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Range of motion and myology support a digging function for the forelimbs of alvarezsauroid dinosaurs

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Numerous lineages of theropod dinosaurs display notable modification of the forelimb, particularly reduction in size and number of digits. Alvarezsauroids are one of the most striking examples of this, exhibiting extreme shortening and increased robusticity of forelimb elements, with a functionally monodactylous manus in late-diverging taxa. These features are generally interpreted as adaptations for digging, possibly as part of a myrmecophagous ecology. Here, we test this hypothesis, using computational range of motion analysis of the shoulder and elbow joints to demonstrate the feasibility of digging behaviours in *Mononykus olecranus*, a highly specialized alvarezsauroid, and the less specialized *Bannykus wulatensis*. We find that *Bannykus* has the capacity for various digging styles and generalized forelimb function, while *Mononykus* has more restricted motion and may have employed a highly specialized digging style. We also identify similarities in forelimb muscle moment arms between alvarezsaurs and specialized mammalian diggers, supporting adaptation for digging. These findings are consistent with interpretations of insectivory in alvarezsauroids, and suggest increasing specialization to myrmecophagy throughout their evolutionary history, shedding new light on the evolution of this enigmatic clade and the ecological diversity of non-avian theropod dinosaurs.

1. Introduction

The forelimbs of theropod dinosaurs exhibit a remarkable diversity of form, partially enabled by bipedalism and the release of the forelimb and pectoral girdle from functional constraints relating to locomotion [1–3]. One of the most dramatic examples of theropod forelimb modification is found in the Alvarezsauroidea, a lineage of maniraptorans (figure 1A). The forelimb of late-diverging alvarezsauroids is highly shortened and features a reduced manus (hand) characterized by one large digit bearing a hypertrophied ungual, with the other digits significantly reduced, and in some cases presumed to be wholly vestigial [7–9]. Because of these bizarre and unique characteristics, the function of the alvarezsauroid forelimb has been subject to long-standing speculation [8–12].

The forelimbs of late-diverging alvarezsauroids possess a number of characters, such as an enlarged deltopectoral crest and olecranon process, that are also observed in extant forelimb-digging mammals, in which they are recognized as functional adaptations for digging behaviours [13,14]. More specifically, the combination of these features with reduced digital number and enlarged, hypertrophied unguals in alvarezsauroids is similar to the state observed in extant mammals such as pangolins and anteaters, which use their forelimbs to break into insect nests as part of a myrmecophagous (termite or ant-eating) ecology [15]. As a result, although anatomical features like an expanded olecranon and deltopectoral crest also occur as adaptations for other behaviours such as climbing [16] and swimming [17], various authors have suggested some sort of digging function as the most plausible explanation for the highly derived forelimb of alvarezsauroids, given indications from hindlimb morphology that these animals were terrestrial cursors [18–20]. Because the forelimbs of derived alvarezsauroids are too short for tunnelling or burrowing behaviour, the prevailing hypothesis is that alvarezsauroids may have used their forelimbs to break into substrates housing insects—for example, wood containing wood-boring termites [7–9,12,20]. This is supported by other morphological features: alvarezsauroids possess simplified, reduced teeth and slender jaws, common adaptations to myrmecophagy [7,20–22]. A feeding ecology similar to pangolins, involving above-ground 'digging' behaviours, appears feasible even with the short length of the forelimb, as it is not necessary to reach all the way to the ground, and is compatible with an otherwise cursorial lifestyle. In line with other authors (e.g. [5,20]), we use the term 'digging' as general shorthand for forelimb function concerned with breaking into hard substrate, i.e. not exclusively to refer to below-ground burrowing. Digging in alvarezsauroids is also supported by a reduced pubic symphysis and increased numbers of sacral vertebrae in several members of the clade, features characteristic of mammals that engage in forelimb digging [11,13,15,20,23,24]. This extreme degree of specialization and the discrepancy in size between the fore- and hindlimbs of derived alvarezsauroids are features not observed in extant mammals, which must retain relatively equivalently sized fore- and hindlimbs to facilitate quadrupedal locomotion. Alvarezsauroids may therefore have occupied a unique ecological niche combining cursoriality and digging behaviours, facilitated by their bipedal locomotion as theropod dinosaurs.

Despite the support for this hypothesis provided by comparative morphology, it has received little biomechanical testing. The few studies to explicitly investigate alvarezsauroid forelimb function used manual manipulation of casts of the bones of the forelimb of the parvicursorine *Mononykus* to assess the range of motion (ROM) permitted at joint articulations and concluded that forelimb digging was feasible in this taxon [11,25]. ROM analysis can also inform more specific interpretations of digging style, which is known to correlate with ecology in extant animals: numerous extant mammals engage in subparasagittal scratch digging, but hook-and-pull digging strategies involving retraction and flexion of the whole arm are solely used by termite-eating myrmecophages like pangolins and anteaters [13,15]. A capacity for both scratch and hook-and-pull digging behaviours have been suggested for *Mononykus* [11,25], and similarity of the humeral head of *Mononykus* to extant 'humeral rotation' diggers like echidnas has also been noted [20]. This relatively poor understanding of the specific mechanism that alvarezsauroids may have used for digging, and potential variation among different alvarezsauroids in this regard, can be informed by resolving forelimb function in greater detail.

Computational methods of estimating ROM developed in recent years offer the potential to capture range of motion more thoroughly than non-computational approaches. In particular, these methods can capture interactions between rotational degrees of freedom, where rotation in one axis influences the simultaneous rotation possible in another [26,27]. These methods represent an ideal framework to elaborate on previous studies of forelimb mobility in these dinosaurs. Muscle moment arms are another useful indicator of the importance of certain muscle groups for particular motions and can be used as indices of function [5,28,29]. While the likely expansion of forelimb muscle moment arms has been noted in alvarezsauroids [20], these metrics have not been thoroughly investigated.

Here, we apply computational ROM and moment arm analysis to the alvarezsauroid forelimb for the first time to our knowledge, to quantitatively assess functional capacity, with the aim of evaluating the feasibility of digging behaviours. We include two alvarezsauroids in the analysis: *Mononykus olecranus*, a Late Cretaceous parvicursorine alvarezsauroid with highly derived forelimbs [7,10], and *Bannykus wulatensis*, an Early Cretaceous alvarezsauroid exhibiting more plesiomorphic forelimb morphology but some reduction in length [4] (figure 1A). We reconstruct estimated forelimb muscle attachments for *Mononykus* and *Bannykus*, using these to calculate muscle moment arms and quantitatively compare them with extant mammals. We aim in particular to assess whether alvarezsaurs resemble forelimb-digging mammals in these functional metrics [5,15]. We hypothesize that the forelimbs of both taxa possess the requisite joint mobility for digging, and that moment arms for muscles typically involved in forelimb digging will be emphasized in *Mononykus* and *Bannykus* relative to unspecialized theropods. Earlier-diverging alvarezsauroids like *Bannykus* have received very little research attention, especially from a functional perspective, but nonetheless show features indicative of specialized forelimb function such as elaborated deltopectoral crest and olecranon [4]. We suggest that function in *Mononykus* may be more specialized than in *Bannykus* because of its more extreme forelimb shortening, digital reduction and more derived joint morphology. Comparing functional metrics and ROM between these two taxa will enable us to test this hypothesis with multiple functional metrics, providing some of the first direct investigation into functional evolution in alvarezsauroids and shedding light on how the unique features of this clade developed.

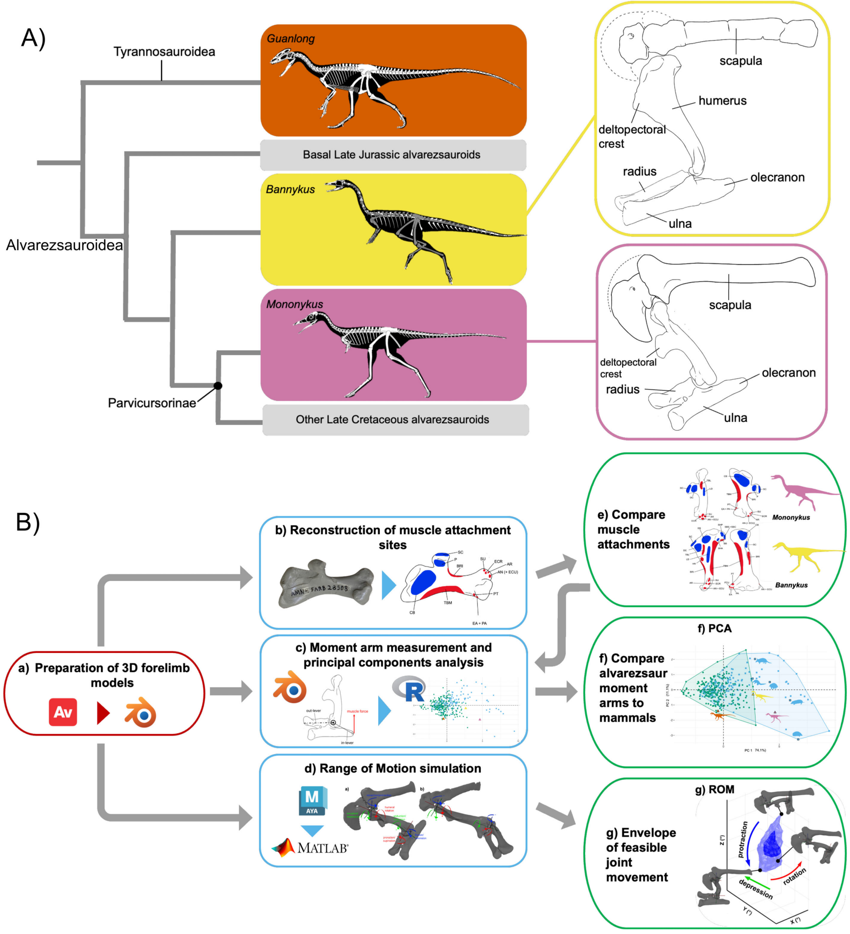

Figure 1. (A) A simplified phylogeny showing the positions of *Guanlong*, *Bannykus* and *Mononykus*, with illustrations of forelimb elements of *Bannykus* and *Mononykus*. Skeletals copyright Scott Hartman; *Bannykus* skeletal from [4] (not to scale). (B) A schematic summarizing the workflow and outputs of the study, with red box indicating data preparation and acquisition, blue boxes showing data processing and analysis, and green the outputs of these analyses. (B) Detail of individual steps in the workflow: (a) segmentation and repair of 3D digital models of *Mononykus* and *Bannykus* forelimb elements in Avizo and Blender; (b) use of the extant phylogenetic bracket and examination of the scans to reconstruct attachment sites for pectoral and forelimb musculature; (c) measurement of moment arms for functional groups of muscles in *Mononykus* and *Bannykus*, and principal components analysis (PCA) of these metrics in combination with a large dataset derived from extant mammals [5]; (d) articulation of digital models in Autodesk Maya, and range of motion (ROM) analysis of the shoulder and elbow joints of both taxa in MATLAB [6]; (e) visualization of muscle attachment sites for comparison between the two taxa; (f) PCA plot showing alvarezsauroid moment arms alongside those of extant mammals; (g) envelope of feasible joint mobility produced by ROM simulation.

2. Material and methods

(a) Institutional abbreviations

AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology; CAS, Chinese Academy of Sciences.

(b) Data acquisition and reconstruction

Three-dimensional models of the forelimb elements, scapula and coracoid of *Mononykus olecranus* (AMNH FARB 28508), derived from surface scans, were used for this study. The *Bannykus wulatensis* specimen (IVPP V25026) was scanned and segmented as part of a previous study [4] (see electronic supplementary material, supplementary methods 1). A specimen of the tyrannosauroid *Guanlong wucaii* (IVPP V14531) was included in the moment arms analysis for comparison with the alvarezsauroids, and had been computed tomography (CT) scanned as part of a previous study [30] (see electronic supplementary material). Segmentation was performed in Avizo (v. 2022.1; www.thermofisher.com), and forelimb elements were exported as .stl files. Preservational artefacts such as cracks and missing pieces were digitally repaired in Blender (v. 3.4.1) to produce complete left forelimbs of all three taxa (methods following [31,32], full details in electronic supplementary material). The articular surfaces of all elements were intact except for a small missing piece of the proximal radius of *Bannykus*, which was repaired by extrapolation of the existing morphology and reference to other alvarezsauroids such as *Shishugounykus* and *Haplocheirus* [33,34]. We acknowledge this as a possible source of error in our analysis, but consider it preferable to leaving the bone unrepaired, which would likely have caused an overestimation of ROM.

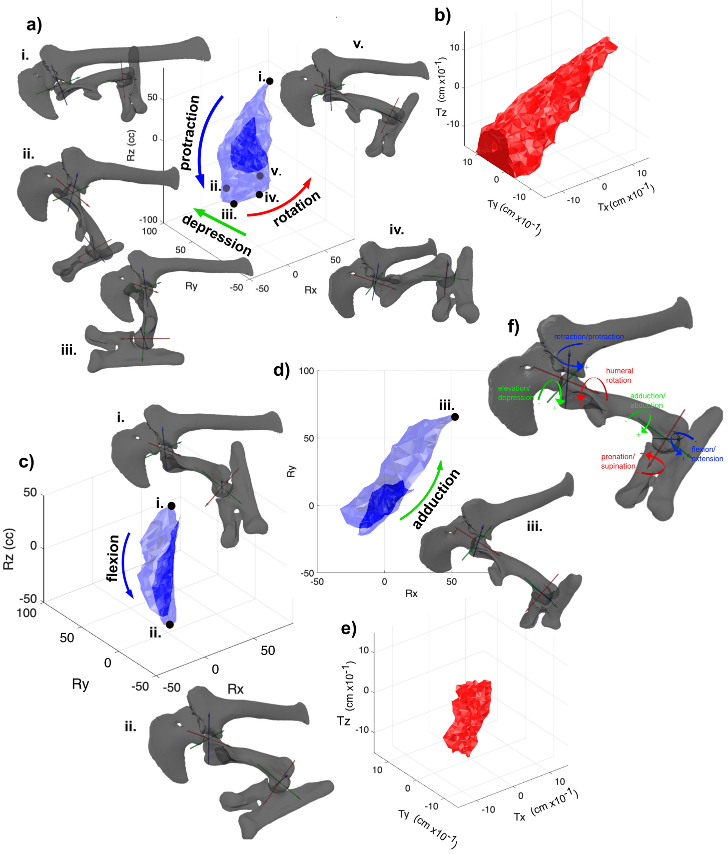

Figure 2. Envelopes of viable poses for the shoulder and elbow of *Mononykus*. (a) Shoulder range of motion (ROM) map; (b) translational shoulder ROM; (c,d) elbow ROM maps: (d) shows (c) viewed perpendicular to the *Y*-axis. (e) Translational elbow ROM. (f) Shows the Z pose from which all ROM excursions were measured; joint coordinate system axes show orientation and rotation directions in which ROM was measured: *X*-axis, red; *Y*-axis, green; *Z*-axis, blue. ROM maps are plotted according to the *X*, *Y* and *Z* rotation of viable poses. Example poses approximate numbered points on the ROM maps representing extremes of ROM excursion; results from cartilage simulations in paler blue are superimposed on osteological simulation results. Units are degrees for rotation and millimetres for translation maps. Results in (a) are from simulations MSO, MSC; ROM maps in (c) and (d) are from simulations MEO, MECcu (table 1).

(c) Range of motion analysis

ROM is measured in six degrees of freedom: three rotational degrees of freedom and three translational degrees of freedom, along three orthogonal axes (X, Y and Z) known as a joint coordinate system (JCS). The JCS for the shoulder and elbow joints of *Mononykus* and *Bannykus* were established in Blender (v. 3.4.1), following the general approach of [27] and [35] (see also electronic supplementary material, supplementary methods 2). The radius and ulna of *Bannykus* were modelled as one combined element, as this more closely resembles *in vivo* forelimb motion than simulating them independently of one another [36]. Geometric primitives were fitted to the articular surfaces of forelimb elements, the centroids of which designated the 'joint centre', where the origin of the axes of the joint coordinate system was placed. Individual anatomical coordinate systems (ACSs) were then established at the ends of each bone, and these were superimposed to articulate the forelimb. If necessary the distal element was translated distally so that the articular surfaces of the two bones were not intersecting. The JCS for each joint was then established at the 'joint centre', describing the movement of the distal ACS relative to the proximal ACS. For the elbow JCS, the X-axis describes long-axis rotation of the forearm, The Z-axis describes extension and flexion of the antebrachium, and Y is orthogonal to these and represents adduction and abduction at the elbow. For the shoulder JCS, the X-axis describes long-axis rotation of the humerus, the Z-axis describes retraction and protraction of the humerus, and Y is orthogonal to X and Z, and describes elevation and depression of the humerus. The joints were positioned in a zero pose (Z pose), from which ROM is measured. While Z poses are typically set up with elements extended straight down or laterally at 90° to the body, owing to highly derived morphology this is not achievable in *Mononykus* without intersection of the meshes. A Z pose need not be anatomically feasible, but because the algorithm used for the ROM analyses performed here requires a non-intersecting starting pose [6], a single suitable non-intersecting pose that was feasible for both taxa was chosen and used as a Z pose in order to easily compare results. In this pose, the humerus is positioned at an angle of 65° with the scapula, and 65° with the sagittal plane, and the forearm is positioned at 90° to the humerus (figures 2f and 3f).

ROM analysis of the shoulder and elbow joints of *Mononykus* and *Bannykus* was performed using the 'APSE' algorithm [6], implemented in MATLAB (figure 1B,G). Meshes of articulating elements and axes for each joint are input in a Z pose to the algorithm, which iteratively searches pose space until converging on an envelope of joint mobility.

For the shoulder and elbow joints of both taxa, a conservative 'osteological ROM' simulation was run, allowing a negligible maximum translation of the origin of the joint coordinate system of ±0.05 mm to simulate articulation of the bones directly against each other (table 1; MSO, MEO, BSO, BEO; electronic supplementary material, table S3).

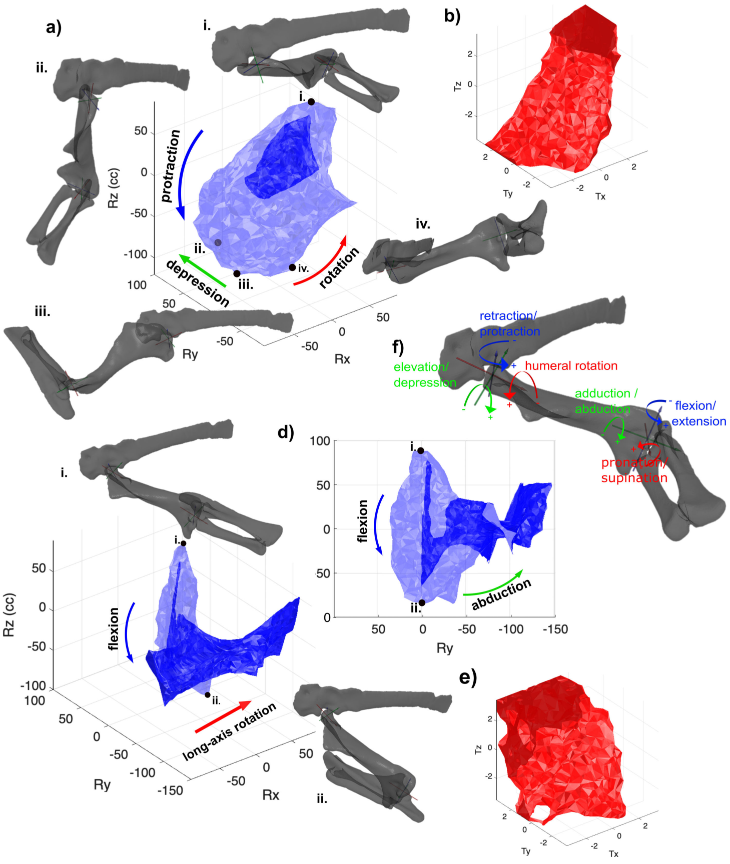

Figure 3. Envelopes of viable poses for the shoulder and elbow of *Bannykus*. (a) Shoulder range of motion (ROM) map; (b) translational shoulder ROM; (c–d) elbow ROM: (d) shows (c) viewed perpendicular to the *Y*-axis; (e) translational elbow ROM. (f) Shows the Z pose from which all ROM excursions were measured; joint coordinate system axes show orientation and rotation directions in which ROM was measured: *X*-axis, red; *Y*-axis, green; Z-axis, blue. Maps are plotted according to *X*, *Y* and *Z* rotation of viable poses. Example poses approximate numbered points on the ROM maps representing extremes of ROM excursion; results from cartilage simulations in paler blue are superimposed on osteological simulation results. Units are degrees for rotation and millimetres for translation maps. Results in (a) are from simulations BSO, BSC; ROM maps in (c) and (d) are from simulations BEO, BECgu (table 1).

Articulating elements in the joints of vertebrates are offset from each other by cartilaginous epiphyses [38]; a set of 'cartilage ROM' simulations was therefore also run. A range of offsets ('cartilage correction factors' or CCFs) was utilized to estimate appropriate offsets for the bone models (electronic supplementary material, tables S1–S3). These values were derived from extant birds [38] and used as the input 'separation distance' for the APSE algorithm. In using separation thresholds derived from measured cartilage thicknesses, we underestimate the actual separation distance that would exist between the bones in the joint of a living animal, which would likely be much larger [39]. However, as these distances are poorly understood [38,40,41], in order to ground estimates in published anatomical data we take a conservative approach and use these CCFs to represent the minimum amount of separation that might result from the presence of articular cartilage. For the alvarezsauroid shoulder joint, avian CCFs were insufficient to fulfil the overlap requirements of the APSE algorithm, so the offsets were iteratively increased to find the closest viable offset (full details in electronic supplementary material, tables S1–S3).

For the elbow joints, four simulations were run each for *Mononykus* and *Bannykus*; using CCFs calculated from both the radius and ulna cartilage of *Gallus*, and for the radius and ulna values of *Coturnix* (table 1; MECcu, MECgu, MECgr, BECgu, BECgr; electronic supplementary material, table S3). This was done to reflect the full spectrum of possible articular cartilage thicknesses suggested by the highly differing morphologies of the elbow joints of *Mononykus* and *Bannykus*: the radius and ulna of *Mononykus* are sutured together, forming a single, subspherical articular surface articulating with a single distal humeral condyle, while *Bannykus* has a more typical elbow morphology, with separate articulations of the radius and ulna on two distal humeral condyles. Running this full set of simulations for each joint enables comparison and repeatability between the two taxa, resolving ROM in greater detail while helping identify the most informative separation threshold for each joint (full details in electronic supplementary material). Cosine-corrected ROM maps for each simulation were generated as APSE converged on an envelope of viable joint mobility; raw results were cosine-corrected following [37].

(d) Muscle reconstruction

Forelimb muscle attachments for *Mononykus* and *Bannykus* were reconstructed using osteological correlates and following the extant phylogenetic bracket (EPB; [42]) methodology, with referral to previously published myological reconstructions of the pectoral girdle and forelimb in theropods [1,43–45] (see electronic supplementary material, supplementary methods 3 for full details).

Table 1. Cosine-corrected results of all viable simulations. Simulation ID codes included for ease of reference, with maximum and minimum rotations. Simulations marked with an asterisk (*) are figured. *Z* rotations are cosine-corrected following [37]. Full ROM map volumes and number of viable poses are available in the electronic supplementary material, Tables S4-8.

		simulation ID	min. *X* (°) (long-axis rotation)	max. *X* (°) (long-axis rotation)	min. *Y* (°) (shoulder elevation/ elbow abduction)	max. *Y* (°) (shoulder depression/ elbow adduction)	min. *Z* (°) (shoulder protraction/ elbow flexion)	max. *Z* (°) (shoulder retraction/ elbow extension)
Mononykus	shoulder osteological	MSO	−27.2	20.37	−14.18	48.53	−45.01	47.64
	shoulder cartilage	MSC	−43.61	33.42	-37.58	49.45	−77.91	79.69
	elbow osteological	MEO	−19.51	21.99	−22.48	18.63	−43.19	40.93
	elbow cartilage (*Coturnix* ulna)	MECcu	−33.32	53.17	−17.32	67.51	−50.10	47.99
	elbow cartilage* (*Gallus* ulna)	MECgu	−90	90	−180	180	−179.49	179.94
	elbow cartilage* (*Gallus* radius)	MECgr	−90	90	−180	79.99	−179.15	179.32
Bannykus	shoulder osteological	BSO	−30.49	59.14	−25.49	46.95	−58.65	61.15
	shoulder cartilage	BSC	−77.31	85.74	−62.97	81.08	−103.23	98.85
	elbow osteological	BEO	−23.02	6.67	−19.20	1.38	−67.44	76.98
	elbow cartilage (*Gallus* ulna)	BECgu	−81.14	40.28	−87.36	36.58	−103.23	100.08
	elbow cartilage* (*Gallus* radius)	BECgr	−83.43	36.47	−87.88	35.08	−101.31	98.44

(e) Moment arm measurement

The moment arm of a muscle group significantly influences its ability to effect rotation about a joint, and larger moment arms may indicate functional emphasis on muscles with actions of behavioural and ecological importance [28,29]. For comparison with a typical theropod, corresponding measurements were made on the forelimb of the early-diverging tyrannosauroid *Guanlong wucaii* (electronic supplementary material, supplementary methods 4). All three models were articulated and measurements made in Blender. Long axes of humeral rotation for this part of the analysis were defined as the axes connecting the joint centres of the shoulder and elbow joints used for the ROM analysis; models were measured with the antebrachium flexed at 90° to this axis (figures 2f and 3f). Moment arms were measured for *Mononykus* and *Bannykus* using the methodology proposed by Nakai & Fujiwara [5], a study of muscle moment arms in forelimb-digging mammals. Forelimb muscles were grouped into five functional categories representing types of motion: shoulder retraction (Sre), shoulder medial rotation (Smr), elbow extension (Eex), elbow flexion (Efl), and elbow adduction (Ead) (full details in electronic supplementary material). The in-lever (Li) and out-lever (Lo) of each muscle were measured and moment arm ratios (Li/Lo) were calculated for each muscle (full details in electronic supplementary material, figure S1). The largest moment arms for each of the five types of motion were selected for further analysis and for comparison with the equivalent measurements for mammals published in [5] (electronic supplementary material, table S14). Analysis of moment arm ratios was performed in R (v. 4.2.2). Maximum moment arm ratios for shoulder retraction, humeral rotation, elbow flexion, extension and adduction for *Guanlong*, *Mononykus* and *Bannykus* were added to the dataset of [5] for comparison. A principal components analysis was performed on moment arm ratios for all taxa in the dataset using the 'FactoMineR' package [46].

3. Results

(a) Range of motion

Both simulations (table 1; MECgu, MECgr) using *Gallus*-derived CCFs for the elbow of *Mononykus* resulted in very large volumes of viable ROM, which are uninformative for interpretation of *in vivo* forelimb function so are not discussed further. Additional simulations run using the *Gallus*-derived CCFs, with a higher overlap threshold of 80% (significantly more conservative than thresholds used in other ROM studies, which often consider 50% overlap still to be in articulation [6,40]), also yield very large volumes of viable ROM, indicating that *Gallus*-derived CCFs are inappropriate for use in *Mononykus*. Therefore, the *Mononykus* simulation using CCFs derived from measurements of the ulna of *Coturnix* (table 1; MECcu) is selected as most appropriate for further discussion and for comparison with the results for *Bannykus*. Both *Bannykus* elbow simulations using CCFs derived from *Gallus* (table 1; BECgu, BECgr) retrieve similar results; the ulna CCF simulation results (table 1; BECgu) are selected for further discussion and comparison, and the radius CCF simulation is not discussed further. Henceforth, discussion of '6DOF' or 'cartilage' ROM simulations for the elbow joints refer to the *Mononykus-Coturnix* ulna simulation MECcu, and the *Bannykus-Gallus* ulna simulation BECgu (table 1).

(i) *Mononykus*

Osteological 3DOF simulations of the shoulder of *Mononykus* find limited protraction, elevation and long-axis rotation of the humerus from the Z pose. Humeral retraction and depression from the Z pose are slightly greater, but overall osteological ROM is fairly restricted (table 1 and figure 2). Osteological ROM for the elbow of *Mononykus* retrieves a maximum 41° of extension and 43° of flexion from the 90° Z pose. Abduction, adduction and long-axis rotation are tightly coupled, and maximum extension of the elbow occurs when these are minimal (table 1 and figure 2). 6DOF cartilage ROM for the shoulder is much less constrained, with greater permitted rotation in all directions except humeral depression; retraction and protraction of the humerus is particularly emphasized. In fact, the degree of retraction retrieved is anatomically unfeasible, taking the humerus underneath the scapular blade, but indicates that this degree of freedom is not significantly constrained by hard tissue morphology. Humeral retraction and long-axis rotation are coupled in both 3DOF and 6DOF, with maximum retraction facilitated by simultaneous long-axis rotation (table 1 and figure 2a). Translation in the 6DOF simulation is tightly coupled in the *X*- and *Z*-axes, reflecting the capacity of the humerus to move laterally/ventrally outwards from the glenoid (figure 2). Simulating the effect of cartilage for the elbow of *Mononykus* permits only slightly increased extension, with possible flexion slightly reduced. Long-axis rotation is increased in both directions, and a much greater degree of adduction is feasible. Abduction/adduction and long-axis rotation remain tightly coupled, and are possible at greater degrees of elbow extension than in the osteological ROM (figure 2c,d). Translation is minimal, restricted in the *Y*-axis, and mainly constrained to the *Z*-axis (figure 2e).

(ii) *Bannykus*

The osteological ROM for the shoulder of *Bannykus* is greater than for *Mononykus*, with relatively limited retraction, protraction and elevation, and a large possible extent of long-axis rotation (table 1 and figure 3a). The osteological ROM map for the elbow of *Bannykus* reconstructs a significant amount of unfeasible ROM, representing abduction of the antebrachium fully around the ectepicondyle to the posterior side of the humerus, where substantial rotation in all three axes is then permitted, reaching to the limits of rotational space allowed by the algorithm (figure 3c,d). This would be impossible *in vivo*, but is retrieved here because 3DOF 'osteological ROM' simulations using APSE class all non-intersecting poses as viable—once an overlap threshold is imposed this additional ROM is excluded as the articular surfaces are no longer within a biologically feasible distance of each other. Nevertheless, the results of this simulation can still be interpreted; the extra ROM is connected by a thin region of pose space to a part of the ROM map showing rotation restricted to the *Z*-axis—the expected hinge-like rotation of the elbow joint. A large degree of both elbow extension and flexion is permitted, and long-axis rotation, abduction and adduction are limited. In the 6DOF simulation for the shoulder, a much greater extent of humeral depression and elevation is feasible, and long-axis rotation is also increased. Similarly to *Mononykus*, biologically unfeasible humeral retraction is reconstructed, and maximum humeral protraction is increased. Translation is mostly restricted to the *Z*-axis (table 1 and figure 3b). For the 6DOF cartilage ROM for the elbow of *Bannykus*, long-axis rotation of the forearm is relatively small (figure 3c,d). A large degree of possible elbow abduction is retrieved; this is biologically unfeasible, but indicates that this motion was not limited by bony morphology in *Bannykus*. Large extents of elbow flexion and extension are feasible in *Bannykus;* these are greater than in *Mononykus*. Translation is almost totally unrestricted within the ± 3.5 mm limits set as the simulation parameters (figure 3e).

(b) Moment arms

Full details of all reconstructed muscle attachments, with references and explanations of levels of inferences, are provided in electronic supplementary material, supplementary results 7-8, figures S2–S5 and tables S9–S10. For all muscle groups except elbow adductors, *Mononykus* has maximum moment arms that exceed those of *Guanlong*, *Bannykus* and the majority of mammals included in the analysis (electronic supplementary material, tables S11-14. In particular, the moment arms for elbow extensors and shoulder medial rotators of *Mononykus* exceed those of almost all digging mammals (figure 4B,D). The forelimb muscle moment arms of *Bannykus* are smaller than those of *Mononykus* but exceed those of most non-digging mammals in the dataset, falling at the top of this range (or above it, in the case of the shoulder medial rotators). The moment arms for *Guanlong* are smaller than for the two alvarezsauroids (except the shoulder retractor, which is slightly greater than that of *Bannykus*), falling within the range observed for non-digging mammals (figure 4). The first principal component (PC1) explains 74.1% of variation in the moment arm data, with PC2 explaining 11.1% (figure 4A). Non-digging mammals with smaller forelimb moment arms cluster towards lower values of PC1 while mammals that use their forelimbs to dig occupy positive areas of this axis. *Mononykus* falls well into this region, with *Bannykus* plotting at the margins of the non-digging hull, and *Guanlong* grouping with non-digging mammals.

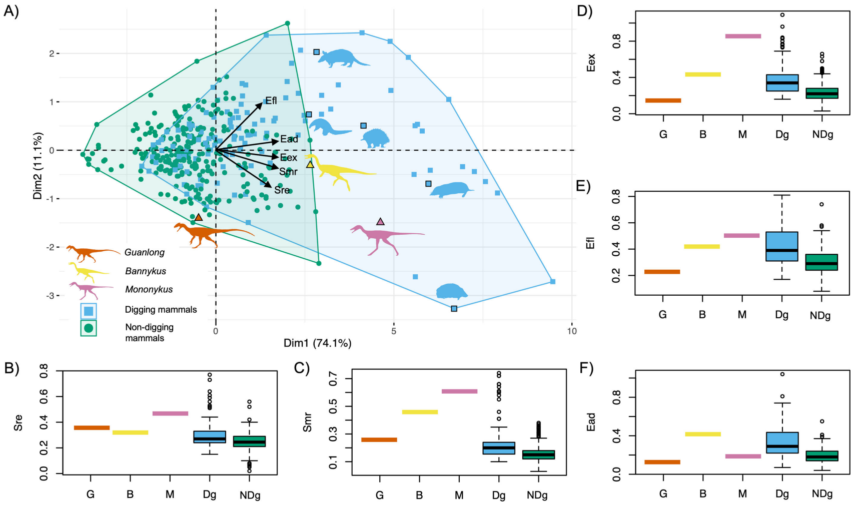

Figure 4. Moment arm analysis results. (A) Morphospace of moment arm ratios for digging and non-digging mammals, the early-diverging tyrannosauroid *Guanlong*, and the alvarezsauroids *Mononykus* and *Bannykus*. Convex hulls designate digging and non-digging mammals in the dataset. Directions of variables are indicated with arrows: Efl, elbow flexor; Ead, elbow adductor; Eex, elbow extensor; Smr, shoulder medial rotator; Sre, shoulder retractor. Points outlined in black are illustrated with silhouettes; mammal silhouettes are (from top to bottom): nine banded armadillo *Dasypus novemcinctus*, giant pangolin *Smutsia gigantea*, short-beaked echidna *Tachyglossus aculeatus*, European mole *Talpa europaea*, and the giant golden mole *Chrysospalax trevelyani*. (B–F) Distribution of maximum moment arm ratios among digging (Dg) and non-digging mammals (NDg), *Guanlong* (G), *Bannykus* (B) and *Mononykus* (M) for: panel (B) shoulder retractors (Sre), panel (C) shoulder medial rotators (Smr), panel (D) elbow extensors (Eex), panel (E) elbow flexors (Efl), and panel (F) elbow adductors (Ead). *Dasypus novemcinctus* silhouette copyright Gabriela Palomo-Munoz, https://creativecommons.org/licenses/by-nc/3.0/. *Chrysospalax trevelyani* silhouette copyright Mo Hassan, https://creativecommons.org/licenses/by-nc-sa/3.0/). *Guanlong* and *Mononykus* silhouettes copyright Scott Hartman, https://creativecommons.org/licenses/by-sa/3.0/). *Bannykus* silhouette modified from [4].

4. Discussion

ROM analysis indicates that *Bannykus* would have been capable of generalized forelimb function and styles of forelimb digging including both scratch and hook-and-pull digging. *Mononykus*, however, has more restricted ROM and likely highly specialized forelimb function, and may have utilized a unique digging style combining aspects of both hook-and-pull and humeral rotation digging. Moment arm analysis supports these interpretations, indicating functional similarity to forelimb-digging mammals and adaptation for digging in both alvarezsauroids, with *Mononykus* showing more extreme specialization. These findings are consistent with previous hypotheses of myrmecophagy and obligate insectivory in parvicursorine alvarezsauroids like *Mononykus*, and may suggest that some adaptation to such an ecology had already occurred in *Bannykus* and other Early Cretaceous alvarezsauroids, possibly as part of a faunivorous ecology.

(a) Forelimb function in *Mononykus* and *Bannykus*

The range of motion analysis presented here supports the feasibility of digging behaviours in both taxa. In *Bannykus*, reconstructed ROM at both joints is sufficient to have permitted a wide range of forelimb functionality, including the 'digging' behaviours necessary to extract insects from hard substrates; the relatively longer forelimbs of *Bannykus* likely also granted it a wider functional repertoire than later-branching, highly derived parvicursorines. In *Mononykus*, however, the highly modified morphology of the forelimb appears to have resulted in a reduction in ROM at the shoulder and elbow joints. Elevation and depression of the humerus are lessened, as are extension and flexion of the elbow, indicating that forelimb function may have been more specialized. However, both joints still possess adequate mobility to enable forelimb 'digging' motions. Mobility at the shoulder of *Mononykus* is characterized by an emphasis on humeral retraction and long-axis rotation, and motion at the elbow appears to have been mostly constrained to the extension/flexion axis, but with potentially significant capacity for adduction. These movements also characterize the digging styles of extant humeral rotation diggers like the echidna, supporting interpretations of a similar digging style in *Mononykus* to these animals [13,15,20,47].

The highly derived morphology of the elbow joint of *Mononykus*, with the single antebrachial condyle medially deflected and rotated [7], means that the arc of flexion and extension for the forearm is almost parallel to the midline when the humerus is held out laterally (noted previously by [11]). This may have enabled humeral retraction and rotation to act together with extension of the elbow to increase the maximum arc travelled by the manus, allowing the shoulder retractor and rotator muscles to contribute to the force exerted through the manus and enabling a digging motion combining aspects of both hook-and-pull and humeral rotation digging. The observed emphasis on the moment arms for elbow extension and humeral retraction, and the feasible ROM for these motions, are consistent with a capacity for forelimb digging in *Mononykus*. The highly congruent articular surfaces of the elbow joint of *Mononykus* are also consistent with this, indicating that the joint was tightly interlocking, which may have increased the stability of the joint during the transmission of forces during digging. The fact that increasing the separation distance in the elbow joint of *Mononykus* dramatically increases available ROM to biologically unfeasible extremes (electronic supplementary material, tables S4–S8), also supports this interpretation. Further work simulating function under a greater range of parameters, and considering the effects of soft tissue structures in constraining ROM is needed to further explore the functional capabilities of this highly unusual structure.

Observations of muscle moment arms and attachment sites are also consistent with digging function in both taxa. Both retain large, well developed osteological correlates of muscle attachment that are absent or reduced in the forelimbs of other short-armed theropods [1,3,48], strongly supporting an important functional role for alvarezsauroid forelimbs (electronic supplementary material, figures S2–S4). The humeri of *Mononykus* and *Bannykus* are highly modified from the basal theropod [45] and basal maniraptoran condition (exemplified by *Haplocheirus* [34]). They both possess a distinctive robust 'hourglass' shape with epiphyses that are significantly expanded in the mediolateral plane, an enlarged internal tuberosity, and a distally placed and prominent deltopectoral crest. These features are all morphologically convergent on extant forelimb-digging mammals [9,13,15,47] and result in increased moment arms for humeral retractors and rotators compared with *Guanlong*; this is especially marked in *Mononykus* (figure 4B,C). The keeled sternum of *Mononykus* [7] also indicates significant expansion of the pectoralis (which takes its origin from this region) and adaptation for humeral adduction and protraction to a degree that is not observed in non-avian theropods, or in earlier-branching alvarezsauroids like *Bannykus*. To our knowledge, the only other tetrapods with a prominent sternal keel that are not specialized for diving or flight are mammalian diggers: golden moles [49], talpid moles [50] and marsupial moles [51]. All possess an independently-evolved keeled sternum, recognized as an adaptation to anchor the powerful pectoral musculature required for forelimb digging.

Both alvarezsauroids have an enlarged olecranon process of the ulna resulting in large moment arms for elbow extension; this is also functionally convergent with extant diggers and is not present in *Guanlong*, other maniraptorans or basal theropods [15,34,45]. In *Mononykus*, this feature along with the extreme shortening of the antebrachium gives a very large moment arm for the triceps brachii, rivalling almost all extant diggers in the dataset (figure 4D; electronic supplementary material, table S14), suggesting a capacity for extremely forceful elbow extension, and a higher degree of functional specialization than *Bannykus*. The distal humeral morphology of both taxa also indicates well developed muscle attachments for muscles controlling motion of the wrist joint, and both taxa have enlarged carpal and digital elements; the fused carpometacarpus and hypertrophied first phalanx of *Mononykus* is especially notable. This further supports the importance of flexion and force transmission at the wrist, consistent with adaptation for digging.

ROM and musculoskeletal morphology indicate adaptation of the forelimbs of *Mononykus* and *Bannykus* to deliver powerful force along multiple axes, providing evidence for similarities between forelimb-digging mammals and alvarezsauroids. PCA reinforces this interpretation: *Mononykus*, in particular, plots close to talpid moles and golden moles—highly specialized humeral-rotation and scratch-diggers, respectively—potentially supporting digging in *Mononykus* combining aspects of different digging styles [5,13,15] (figure 4A). *Bannykus* plots at the edge of the non-digging hull, consistent with an aptitude for digging but a lesser degree of functional specialization. *Bannykus* falls near to the tachyglossids (echidnas), and some anteaters and pangolins, suggesting convergence in moment arm ratios between these taxa. We also note that while moment arm proportions do broadly discriminate between digging- and non-digging taxa, there is significant overlap in PCA space between convex hulls enclosing different digging styles (electronic supplementary material, figure S6), reinforcing the importance of considering a variety of morphological and biomechanical data when making inferences about behaviour. Nevertheless, the enlarged moment arms for the elbow flexors, extensors and adductors of *Bannykus* support both scratch digging and hook-and-pull digging—capacity for strong adduction is particularly similar to extant pangolins, which engage in hook-and-pull digging to break into wood and extract termites, with the palms facing medially [5]. In their original description of the specimen, Xu *et al.* also noted that as well as an enlarged digit II, digit III in *Bannykus* appears to have borne powerful flexor muscles, and had an unusually flexible articulation for the ungual similar to the condition in extant insectivores like the aye-aye, in which is it is used to extract insects from crevices in wood [4,52]. This may indicate that *Bannykus* was performing behaviours more similar to those observed in extant mammals than *Mononykus*, which falls in an empty area of PCA space, reinforcing the idea that it was performing highly specialized behaviours. Recent analysis of preserved intestinal contents suggest *Bannykus* had a carnivorous diet, with no evidence of insect chitin in the individual's last meal [53]. This does not mean these animals could not also have been preying on insects, however—it is plausible that *Bannykus* may have used its forelimbs to break into wood and feed on insects inside, though perhaps as part of a faunivorous or opportunistic dietary ecology. This further suggests *Bannykus* as transitional in its morphology and ecology between early-branching alvarezsauroids and potentially obligately myrmecophagous parvicursorines like *Mononykus*.

(b) Functional and ecological evolution in alvarezsauroids

Despite adaptations for digging, the forelimb of *Bannykus* still possesses sufficient mobility at the shoulder and elbow to perform a range of behaviours, further consistent with a more generalist, faunivorous lifestyle. By contrast, the highly modified elbow joint, dramatic shortening of the forelimb, and loss or fusion of manual and carpal elements in *Mononykus*, have resulted in loss of generalized function in favour of a tool optimized to perform a highly specialized function with significant force. The extreme specialization of parvicursorine alvarezsauroids has been suggested to have been driven by increased ecological specialization to obligate myrmecophagy as social insects diversified during the Cretaceous. Alvarezsauroids were thought to have undergone a period of rapid body size miniaturization during this time, associated with the radiation of late-diverging taxa like *Mononykus* and interpreted as evidence for small body size being correlated to the evolution of myrmecophagy [20,24,54,55]. However, the recent discovery of *Alnashetri cerropoliciensis*, a basal non-alvarezsaurid alvarezsauroid with very small body size but unreduced forelimbs comparable with the ancestral coelurosaur condition [56], suggests that alvarezsauroids evolved small body sizes multiple times throughout their evolution, independent of forelimb reduction. The presence of possible adaptations for digging alongside large body size in *Bannykus* provides further support for this interpretation that the evolution of insectivory did not drive miniaturization, with alvarezsauroids evolving small body sizes under different ecologies. Indeed, small body size is not a prerequisite for obligate insectivory; numerous extant obligate myrmecophages exceed the estimated mass of *Bannykus* [54,57].

Disentangling whether a transition from faunivory to obligate myrmecophagy played a role in driving miniaturization and morphological specialization remains challenging, as does resolving the drivers of the extreme forelimb reduction observed in alvarezsauroids. Unlike tyrannosaurids and abelisaurids, in whom extreme forelimb reduction can be interpreted as part of an overall ecology relying solely on prey capture using the head, with no benefit in retaining long arms, alvarezsaur forelimbs are proportionately restructured and morphologically modified to maximize forelimb muscle moment arms, strongly suggesting their ecological importance [48]. While digital reduction has been interpreted as adaptation for digging [24], it still seems paradoxical that the entire forelimb would evolve to be smaller. More detailed integrative biomechanical analyses are needed to thoroughly investigate the consequences of both limb reduction and musculoskeletal apomorphies on forelimb function in alvarezsaurs. Nevertheless, we present a starting point that joins a growing body of work indicating that hypothesized pick-like 'digging' motion was feasible [20,25,58].

While aspects of alvarezsauroid ecology remain mysterious, our results are consistent with previous hypotheses of myrmecophagy and a diet of wood-boring termites: despite their short length, the powerful forelimbs could have been used to break into above-ground substrates like dead logs (and indeed, fossilized wood containing termite boreholes has been found in the same location as alvarezsaur fossil material [20]), which would be accessible to the alvarezsaur forelimb even despite its short length, especially given the tiny body size of late-diverging taxa. Small body size may also have aided foraging; the forelimbs of *Mononykus* are too short to have been inserted far into crevices to extract insects, so a small head with slender jaws was likely advantageous, enabling the animal to insert its whole head to extract prey, with no need to use the forelimb other than as an initial tool to open the crack. Other hypotheses for alvarezsaur forelimb function have been proposed, including the idea that they were specialized for egg predation [12,59], but given alvarezsaurs' suite of shared features with forelimb-digging mammals we consider a similar digging function the most plausible. This does not preclude other uses for the forelimb such as display, grooming or in mating, as have been suggested for the reduced forelimbs of other theropods [1,48]. Various authors have also cited the disparity in length between the fore and hindlimbs of alvarezsaurs as evidence against any forelimb digging behaviours [9,10,12,59], but long hindlimbs would not preclude the proposed behaviour above, perhaps even aiding reach of the forelimb, and can additionally be interpreted as adaptation to move between foraging sites and evade predators. We also note that comparisons with extant digging mammals are imperfect; as bipedal theropods, alvarezsauroids exhibit a decoupling between their fore-and hindlimb morphology that quadrupeds cannot achieve owing to locomotor constraints—this decoupling is exemplified by multiple instances of evolutionary shortening and lengthening of the forelimb across a diverse range of theropod clades. This has resulted in a unique mosaic of cursorial and digging-adapted features with no obvious modern analogue, complicating interpretations of alvarezsauroid ecology.

Considerable functional diversity exists within broad digging categories; even closely related taxa may exhibit morpho-functional differentiation corresponding to more subtle differences in digging behaviour [60]. Similarity in functional metrics (moment arms) indicates that alvarezsaur forelimbs functioned in a similar manner to those of digging mammals—but the digging kinematics of alvarezsauroids were likely unique and not directly analogous to anything seen in extant taxa. Alvarezsauroids represent only one example of how the evolutionary lability of the theropod forelimb has permitted the evolution of highly specialized and unusual morphotypes not seen in extant taxa. Other examples include the very large crania and tiny forelimbs of tyrannosauroids and abelisauroids [1,48], the highly elongated manual unguals of therizinosaurs [58], and extension of the forelimb and manus facilitating the evolution of flight in the maniraptoran lineage leading to birds.

5. Conclusion

The analyses presented here offer a starting point for further quantitative biomechanical analyses of these animals, to resolve the functional drivers of their striking miniaturization, forelimb reduction and specialization. Alvarezsauroids are an intriguing potential example of functional and ecological convergence between dinosaurs and myrmecophagous mammals, illustrating how selection for similar specialized ecological function may be expressed across two very different bodyplans. Our findings not only enhance our understanding of the ecology and function of a unique and enigmatic group of dinosaurs, but also provide insight into forelimb and bodyplan evolution in theropods as a whole. Alvarezsauroid forelimb reduction is among the most dramatic observed in theropods, but did not result in functional degeneration, as in other lineages [1,48], instead reflecting active adaptation to a myrmecophagous niche potentially unique among non-avian dinosaurs. Along with other maniraptorans possessing specialized forelimb morphology, such as therizinosaurs [58] and scansorioterygids [61], alvarezsauroids indicate how experimentation in forelimb morphology was particularly key in facilitating ecological diversity in this clade, and provide important context for the evolution of the avian wing, one of the most significant innovations in vertebrate evolution.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data required to reproduce the analyses, as well as complete ROM and PCA results, are available on Zenodo [62]. Supplementary material is available online [63].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.L.: conceptualization, formal analysis, investigation, methodology, project administration, writing—original draft, writing—review and editing; Z.Q.: conceptualization, resources, supervision, writing—review and editing; B.W.G.: supervision, writing—review and editing; A.B.: supervision, writing—review and editing; Y.Y.: funding acquisition, resources, writing—review and editing; X.X.: funding acquisition, resources, writing—review and editing; E.R.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

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