Alvarezsauria and 5. Body length-Alvarezsauria).

European alvarezsaurians are only represented by alvarezsaurids from the Upper Cretaceous. *Heptasteornis andrewsi* (Harrison and Walker, 1975; Naish and Dyke, 2004), from the Maastrichtian Sânpetru Formation (Haţeg Basin, Romania), was estimated to have a body mass of 6.16 kg and a body length of 1.87 m. Likewise, North American alvarezsaurids also are known from the Maastrichtian and from scarce alvarezsaurid fossil material. Body-mass estimates for *Albertonykus borealis* (Longrich and Currie, 2009) (lower Maastrichtian Horseshoe Canyon Formation of Alberta, Canada) and *Trierarchuncus prairiensis* (Fowler et al., 2020) (late Maastrichtian Hell Creek Formation of Montana, United States) were estimated to be 4.65 and 4.30 kg, respectively, with body-length-estimations of 1.75 and 1.71 m respectively (Fig. 3; Supporting Information S1: 3. Body mass-Alvarezsauria and 5. Body length-Alvarezsauria).

Body-mass evolution and phylogenetic trends

The results obtained show that the common ancestor of Alvarezsauria would have weighed ~11.4 kg (Fig. 4a; Fig. S1: Supporting Information S5), less than half of the ~23 kg value recovered by Qin et al. (2021). With respect to the Chinese non-alvarezsaurid alvarezsaurians (i.e. unnamed node including *Bannykus*, *Xiyunykus,* and *Tugulusaurus*), their hypothesized ancestor remained at a median body size of ~17.3 kg during the Tithonian (Fig. 4a; Fig. S1: Supporting Information S5). Subsequently, this clade evolved significant body-size variations in Asia ranging from ~15.42 to ~17.14 kg (i.e. *Xiyunykus* and *Tugulusaurus*) up to ~29.55 kg (i.e. *Bannykus*) accentuated during the Barremian-Aptian (Fig. 4a; Fig. S1: Supporting Information S5).

In Patagonia, the ancestor of the alvarezsaurian clade including *Alnashetri* as an early diverging non-alvarezsaurid member would have been ~13.3 kg (Fig. 4a; Fig. S1: Supporting Information S5). Additionally, our estimates suggest a body mass of ~23.1 kg for the common ancestor of Alvarezsauridae, which is more than threefold heavier than the ~7.4 kg recovered by Qin et al. (2021) (Fig. 4a; Fig. S1: Supporting Information S5). Alvarezsauridae split into two branches around the Turonian. The first branch contains all of the Patagonian forms which had a common ancestor that evolved a greater mass of ~33.4 kg and gave rise to a diversification event during the late Coniacian (Fig. 4a; Fig. S1: Supporting Information S5). The parvicursorine common ancestor of the second branch is lighter than the alvarezsaurid common ancestor (estimated body mass of ~17.2 kg rather than ~23.1 kg) that gave rise to a branching event during the early Coniacian (Fig. 4a; Fig. S1: Supporting Information S5). Regarding the hypothetical ancestor of Patagonykinae, our data suggest an even heavier estimated body mass of ~47.9 kg giving rise to a diversification event during the late Coniacian (Fig. 4a; Fig. S1: Supporting Information S5). Finally, the common ancestor of Mononykini is reconstructed to the Coniacian–Santonian with a much lighter estimated body mass of ~5.5 kg (Fig. 4a; Fig. S1: Supplementary Information S5).

Our palaeodiversity analysis using the resultant tree topology for Alvarezsauria shows a low but consistent range of diversity during the Oxfordian–early Hauterivian (Fig. 4b), followed by two events of evolutionary stasis between the Barremian and early Albian, and the late Albian and Santonian (Fig. 4b). Our data also reveal a major diversification event during the Santonian to Campanian transition which resulted in a threefold increase in the number of taxa (Fig. 4b).

Results obtained from Campione et al. (2014)'s body-mass equation show a pattern similar to that obtained from Christiansen and Fariña (2004)'s equation. For example, the common ancestor of Alvarezsauria would have weighed ~8.75 kg, whereas the hypothesized ancestor of Chinese non-alvarezsaurid alvarezsaurians would have weighed ~16.87 kg. The ancestor of the alvarezsaurian clade that includes *Alnashetri* as a non-alvarezsaurid early diverging member would have been ~10 kg. Our estimates suggest that the common ancestor of Alvarezsauridae would have weighed ~15 kg, whereas the common ancestor of Patagonian taxa would have weighed ~22.5 kg. For

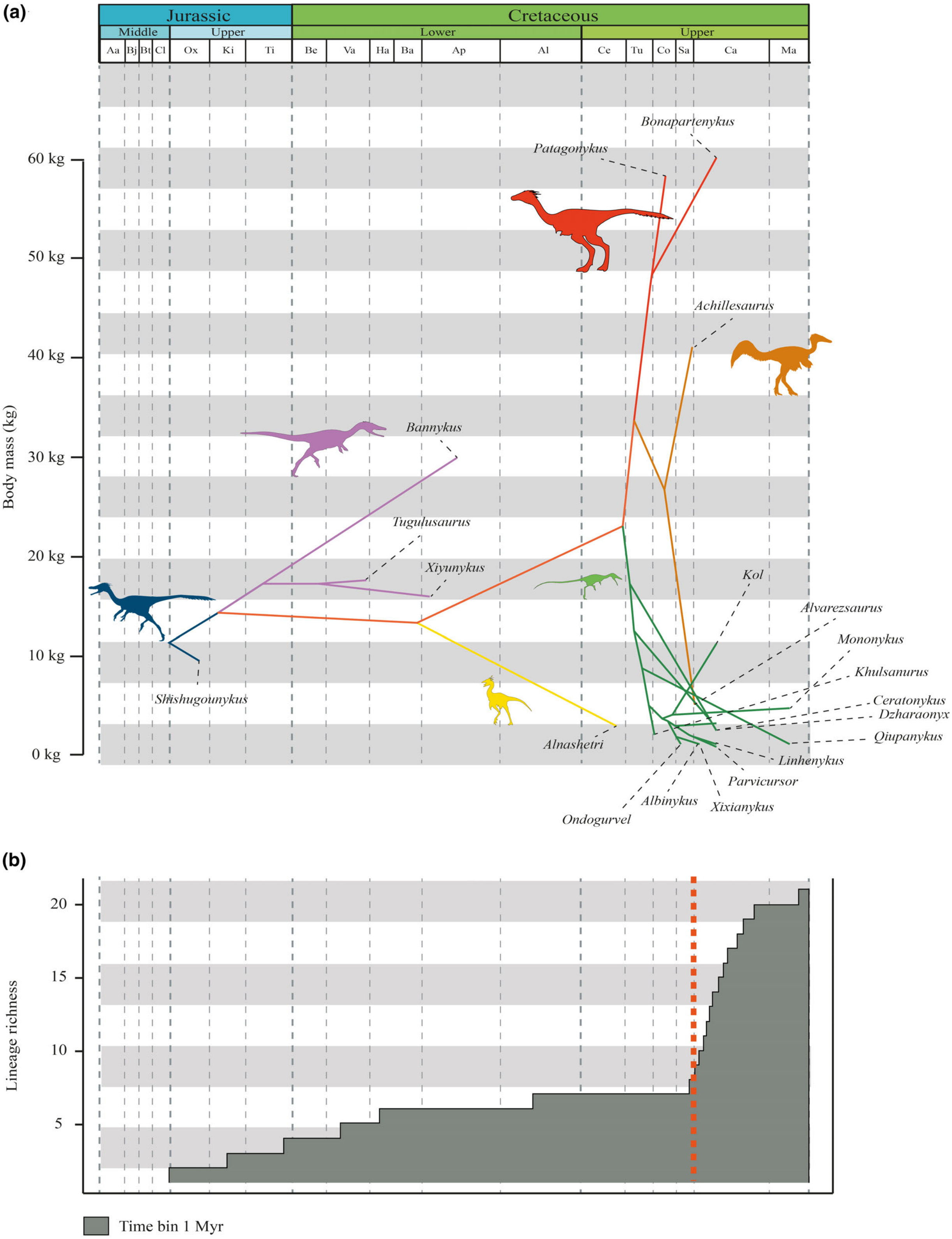

Fig. 4. Body-mass evolution of Alvarezsauria and its diversification through time. (a) Body-mass evolution within Alvarezsauria, showing trends at each node; and (b) explosive speciation and diversification that occurred within Alvarezsauria after the red line. The range of blues represents the forms of the Upper Jurassic, the range of pink represents the forms of the Lower Cretaceous, the range of reds represents the forms of the Upper Cretaceous of Patagonia, and the range of greens represents the Parvicursorinae.

the common ancestor of Patagonykinae, the estimated body mass is ~31.25 kg, and with Parvicursorinae ~11.2 kg. Finally, the common ancestor of Mononykini is estimated with a body mass of 3.75 kg (Figs S2 and S3: Supporting Information S5).

The results obtained from our primary reduced consensus tree, with body masses calculated using the equations from Christiansen and Fariña (2004) and log-transformed to normalize the data, reveal the same hypotheses proposed previously. However, these data made it easier to visualize the events mentioned above (Figs S4 and S5: Supporting Information S5). The results from the subset of MPTs, including the Parvicursorinae taxa excluded from the reduced consensus tree, show very similar outcomes to those obtained in the reduced consensus tree (Figs S6 and S17: Supporting Information S5). The results show that despite the various positions of the unstable taxa, they do not affect our interpretations. The entire subset of the most parsimonious trees analysed here supports our hypothesis.

Finally, the results obtained from our reduced consensus tree, utilizing the branch temporal calibration methods MBL and Cal3, support the three events of miniaturization and the trend towards large body masses in Patagonykinae proposed using the DatePhylo calibration method. The only variation observed is in the branch interval leading to *Alnashetri*; depending on the method used, this event is either similar to the proposed scenario or occurs during the Albian–Cenomanian interval (Figs S18 and S23: Supporting Information S5).

Morphological evolutionary rates of the alvarezsaurian skeleton

Analyses of morphological evolutionary rates derived from all characters show relatively low values with the exception of four specific time intervals with elevated evolutionary rates (Fig. 5): (i) Bathonian to Callovian, (ii) late Hauterivian to early Berriasian (i.e. the branch leading to the clade composed by *Bannykus*, *Tugulusaurus,* and *Xiyunykus*), the early Cenomanian (i.e. the branch leading to Alvarezsauridae and the early diverging parvicursorines), and the late Cenomanian–Turonian (i.e. in Patagonykinae and Mononykini). The branches that cross these lapses are temporally short and concentrate a large number of character changes, resulting in high rates of morphological evolution. This pattern is common to other parsimony-based estimates (see Pol et al., 2024) but it is worth noting there are many other branches in the tree with minimum temporal length that do not have concentrated anatomical changes and are therefore depicted as having low evolutionary rates. The analyses using only specific anatomical regions (e.g. pectoral girdle and forelimb, hind limb, and tail) show a similar pattern (Figs 6 and 7); an exception is the hind limb and tail that show a uniform evolutionary rate within Parvicursorinae (Fig. 7). We were unable to calculate evolutionary rates for the skull because there was insufficient preservation of elements across the sample to recover a meaningful result (as parsimony estimates tend to result in extremely low rates when missing data is extremely abundant).

Discussion

Our phylogenetic analysis recovered a novel topology for the early diverging Asian alvarezsaurian lineages and for Late Cretaceous taxa nested within Alvarezsauridae. These results support the monophyly of Alvarezsauridae and recover *Alvarezsaurus* and *Achillesaurus* as early diverging members of this clade. *Alnashetri* is nested as a non-alvarezsaurid alvarezsaurian. Patagonykinae is nested within Alvarezsauridae, and together with *Alvarezsaurus* and *Achillesaurus*, they are recovered as the sister-group of Parvicursorinae. The applied scripts in the analysis ensure that low-supported nodes were not to the result of unstable taxa. Support for the [*Bannykus* + (*Tugulusaurus* + *Xiyunykus*)], Patagonykinae, and Parvicursorinae nodes are strongly supported. These high-support values may be indicative of an endemic clade originating in Asia early in the evolutionary history of alvarezsaurians. Likewise, these support values indicate that Patagonykinae is endemic to South America and is currently known only from Patagonia.

Our body-mass analysis enabled by our improved phylogenetic framework reconstructs a body mass of 11.4 kg for the common ancestor of Alvarezsauria. This is lighter than early diverging alvarezsaurians which maintained median body sizes of 15.4–29.0 kg, showing a significant body-mass variation during the Valanginian to Aptian stages of the Cretaceous. We infer body masses of 23.1 and 47.9 kg for the common ancestors of Alvarezsauridae and Patagonykinae, respectively, and 17.2 kg for the common ancestor of the Parvicursorinae. Such inferences suggest the presence of at least three independent miniaturization events within Alvarezsauria, two in Gondwana (Patagonia) and one in Laurasia (Asia).

The first independent miniaturization event was during the Aptian to Cenomanian within the lineage leading to the non-alvarezsaurid *Alnashetri* (~2.4 kg subadult), which directly follows higher morphological rates detected during the Bathonian–Callovian stages of the Jurassic and the Hauterivian–early Berremian stages of the Cretaceous. In contrast to previous work (*contra* Xu et al., 2013, 2018; Ding et al., 2020), our results indicate that alvarezsaurians had already

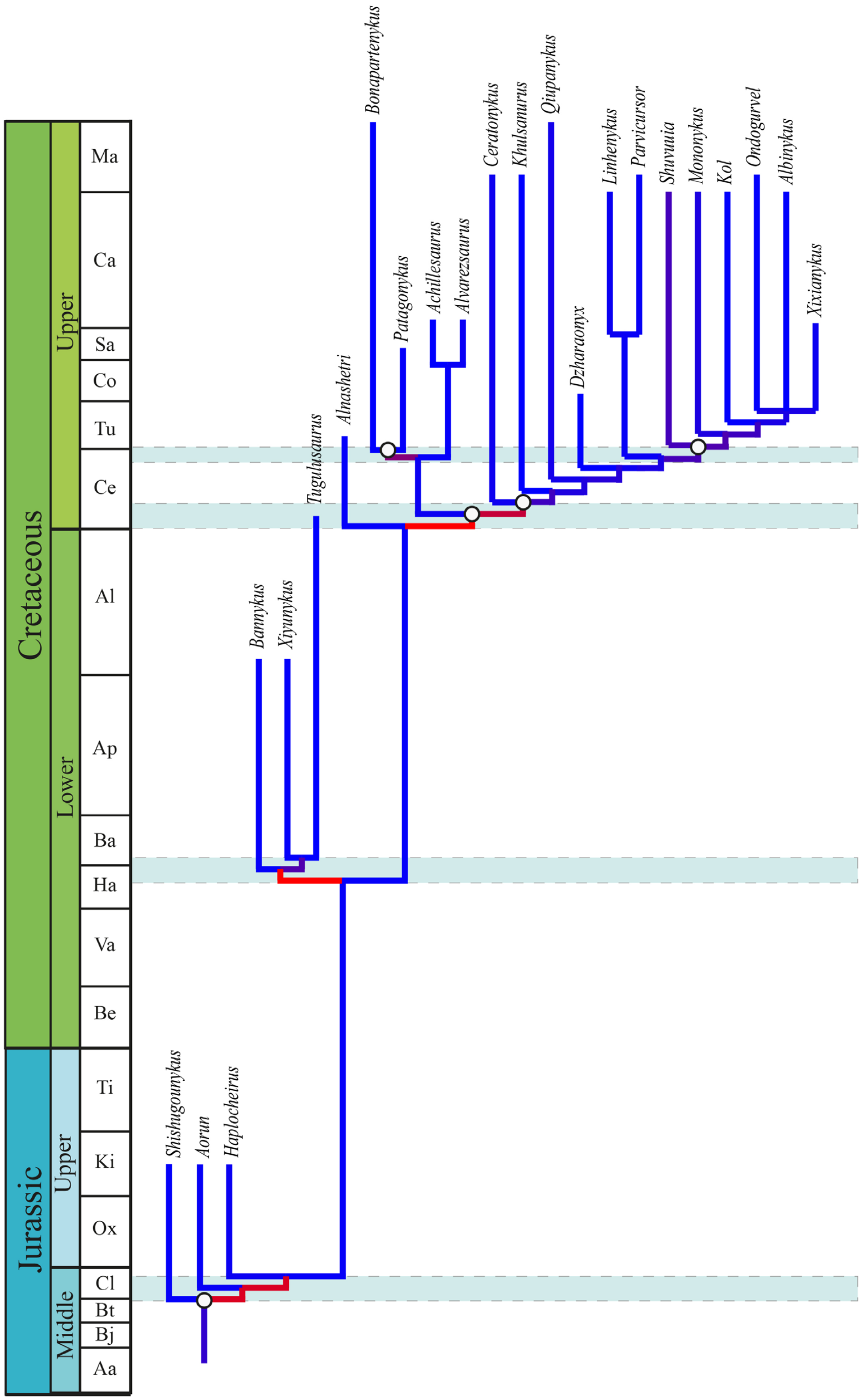

Fig. 5. Evolutionary morphological rates calculated from all phylogenetic characters and time-calibrated reduced consensus tree.

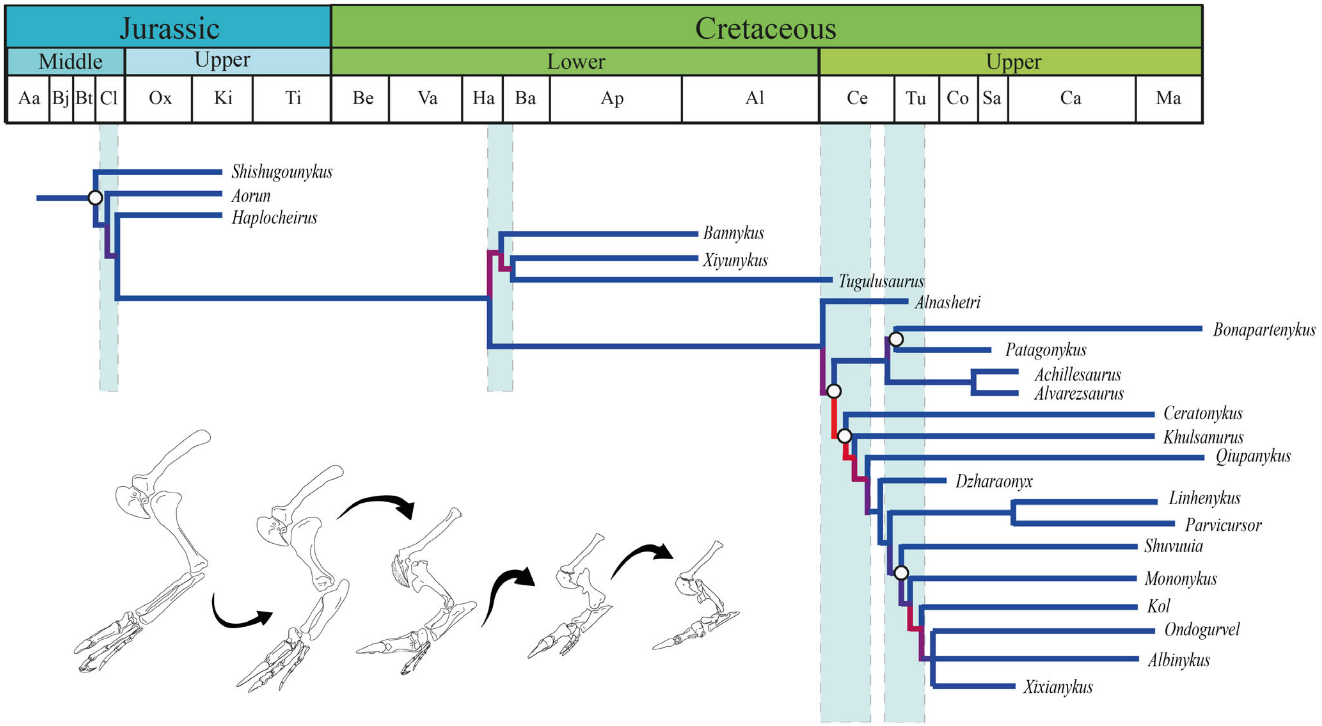

Fig. 6. Evolutionary morphological rates calculated from phylogenetic pectoral girdle and forelimb characters, and a time-calibrated reduced consensus tree.

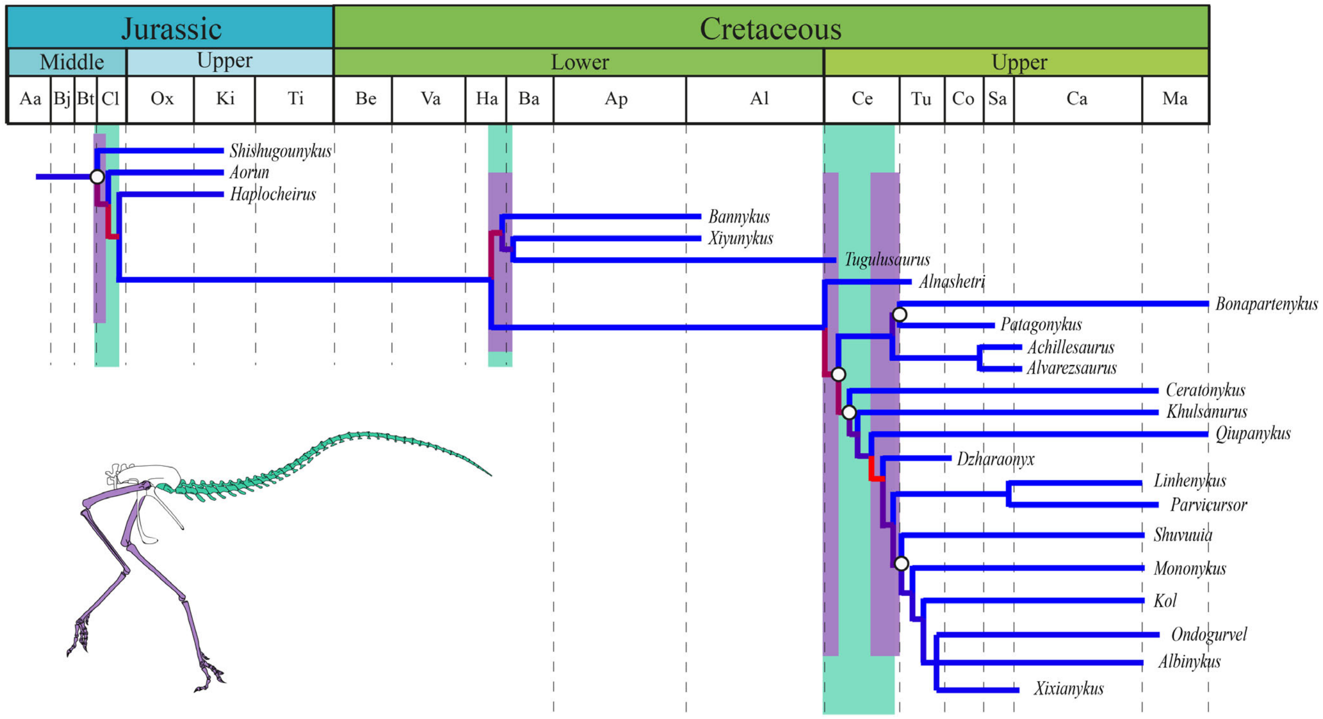

Fig. 7. Evolutionary morphological rates calculated from phylogenetic hind limb and tail characters, and a time-calibrated reduced consensus tree.

dispersed to South America between the Kimmeridgian and Aptian. During the end of the Jurassic and the beginning of the Cretaceous, there was a brief "Cold House" period (Iglesias et al., 2011) that was likely to have been a climatic event contributing to the intercontinental dispersal of alvarezsaurians that potentially stimulated their miniaturization. In fact, Ding et al. (2020) mentioned that continental-scale vicariance induced by the breakup of Pangaea in the ate Jurassic was an important biogeographical process that influenced coelurosaurian evolution more broadly. During the Aptian–Albian of Gondwana, large theropod faunae comprising ceratosaurians, spinosaurids, carcharodontosaurids, and early diverging coelurosaurians diversified (Novas et al., 2013; Meso et al., 2021a). These faunae were part of the broader "Middle Cretaceous Faunal Assemblage of Gondwana" (MCFAG) that spanned the Aptian–middle Turonian interval (Meso et al., 2021a). Its coincidence with this alvarezsaurian miniaturization event suggests this diversification also was a contributing factor, presumably through saturation of theropod body-size niches in terrestrial ecosystems (Peris and Condamine, 2024) that compelled alvarezsaurians to explore new frontiers in their body plan. The initial breakup of Gondwana during the Early Cretaceous also coincides with this miniaturization event which significantly influenced plant distribution by geographically restricting palaeofloras leading to new biome development (Iglesias et al., 2011), which may too have influenced evolution towards miniaturization. Specifically, Patagonian palaeofloras show a considerable increase in floristic diversity including groups such as Cyatheaceae, Cycadales, and Cheirolepidiaceae, and document the diversification of Araucariaceae, Podocarpaceae, and Taxodiaceae (Iglesias et al., 2011). In fact, Patagonia, West Antarctica (Antarctic Peninsula, Thurston Island, and Marye Bird Land), New Zealand, New Caledonia and other smaller islands, Tasmania, and mainland Australia all shared a floristic similarity and could have belonged to the same Warm Temperate climatic zone (Iglesias et al., 2011). It also is noteworthy that divergence of early diverging isopteran termites (e.g. Kalotermitidae and Stolotermitidae) also happened during the Early Cretaceous when New Zealand was part of West Antarctica (Engel et al., 2009), which is one of the possible insect food sources traditionally suggested for certain alvarezsaurids (Qin et al., 2021). Although the termite fossil record is scarce and fragmentary worldwide, in Argentina, there are records of borings and coprolites in Early Cretaceous conifer wood from the Kachaike Formation (early Aptian–early Turonian) and from a cycad stem from the Upper Cretaceous Allen Formation (Genise, 1995; Greppi et al., 2023). Thus, the apparent diversification of alvarezsaurs in South America during the Aptian, and the first miniaturization event of this clade, seems to correlate with the rapid expansion of herbivorous and social insects, suggesting an evolutionary radiation that was in some way connected to the fulfillment of ecological niches that use food resources that became available in terrestrial ecosystems. At the same time, some authors highlight important morphological specializations in eusocial termites associated with large termite mounds (Lloyd et al., 2008; Engel et al., 2016; Zhao et al., 2020). This complexity at the level of both colony architecture and termite specialization could be attributable to coevolution in which a new ecological niche exploited by alvarezsaurids may have contributed to the rapid specialization of these insects.

The second independent miniaturization event was during the Turonian to Coniacian within Parvicursorinae (partly supported by an alvarezsaurid from the Turonian Bissekty Formation (Averianov and Sues, 2017, 2021) with an estimated body mass of ~1.5 kg). The third independent miniaturization event was during the Coniacian to Santonian stage of the Cretaceous at the base of Alvarezsauridae sustained by *Alvarezsaurus* (~4.3 kg subadult). These second and third miniaturization events follow elevated evolutionary rates detected in the early Cenomanian and late Cenomanian–Turonian stages. Our results also provide the first quantitative support for an increasing body-size trend within Patagonykinae, providing robust evidence of the complex body-size patterns among alvarezsaurians (Fig. 8). Regarding the radiation of alvarezsaurids in Patagonia during the Turonian, the second Coniacian–Santonian miniaturization event, alvarezsaurid dispersal into Laurasia, and the Cenomanian–Turonian "gigantism" event in Patagonykinae, they all appear to correlate with faunistic turnover leading up to the end of the MCFAG in South America. For example, the common MCFAG lineages of ceratosaurids, elaphrosaurine noasaurids, carcharodontosaurids, rebbachisaurids, early-diverging titanosaurians, and uruguaysuchid mesoeucrocodylians all disappear from the fossil record of Patagonia (Coria and Salgado, 2005; Novas et al., 2013; Meso et al., 2021a). This event is likely to have contributed to a subsequent adaptive radiation of clades including patagonykine alvarezsaurians as well as furileusaurian abelisaurids, megaraptorids and later-diverging unenlagiids (Coria and Salgado, 2005; Novas et al., 2013; Meso et al., 2021a).

Finally, another event that was likely to have influenced all three miniaturization events to some extent was the Cretaceous Terrestrial Revolution (KTR). This event involved the earliest radiation of angiosperms and contributed to the emergence of new lineages across terrestrial ecosystems, including the diversification of insects (Lloyd et al., 2008; Peris and

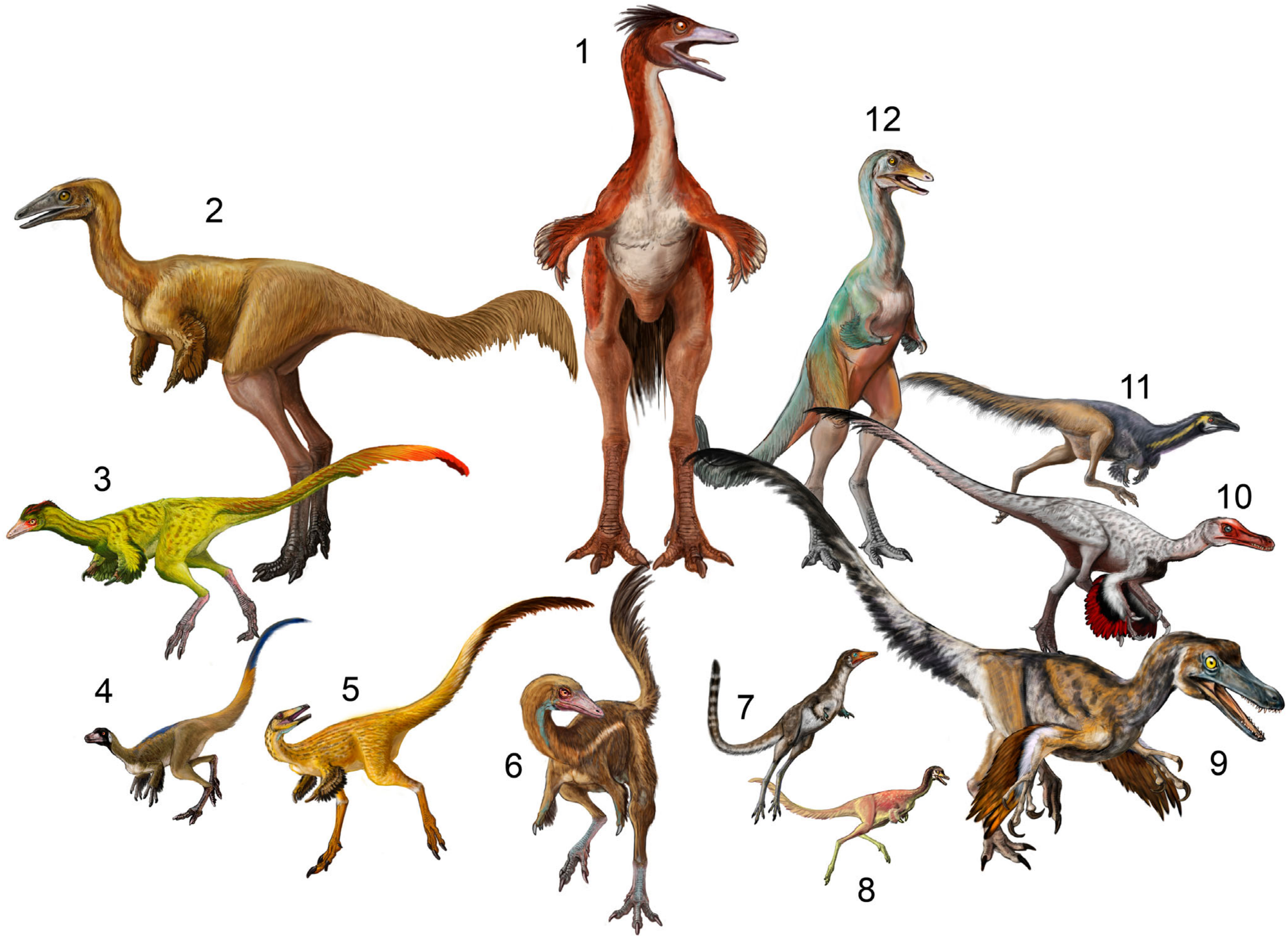

Fig. 8. Life reconstruction of 12 alvarezsaurians that illustrate body-size change in the clade. 1, *Bonapartenykus*; 2, *Patagonykus*; 3, *Alvarezsaurus*; 4, *Alnashetri*; 5, *Albertonykus*; 6, *Heptasteornis*; 7, *Dzharaonyx*; 8, *Linhenykus*; 9, *Haplocheirus*; 10, *Shishugounykus*; 11, *Kol*; 12, *Bannykus*. Artwork by Abel G. Montes.

Condamine, 2024), which are one of the food sources suggested for large-diverging alvarezsaurians in particular (Qin et al., 2021).

In contrast to Xu et al. (2018), our evolutionary rate data does not support mosaicism, but rather an incremental acquisition pattern of osteological specializations. Our analyses show that the forelimb, pelvis, hind limb, and tail acted as independent locomotor units, yet our results support a gradual evolution for the whole skeleton, at least for the body regions analysed. However, our results do show that the hind limb and tail were much more deeply transformed within Mononykini compared to other alvarezsaurians (Fig. 7).

In Laurasia, we observed an event of speciation and explosive diversification with Parvicursorinae during the Campanian that tripled clade diversity (Fig. 4b). We also observed body-mass variability suggesting that this event may best fit an adaptive radiation model of niche-filling. This is potentially related to faunal change associated with the separation (at least partially) between northern and southern Patagonia at the time (Novas et al., 2019).

Within lineages it is more common to observe a trend towards increasing body size (Depéret, 1907; Mcshea, 1994; Carrano, 2006; Zanno and Makovicky, 2013; Benson et al., 2018) with "founding" ancestors of "successful clades" that are fewer in number, lower in diversity and shorter in longevity (Hanken and Wake, 1993; Turner et al., 2007; Novas et al., 2012; Brusatte et al., 2014; Lee et al., 2014). However, miniaturization has been postulated as a key feature in the evolution of many important animal groups, including birds, lizards, snakes and bivalves (Carroll, 1969, 1970; Bolt, 1977; Alberch et al., 1979; Carroll and Holmes, 1980; Rieppel, 1984, 1988; Seilacher, 1984; Turner et al., 2007; Brusatte et al., 2014; Lee et al., 2014). According to Hanken and Wake (1993), this occurs when morphological novelty, commonly associated with miniaturization, involves fundamental changes in the bauplan and can result in completely new patterns of organization. Even in examples where such a bauplan is maintained, miniaturization can drive the evolution of new morphological and developmental relationships, and often results in morphological homoplasy, which can obscure phylogenetic interrelationships and understanding about declining body size (see Hanken and Wake, 1993). Although the consequences of miniaturization for the biology of organisms are complex, there are several general effects (Hanken and Wake, 1993) that are expected in miniaturized alvarezsaurians that we evaluate in detail for the first time.

Morphological novelty is the most common effect seen in modern animals (Hanken and Wake, 1993) and is perhaps the effect that we most expect to see in alvarezsaurian. Hanken and Wake (1993) noted a close correlation between size and the relative development of certain anatomical structures in several living vertebrates and insects. These examples range from the presence of a bilaterally asymmetrical subcephalic copulatory organ derived from the pelvic fins in Asian phallostethid fishes to a “ciliated” wing in some trichopterigid beetle species (see Hanken and Wake, 1993). These authors highlight that in many vertebrates (for example, miniaturized amphibians and reptiles) there is a negative allometric relationship between the size of the inner ear, the size of the head and body size (Hanken and Wake, 1993). This relationship produces an abrupt and novel rearrangement of the entire skull with functional and behavioral consequences (Hanken and Wake, 1993). In this context, the miniaturized parvicursorines appear to exemplify the morphological novelty effect of miniaturization as novel skull characteristics including enlarged foramen magnum, basal tubera that are not medially expanded, enlargement of the forebrain and anterior spinal cord, as well as enlarged orbit and scleral ring. These traits suggest the development of specialized scotopic vision and highly developed somatosensation (Alifanov and Saveliev, 2011; Choiniere et al., 2021; Agnolín et al., 2022).

A second expected effect in alvarezsaurians is structural reduction and simplification, which can occur in different ways in living animals and can involve multiple body regions (Hanken and Wake, 1993). Adult minute salamanders of the genus *Thorius* lack several cranial and postcranial bones found in more ancestral forms, have a largely unprotected brain and lack teeth (Hanken, 1993). These structural reductions and simplifications have been mentioned as special adaptations of the animals concerned or as their dramatic dependence on the reduction and simplification of their bauplans (Te Winkel, 1935; Roth et al., 1988; Hanken and Wake, 1993). Many miniaturized invertebrates lost entire organs that also have been linked to changes in ecology, behavior, and other characteristics (Matsuda, 1987). In this context, structural reductions and simplifications are observed in alvarezsaurian skulls (Choiniere et al., 2014b; Agnolín et al., 2022). Early diverging alvarezsaurians such as *Haplocheirus* and *Aorun* (Choiniere et al., 2010, 2014a) have a triradiate jugal that becomes a simpler rod-shaped in later-diverging parvicursorine alvarezsaurids such as *Shuvuuia*, *Ceratonykus*, and *Jaculinykus* (Chiappe et al., 1998; Alifanov and Barsbold, 2009; Kubo et al., 2023). Other early diverging alvarezsaurians have an unfused quadratojugal and jugal that becomes fused in later-diverging forms such as *Shuvuuia*, *Ceratonykus,* and *Jaculinykus* (Chiappe et al., 1998; Alifanov and Barsbold, 2009; Kubo et al., 2023). Other early diverging alvarezsaurians have a postorbital process on the jugal that becomes absent in later-diverging forms such as *Shuvuuia*, *Ceratonykus,* and *Jaculinykus* (Chiappe et al., 1998; Alifanov and Barsbold, 2009; Kubo et al., 2023).

A third effect of miniaturization expected in miniaturized alvarezsaurians is elevated homoplasy (Ford, 1980; Rieppel, 1988; Hanken and Wake, 1993). This is often called “compensatory convergence” and involves the evolution of similar features that compensate for the detrimental effects of downsizing (Wake, 1986). In this context, miniaturization within Alvarezsauria can at least partly explain why their phylogenetic relationships were highly controversial during early periods of their discovery history (Meso, 2022).

A fourth effect of miniaturization expected in miniaturized alvarezsaurians is behavioral change. Miniaturization can be associated with reduced fecundity and increased egg size in birds, resulting in many cases where females produce only a single large egg per clutch (Dybas, 1966; Grandison, 1980; Shine and Greer, 1991; Hanken and Wake, 1993). In the case of the living kiwi bird (*Apterix*), their eggs are ~20% of their weight (Calder III, 1979). The small alvarezsaurid *Qiupanykus* from the Late Cretaceous of Luanchuan, Henan, China preserves fragments of eggshells located near its tail proposed to be oviraptorosaurian eggs because of their large size (estimated body mass ~0.5 kg and estimated egg mass ~1 kg) and association with a juvenile oviraptorosaur (Lü et al., 2018). However, in light of the considerations discusses above, such a large egg could be interpreted as belonging to a miniaturized alvarezsaurid (i.e. *Qiupanykus*). This interpretation is opposite to that observed in the large body-sized alvarezsaurid *Bonapartenykus*, whose remains were found associated with pieces of a relatively large egg (Agnolín et al., 2012). Altogether, this evidence suggests that alvarezsaurids may have had a reproductive strategy characterized by laying large eggs in relation to their bodies.

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Conflict of Interest

None declared.

DATA AVAILABILITY STATEMENT

All data are available.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting Information S1. Applied equations, calculations of body mass, and estimations of body size.

Supporting Information S2. List of characters, data matrix, and modifications done.

Supporting Information S3. Alvarezsaurians nomenclature history.

Supporting Information S4. Strict and reduced consensus trees.

Supporting Information S5. Macroevolutionary analyses from reduced consensus.