

Ontogeny and miniaturization of Alvarezsauridae (Dinosauria, Theropoda)

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Abstract

The ontogenetic status of the known specimens of alvarezsaurid theropod dinosaurs is revised. We present histological data that the holotype of *Parvicursor remotus* from the Upper Cretaceous Barungoyot Formation of Mongolia is not an adult individual, as previously thought, but a juvenile less than one year old. The miniaturization took place only in the Late Cretaceous Asiatic Parvicursorinae, whereas the Late Cretaceous South American non-parvicursorine alvarezsaurids were large animals. The miniaturization occurred by shifting ossification to earlier ontogenetic stages, in particular, by the closure of the neurocentral sutures on the presacral vertebrae of juvenile animals. There is no morphological support for the myrmecophagy in the alvarezsaurids and a shift to a myrmecophagous ecological niche does not explain the need for miniaturization.

Keywords: Dinosauria, Theropoda, Alvarezsauridae, ontogeny, miniaturization

Introduction

Non-avian dinosaurs are best known for their frequently large body sizes, including the largest creatures to ever roam the Earth. Many phylogenetic lines of non-avian dinosaurs showed a tendency to increase in size over time, a phenomenon known as Cope's Rule (Hone, Keesey, Pisani, and Purvis, 2005; Carrano, 2006; Benson, Hunt, Carrano, and Campione, 2018). In spite of a selective advantage for individuals with larger size within populations (Hone and Benton, 2005), all lineages of non-avian dinosaurs in which there was an increase in size became extinct. The opposite evolutionary trend, miniaturization, is defined as a decrease in body size of at least two orders of magnitude from ancestors to descendants (Qin et al., 2021). This is an important evolutionary phenomenon involved in the origin of higher taxa (Hanken and Wake, 1993). Among non-avian dinosaurs miniaturization occurred in the lineage leading to birds (Brusatte, Lloyd, Wang, and Norell, 2014; Lee, Cau, Naish, and Dyke, 2014; Puttick, Thomas, and Benton, 2014). Alvarezsauroida is the only other group of non-avian dinosaurs in the evolution of which miniaturization took place (Choiniere et al., 2010; Agnolin, Powell, Novas, and Kundrát, 2012; Qin, Clark, Choiniere, and Xu, 2019; Qin et al., 2021). In alvarezsaurids, this process did not lead to the origin of new taxa, apparently because of their extreme specialization. According to Qin et al. (Qin et al., 2021), the alvarezsauroid miniaturization and the phylogenetic radiation of this clade were caused by a shift to the myrmecophagous ecological niche followed by the emergence of ants and termites.

The study of the alvarezsauroid miniaturization presented by Qin et al. (Qin et al., 2021) is important because it includes new data from the early-branching

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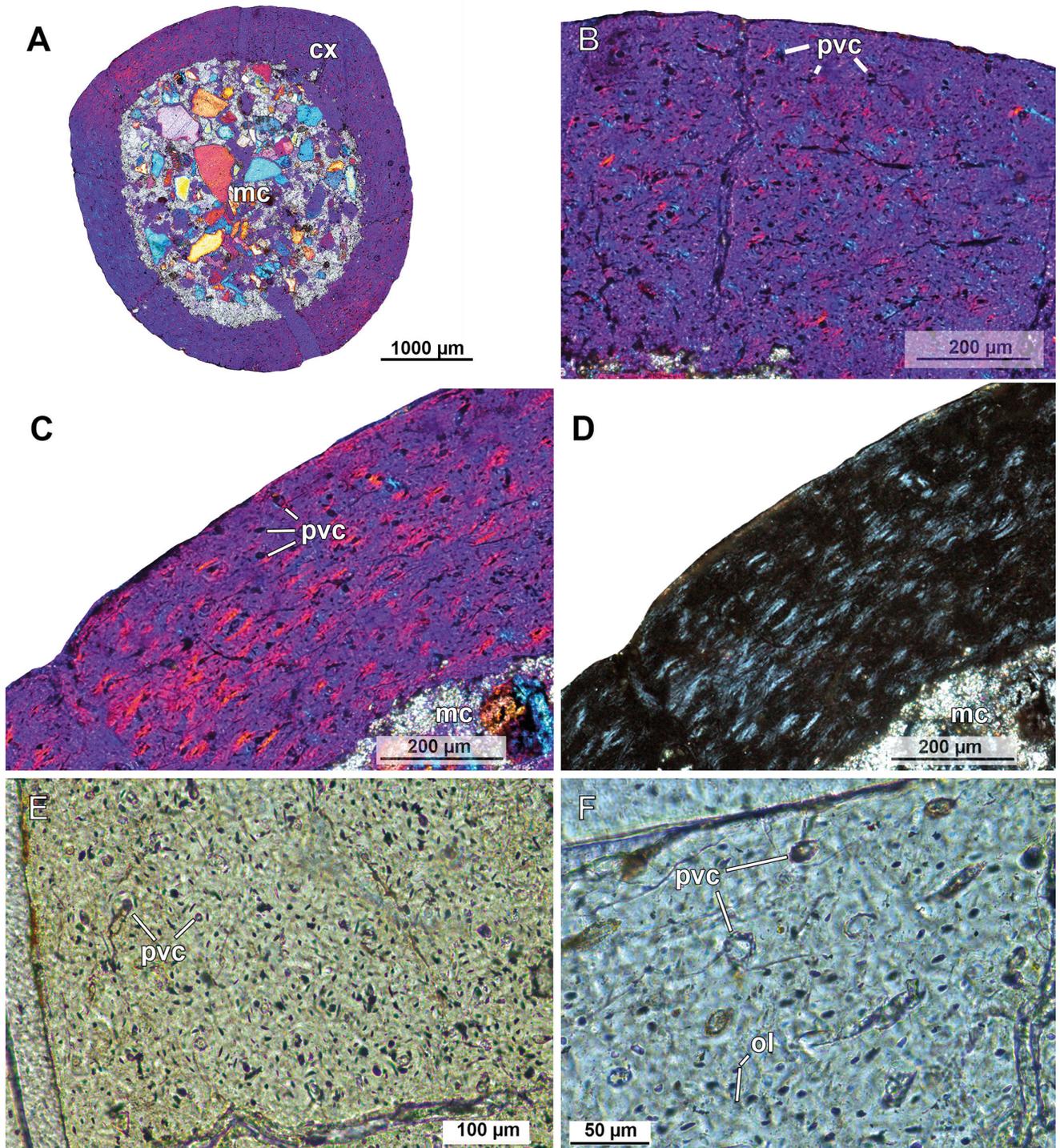


Fig. 1. *Parvicursor remotus*, PIN 4487/25, left femur, histological sections under polarized light with lambda waveplate (A–C), without lambda waveplate (D), and under normal light (E–F). (A) Microanatomical overview. Note the relatively thin cortex entirely composed of primary bone tissues and enlarged medullary cavity. (B–F) Close-ups of the primary cortex showing fibrolamellar complex and longitudinal vascularization. Note the absence of cyclical growth marks and bone remodelling. Abbreviations: *cx* — cortex; *mc* — medullary cavity; *ol* — osteocyte lacuna; *pvc* — primary vascular canal.

alvarezsauroids and considered the ontogenetic effect based on histological data. However, this study contains errors in estimating the individual age of several alvarezsauroid specimens, which are discussed in this paper. In particular, these authors considered the single known specimen of *Parvicursor remotus*, the smallest

known alvarezsauroid, as an adult. Here we present histological data showing that this specimen is a very young individual, not more than one year old. Considering this specimen as an adult has led to a significant reassessment of the scale of alvarezsauroid miniaturization by Qin et al. (Qin et al., 2021).

Institutional abbreviations. 41HIII, Henan Geological Museum, Zhengzhou, China; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN-PV-RN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (RN, Colección Río Negro), Buenos Aires, Argentina; MCFVPH, Museo Carmen Funes, Plaza Huinul, Neuquén, Argentina; MPCA, Museo Provincial “Carlos Ameghino”, Cipolletti, Argentina; MPC-D, Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MUCPV, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China, Xixia, China.

Histological study of *Parvicursor remotus*

For the histological study, we sampled the left femur of the *Parvicursor remotus* holotype (PIN 4487/25). Thin-sections were prepared based on the methodology outlined in Chinsamy and Raath (Chinsamy and Raath, 1992). The sections were examined under normal and polarized light using an optical microscope (Leica 4500, Leica Microsystems, Wetzlar, Germany) in the Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia). Histological terminology follows Francillon-Vieillot et al. (Francillon-Vieillot et al., 1990).

The femur of *Parvicursor remotus* (from the holotype PIN 4487/25; a section taken close to the mid-diaphyseal level; Fig. 1) has a relatively thin cortex (minimal cortical thickness about 0.4 mm; maximal cortical thickness about 0.8 mm) entirely composed of primary bone tissues surrounding a well-defined medullary cavity (Fig. 1A). The cortico-diaphyseal index (CDI, cortical thickness/local bone radius) is between 0.24–0.44. The primary bone organization of the cortex is a fibrolamellar complex. The primary bone of the cortex is vascularized with relatively small, longitudinally oriented primary vascular canals and primary osteons. Other types of orientation are rare and only few reticular and radial vascular canals are present. There are no growth marks (e.g., annuli, lines of arrested growth) in the cortex. The cortex has an irregular perimedullary inner margin, which is the result of bone resorption and the expansion of the medullary cavity). Signs of bone remodelling (e.g., erosion bays, secondary osteons and endosteal bone deposition) of the cortex are absent. Osteocytic lacunae are numerous and their shape varies from rounded to ellipsoid.

The presence of only primary bone cortex entirely composed of fibrolamellar complex, the absence of the bone remodelling in the cortex and the absence of cyclical growth marks in the cortex suggests that the holotype femur belongs to the fast-growing juvenile individual with

the age less than one year. In terms of microanatomical and histological structure, the holotype femur of *Parvicursor remotus* is generally similar to long bones of other juvenile alvarezsaurids (e.g., *Aorun*; see (Choiniere et al., 2014); (Qin et al., 2021)) in the presence of a relatively thin cortex and an enlarged medullary cavity, high degree of vascularization, and the primary bone being entirely formed by a fibrolamellar complex. The predominance of the longitudinal orientation of the vascular canals in the cortex found in *Parvicursor* is common for small-sized alvarezsaurids (e.g., *Shuvuuia*, *Albinykus*, *Xixianykus*; see (Qin et al., 2021)), and other small coelurosaurian theropods, including basal avialans (Erickson et al., 2009; Nesbitt, Clarke, Turner, and Norell, 2011).

Ontogenetic age of alvarezsaurid specimens

The ontogenetic status of the known alvarezsaurid specimens is discussed below and summarized in Table 1. The taxa are ordered according to their geological age, from ancient to young.

***Aorun zhaoui*.** Callovian part of the Shishugou Formation; Wucaiwan locality, Xinjiang, China. The holotype (IVPP V15709) was considered an immature individual because of the lack of complete fusion of any of the neural arches on the vertebral centra (Choiniere et al., 2014). No lines of arrested growth (LAGs) were observed in either the tibial or fibular histological sections. The specimen was identified as hatchling in (Qin et al., 2021). The specimen lacks co-ossification of the proximal tarsals among themselves and with the tibia, of the distal tarsals with the metatarsals, and of the proximal metatarsals, which is consistent with its juvenile status.

***Shishugounykus inexpectus*.** Oxfordian part of the Shishugou Formation; Wucaiwan locality, Xinjiang, China. In the holotype (IVPP V23567), the neurocentral sutures are closed on the dorsal and sacral vertebrae, but open on the anterior caudal vertebra. The fusions between the sacral centra are not complete. Metacarpal II has not incorporated the distal “semilunate” carpal. There are five LAGs in the femoral cortex and the individual age was estimated as nine years (Qin, Clark, Choiniere, and Xu, 2019; Qin et al., 2021). The specimen was considered a nine-year-old adult (Qin et al., 2021).

***Haplocheirus sollers*.** Oxfordian part of the Shishugou Formation; Wucaiwan locality, Xinjiang, China. The holotype (IVPP V15988) was originally interpreted as a young adult or late stage subadult because of the co-ossification of the braincase bones and the still visible neurocentral sutures (Choiniere et al., 2010). The specimen was considered a four-year-old juvenile by Qin et al. (Qin et al., 2021).

***Xiyunykus pengi*.** Barremian–Aptian (?) part of the Tugulu Group; Wucaiwan, Xinjiang, China. The holo-

Table 1. Geological age, individual age, estimated body mass, and ontogenetic status of alvarezsaurid specimens

Taxon and specimen	Age, Ma	Age, years	Body mass, kg	OS
<i>Achillesaurus manazzoni</i> (MACN-PV-RN 1116)	85		30	J
<i>Albinykus baatar</i> (IGM 100/3004)	79.2	3	1.07	A
<i>Alvarezsaurus calvoi</i> (MUCPV 54)	85		3.32	J
<i>Aorun zhaoi</i> (IVPP V15709)	161.6	1	1.27	J
<i>Bannykus wulatensis</i> (IVPP V25026)	119.5	8	29.13	A
<i>Bonapartenykus ultimus</i> (MPCA 1290)	74.8		71.55	A
<i>Ceratonykus oculatus</i> (IGM 100/975)	73		0.26	A
<i>Haplocheirus sollers</i> (IVPP V15988)	160.1	4	20.45	J
<i>Linhenykus monodactylus</i> (IVPP V17608)	77.9		0.45	J
<i>Mononykus olecranus</i> (IGM 107/6)	69.1		4.66	SA
<i>Nemegtonykus citus</i> (MPC-D 100/203)	69.1		3.31	A
<i>Ondogurvel alifanovi</i> (PIN 5838/1)	73		1.16	A
<i>Parvicursor remotus</i> (PIN 4487/25)	73	1	0.18	J
<i>Patagonykus puertai</i> (MCFPVP 37)	90.3		33.6	SA
<i>Qiupanykus zhangji</i> (41HIII-0101)	74.8		0.5	A
<i>Shishugounykus inexpectus</i> (IVPP V23567)	160	9	6.01	A
<i>Shuvuuia deserti</i> (IGM 100/975)	77.9	2	3.05	J
<i>Xixianykus zhangji</i> (XMDFEC V0011)	86.7	11	0.74	A
<i>Xiyunykus pengi</i> (IVPP V22783)	122	9	17.26	A

Data from (Brusatte, Lloyd, Wang, and Norell, 2014; Choiniere et al., 2014; Qin et al., 2021), with some modifications. Ontogenetic stages (OS): J — juvenile; SA — subadult; A — adult.

type (IVPP V22783) is a nine-year-old adult specimen (Qin et al., 2021). The neurocentral sutures on the presacral vertebrae are closed, but the scapula is not fused with the coracoid.

***Bannykus wulatensis*.** Aptian Bayingobi Formation; Chaoge, Inner Mongolia, China. The scapulocoracoid and proximal metatarsals of the holotype (IVPP V25026) are not co-ossified. The specimen was interpreted as an eight-year-old subadult (Xu et al., 2018; Qin et al., 2021). The interpretation of this specimen as a subadult is inconsistent with the interpretation of a much younger, three-year-old specimen of *Albinikus baatar* as an adult by the same authors (Qin et al., 2021). The specimen IVPP V25026 is considered here an adult individual.

***Patagonykus puertai*.** Turonian Rio Neuquen Formation; Sierra del Portezuelo, Argentina. Qin et al. (2021) based their subadult-adult age estimate on the isolated cervical vertebra MCFPVP 38, the attribution of which to the holotype of *P. puertai* (MCFPVP 37) is problematic (Novas, 1997; Longrich and Currie, 2009). On the holotype, the synsacrum is fully co-ossified and the distal tarsal is partially fused with the metatarsus, but

the scapula is not fused with the coracoid and the sutures between the astragalus and calcaneum and the astragalus and tibia are still visible (Novas, 1997: Fig. 27A, D, C). A subadult status is accepted here for MCFPVP 37.

***Xixianykus zhangji*.** Coniacian–Santonian Majiacun Formation; Zhoujiagou, Henan, China. The holotype (XMDFEC V0011) shows the following ontogenetic features according to the original description (Xu et al., 2010) and Qin et al. (2021): 1) neurocentral sutures are visible on most of the adequately preserved vertebrae; 2) the sacral vertebrae are fused into a synsacrum; 3) the astragalus and calcaneum are co-ossified to each other and to the tibia; and 4) the distal tarsals are co-ossified with the metatarsals. Based on character 1, Xu et al. (Xu et al., 2010) concluded that the individual had not yet reached full skeletal maturity. Two LAGs are identified in the histological section of the metatarsal II (Qin, Zhao, and Xu, 2019). The specimen was considered an eleven-year-old adult by Qin et al. (Qin et al., 2021).

***Alvarezsaurus calvoi*.** Santonian Bajo de la Carpa Formation; Boca del Sapo, Argentina. The holotype (MUCPV 54) is a juvenile specimen based on the lack of fusion between the neural arches and centra of the

cervical and dorsal vertebrae (Qin et al., 2021). The sutures between the scapula and coracoid, calcaneum and astragalus, and astragalus and tibia are open, suggesting a very young age for this individual, in spite of its large size (with estimated body mass of 30 kg).

Achillesaurus manazzonei. Santonian Bajo de la Carpa Formation; Paso Córdova, Argentina. The holotype (MACN-PV-RN 1116) was considered a subadult-adult individual based on the fusion between the centra and the neural arches on the sacral and caudal vertebrae (Qin et al., 2021). However, in alvarezsaurids, the neurocentral sutures can be already closed in juvenile specimens (*Parvicursor remotus*). The open sutures between the centra of the sacral vertebrae, calcaneum and astragalus, and astragalus and tibia in MACN-PV-RN 1116 suggest a juvenile status for this specimen. The lack of co-ossification between the astragalus and calcaneum is noteworthy as these bones are already co-ossified in a one-year-old specimen of *Parvicursor remotus*. *Achillesaurus manazzonei* is likely a subjective junior synonym of *Alvarezsaurus calvoi* (Makovicky, Apesteguía, and Gianechini, 2012).

Albinykus baatar. Santonian(?) — Campanian Javkhant Formation; Khugenetslavkant, Mongolia. The holotype (IGM 100/3004) was identified as a subadult (Nesbitt, Clarke, Turner, and Norell, 2011) or a three-year-old adult (Qin et al., 2021) based on the fusion of the proximal and distal tarsals, the fusion of the proximal parts of the metatarsals, and histological data (two intracortical growth lines).

Shuvuuia deserti. Campanian Djadokhta Formation (?); Ukhaa Tolgod, Mongolia. The specimen IGM 100/975 was considered a two-year-old juvenile based on histological data (Qin et al., 2021). The vertebral neurocentral sutures are closed and the proximal metatarsals are not co-ossified in this specimen (Chiappe, Norell, and Clark, 2002).

Linhenykus monodactylus. Campanian Wulansuhai Formation; Bayan Mandahu, Inner Mongolia, China. The holotype (IVPP V17608) was considered a subadult (Xu et al., 2013) or subadult-adult (Qin et al., 2021) based on the completely closed neurocentral sutures and unspecified “appendicular features”. However, in alvarezsaurids the closure of neurocentral sutures itself does not indicate maturity. The neurocentral sutures are closed, for example, on dorsal and caudal vertebrae of PIN 4487/25, the holotype of *Parvicursor remotus*, which is a one-year-old juvenile. The sacral vertebrae of IVPP V17608 are not co-ossified, and the suture between the astragalus and the tibia is not closed, as in PIN 4487/25. The specimen IVPP V17608 is considered here a juvenile. It was described as having co-ossified scapula and coracoid (Xu et al., 2013), which is very unusual for juvenile alvarezsaurids, but the poor preservation of the single known scapulocoracoid does not allow to

exclude the possibility that there was an open suture between the scapula and the coracoid. Qin et al. (Qin et al., 2021) provided a body mass estimate of 2 kg for IVPP V17608, which is much larger than the original estimate of 0.45 kg (Xu et al., 2013) and seems unlikely for such a small individual. We accept here the original estimate.

Parvicursor remotus. Campanian Barungoyot Formation; Khulsan, Mongolia. The holotype (PIN 4487/25) was identified as an adult by Qin et al. (Qin et al., 2021) with reference to Karhu and Rautian (Karhu and Rautian, 1996), although the latter paper clearly stated that this specimen is not an adult. The morphological indicators used by Qin et al. (Qin et al., 2021) for age identification of PIN 4487/25 are the following: 1) the complete obliteration of the neurocentral sutures on the vertebrae; 2) the fusion of two of its synsacral elements; 3) the fusion of the periacetabular bones; and 4) the fusion of the proximal tarsals to the tibia. Character 1 is correct for the dorsal and caudal vertebrae, but, on the sacral vertebrae, the centra are not fused to the neural arches (Averianov and Lopatin, 2021). Only two of sacral centra are fused, with the intercentral sutures still open. The last sacral was not fused to the other sacral vertebrae (Averianov and Lopatin, 2021). The periacetabular bones are not fused; this was based on an erroneous observation made by Karhu and Rautian (1996) (Averianov and Lopatin, 2021). The proximal tarsals adhere to the right tibia with the open sutures and are not fused with the left tibia (Averianov and Lopatin, 2021). As suggested by the histological data presented above, PIN 4487/25 is a juvenile specimen less than one year old. PIN 4487/25 has an estimated body mass of approximately 0.18 kg based on an empirical equation using femoral length (52.6 mm) as a predictor (Christiansen and Fariña, 2004). This estimate is similar to the estimate of 0.15 kg for this specimen by Qin et al. (2021). Thus, PIN 4487/25 is the smallest known alvarezsauroid specimen.

Ceratomykus oculatus. Campanian Barungoyot Formation; Khermiin Tsav, Mongolia. The holotype (IGM 100/975) was considered an adult (Alifanov and Barsbold, 2009) or a subadult-adult (Qin et al., 2021) based on the fusion of the astragali to the tibiae, with partially obliterated sutures. Although not described, this specimen might have proximally co-ossified metatarsals II and IV, which confirm its adult status.

Ondogurvel alifanovi. Campanian Barungoyot Formation; Nemegt, Mongolia. The holotype (PIN 5838/1) is an adult specimen with a co-ossified synsacrum, astragalus fused to the tibia, and co-ossified proximal metatarsals (Averianov and Lopatin, 2022). The femur of *Ondogurvel alifanovi* is 96.7% complete compared with the similar femur of *Mononykus olecranus* (Perle et al., 1994). Thus, its complete length would be 93.7 mm, which gives the estimate of 1.16 kg of body mass using the equation from Christiansen and Fariña (Christiansen and Farina, 2004).

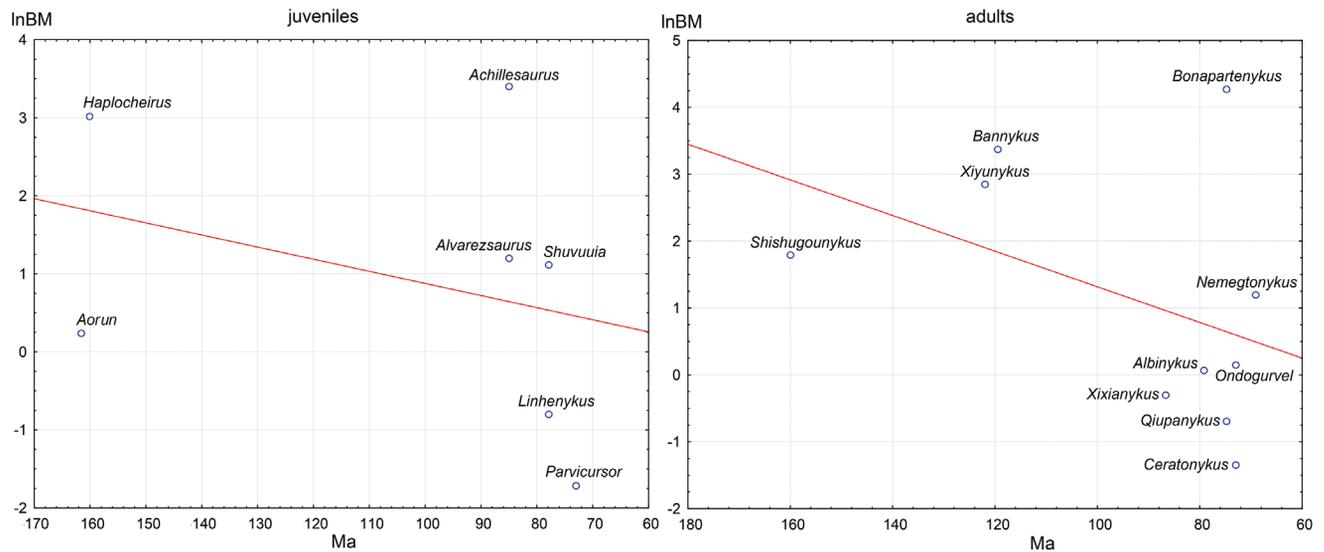


Fig. 2. Scatterplots of estimated body mass (in kg, natural logarithms) versus geological age (Mya) in juvenile and adult alvarezsaurid specimens (see Table 1 for the list of specimens).

Geological age	Ontogenetic stage	Ontogenetic characters						
		1	2	3	4	5	6	7
Campanian-Maastrichtian	Adult (8)	Red	Green	Green	Red	Green	Red	Red
	Subadult (7)	Red	Green	Green	Red	Green	Green	Green
	Juvenile (6)	Red	Green	White	Red	Green	Green	Green
Turonian-Santonian	Adult (5)	Green	Red	White	Red	Red	Red	Red
	Subadult (4)	Red	Red	Green	Green	Green	Green	Green
	Juvenile (3)	Green	Green	Green	Green	Green	Green	Green
Late Jurassic - Early Cretaceous	Adult (2)	Red	Green	Green	White	Green	Green	Green
	Subadult	White	White	White	White	White	White	White
	Juvenile (1)	Green	White	White	Green	Green	Green	Green

Fig. 3. Ontogenetic changes in Late Jurassic — Early Cretaceous, Turonian-Santonian, and Campanian-Maastrichtian alvarezsaurids. Red color indicates co-ossified elements or closed neurocentral sutures, green color — separate elements or open sutures. Ontogenetic characters: 1) neurocentral sutures of presacral vertebrae; 2) centra of sacral vertebrae; 3) scapula and coracoid; 4) astragalus and calcaneum; 5) astragalocalcaneum and tibia; 6) distal tarsals and metatarsus; 7) metatarsals II and IV. Specimens: 1) *Aorun zhaoi*; 2) *Shishugounykus inexpectus*, *Xiyunykus pengi*; 3) *Alvarezsaurus calvoi*, *Achillezaurus manazzoni*; 4) *Patagonykus puertai*; 5) *Xixianykus zhangii*; 6) *Parvicursor remotus*, *Linhenykus monodactylus*; 7) *Mononykus olecranus*; 8) *Albinykus baatar*, *Ondogurvel alifanovi*, *Nemegtomykus citus*, *Bonapartenykus ultimus* (see Table 1 for specimen numbers).

Bonapartenykus ultimus. Campanian-Maastrichtian Allen Formation; Salitral Ojo de Agua, Argentina. The holotype (MPCA 1290) was considered adult because it was found in association with an egg (Qin et al., 2021). The scapulocoracoid is fully fused, which confirms the adult status of the holotype.

Mononykus olecranus. Maastrichtian Nemegt Formation; Bugin Tsav, Mongolia. The holotype IGM

107/6 was identified as a subadult because of the well-developed fusion between astragalus and calcaneum, ilium and ischium, and the vertebral neural arches and centra (Qin et al., 2021). The ilium and ischium do not fuse in other alvarezsaurids and this might be an autapomorphy of *Mononykus* rather than an ontogenetic trait. The scapula and coracoid are not fused and the suture between the astragalocalcaneum and the tibia is

not closed, which confirms the status of GIN 107/6 as a subadult individual.

Nemegtonykus citus. Maastrichtian Nemegt Formation; Altan Uul III, Mongolia. On the holotype (MPC-D 100/203), the preserved vertebrae do not show any open neurocentral sutures, and the hind limb bones show considerable co-ossification according to (Qin et al., 2021). Nevertheless, these authors consider this specimen a subadult. We consider this specimen here an adult individual. It is unusual in having distal fusion of metatarsals II and IV, whereas they are fused proximally in other adult alvarezsaurids. The majority of the characters included in the diagnosis of *Nemegtonykus citus* by Lee et al. (Lee et al., 2019) are ontogenetically correlated. This taxon could be a subjective junior synonym of the very similar and coeval *Mononykus olecranus*.

Qiupanykus zhangii. Maastrichtian Qiupa Formation; Guanping, Henan, China. In the holotype (41HIII-0101), the neural arches of caudal vertebrae are completely fused with the centra without any trace of sutures. The specimen was considered adult (Lü et al., 2018) or subadult (Qin et al., 2021).

Miniaturization and ontogenetic heterochrony in Alvarezsauridae

We plotted the body mass versus geological age separately for the juvenile and adult alvarezsaurid specimens (Fig. 2). Both scatterplots show significant decrease in body size through geological time, but it is more pronounced in adult specimens. The body size decrease occurred in Asiatic taxa, whereas the South American *Achillesaurus* (Santonian) and *Bonapartenykus* (Campanian–Maastrichtian) have the largest juvenile and adult alvarezsaurid specimens, respectively (Fig. 2). Thus, the miniaturization occurred only within the lineage leading to the Parvicursorinae.

The miniaturization was, at least partially, due to a progressive shift in the ossification of certain postcranial elements to the earlier ontogenetic stages (Fig. 2). Thus, in the Late Jurassic — Early Cretaceous and Turonian–Santonian alvarezsaurids the neurocentral sutures of the presacral vertebrae are open in juveniles and closed in adults or subadults, but, in the Campanian–Maastrichtian taxa, these sutures are closed even in the juvenile specimens. All other ontogenetic markers shown in Fig. 3 are in the immature state in the adult specimens of Late Jurassic — Early Cretaceous alvarezsaurids but become mature in the adult specimens of the Late Cretaceous taxa. The astragalus is co-ossified with the calcaneum even in the smallest juveniles of the Late Cretaceous Parvicursorinae (*Parvicursor*, *Linhenykus*), whereas these elements remained separate in a subadult specimen of South American *Patagonykus*. Among the alvarezsaurids, the scapulocoracoid is co-ossified only

in *Bonapartenykus*, which is represented by a largest and possibly the ontogenetically oldest specimen in the sample (for a possible co-ossification of the scapulocoracoid in *Linhenykus* see discussion above).

Paleoecology of Alvarezsauridae

Qin et al. (Qin et al., 2021) found that alvarezsaurid miniaturization and associated phylogenetic radiation are coincident with the emergence of ants and termites. They refer to the previous functional morphological data in support to their conclusion that alvarezsaurid miniaturization was possibly driven by a shift to a myrmecophagous ecological niche. These data come from three sources cited by Qin et al. (Qin et al., 2021): Xu et al. (Xu et al., 2010); Longrich and Currie (Longrich and Currie, 2009), and Senter (Senter, 2005). Xu et al. (Xu et al., 2010) reasoned that alvarezsaurids needed the cursorial hind limbs to escape predators and to move efficiently among termite colonies. However, none of the modern myrmecophagous species shows the extreme specialization to fast running seen in the parvicursorines. Longrich and Currie (Longrich and Currie, 2009), speculated that the North American alvarezsaurid *Albertonykus* preyed on wood-nesting termites. They found that silicified wood from the Horseshoe Canyon Formation, where the remains of *Albertonykus* come from, frequently contains borings, which resemble the galleries of dampwood termites. This, however, does not prove that *Albertonykus* fed on these termites. Senter (Senter, 2005) showed that the forelimb of *Mononykus* was well suited for scratch-digging or hook-and-pull movements such as are used by extant anteaters and pangolins to open tough insect nests. However, none of the extant myrmecophagous animals shows the shortening of the forelimb and reduction of the fingers, which is characteristic of the Late Cretaceous parvicursorines. It is difficult to imagine how it is possible to break the thick walls of termite mounds with such short arms as those of parvicursorines, especially considering the small size of these animals. How would miniaturization help in feeding on ants and termites? We find no compelling morphological data that would suggest that parvicursorines fed on colonies of social insects.

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