Elbow joint adductor moment arm as an indicator of forelimb posture in extinct quadrupedal tetrapods

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Forelimb posture has been a controversial aspect of reconstructing locomotor behaviour in extinct quadrupedal tetrapods. This is partly owing to the qualitative and subjective nature of typical methods, which focus on bony articulations that are often ambiguous and unvalidated postural indicators. Here we outline a new, quantitatively based forelimb posture index that is applicable to a majority of extant tetrapods. By determining the degree of elbow joint adduction/abduction mobility in several tetrapods, the carpal flexor muscles were determined to also play a role as elbow adductors. Such adduction may play a major role during the stance phase in sprawling postures. This role is different from those of upright/sagittal and sloth-like creeping postures, which, respectively, depend more on elbow extensors and flexors. Our measurements of elbow muscle moment arms in 318 extant tetrapod skeletons (Lissamphibia, Synapsida and Reptilia: 33 major clades and 263 genera) revealed that sprawling, sagittal and creeping tetrapods, respectively, emphasize elbow adductor, extensor and flexor muscles. Furthermore, scansional and non-scansional taxa, respectively, emphasize flexors and extensors. Thus, forelimb postures of extinct tetrapods can be qualitatively classified based on our quantitative index. Using this method, we find that Triceratops (Ceratopsidae), Anhanguera (Pterosauria) and desmostylian mammals are categorized as upright/sagittal locomoting taxa.

Keywords: elbow; moment arm; posture; reconstruction; Triceratops; Desmostylian

1. INTRODUCTION

Forelimb function has diversified dramatically within the clade Tetrapoda. Evolutionary shifts of forelimb posture are considered to be major events in many lineages (e.g. in basal mammals [1–3], dinosaurs [4], archosaurs [5] and crocodylomorphs [6]). Reconstruction of limb orientation in any extinct taxon is important not only for reconstructing parameters relevant to their palaeoecology, such as locomotor behaviour, gait, and speed, (which might influence metabolic energy budgets and interactions with other individuals), but also for reliably estimating the timings of limb postural transitions in evolution. For example, reconstructing the forelimb posture of ceratopsian dinosaurs such as the early, smaller form Protoceratops and the later, massive form Triceratops would help illuminate how these animals moved (slower or faster speeds, or the controversial usage of trotting/galloping gaits [7,8]; and how locomotor mechanics and body size co-evolved within Ceratopsia. Such evidence would also be an important independent test of inferences drawn from fossil footprints and trackways [9]. More broadly, reconstructing limb poses brings such animals more dynamically to life and helps further public understandings of engagement with palaeontology, including an explanation of how (or which) such reconstructions are even scientifically achievable.

Previous studies generally have reconstructed the forelimb poses of extinct tetrapods by qualitatively dichotomizing them into upright/sagittal or sprawling categories. Yet as noted above, a consensus on forelimb posture has yet to be achieved in many cases: e.g. early mammals [3,10], ceratopsid dinosaurs [11–18] and desmostylian mammals [19–22]. The popular approach for reconstructing forelimb postures has been to estimate suitable articular relationships between the two components of the glenohumeral (shoulder) joint [3,12,15,20,21,23]. However, this joint tends to have a wide range (or wide interpretations of range) of three-dimensional motion in most taxa, and bony articulations alone may be unreliable indicators of limb orientation and motion [24]. Furthermore, determination of the typical scapular position and orientation on the ribcage still remains problematic or even overlooked [25]. Differences in the shapes of articular cartilage caps and calcified epiphyses can also be a problem, especially in fossil archosaurs whose cartilages are often expected to be thick [26–30].

Another, less commonly used approach favours quantitative parameters for estimating the most mechanically effective postures (angles of abduction/adduction or extension/flexion) of extinct taxa. This includes approaches that focus on bone bending loads [1,5]; or magnitudes of moment arms [22,31,32]. While no approaches are expected to have high precision, these quantitative approaches are at least more explicit and specific, and more closely linked to the fundamental principles governing terrestrial support and movement. However, to date there are few such mechanical approaches for indicating...
the difference between sprawling and upright/sagittal forelimb postures.

Here, we develop a new method for indicating typical forelimb postures in terrestrial tetrapods. A reliable method of reconstruction should be consistent with biomechanical principles and anatomy. Its validity should also be tested by applying it to a broad sample of extant taxa before applying it to extinct taxa, so that its reliability can be determined [33]—are any taxa of known posture falsely classified? We focused on the mechanics of the elbow joint, using the quantitative shape of bones and biomechanical parameters (moment arms) to determine differences in forelimb posture for the first time. This approach has the merit that shoulder joint position/orientation does not need to be inferred (see details later). According to simple mechanical models of forelimb postural relationships with muscle function (see §2), we formulated two main hypotheses: (i) upright/sagittal, sprawling and creeping tetrapods, respectively, emphasize elbow extensor, adductor and flexor muscles and (ii) scansorial and non-scansorial tetrapods, respectively, emphasize flexor and extensors. We tested these hypotheses with our new forelimb postural indicator method, in order to assess how well it would apply to estimating postures for the extinct taxa we investigated.

We then applied our method to six extinct tetrapod genera (*Triceratops* and *Protoceratops* (Ceratopsia), *Anhanguera* (Pterosauria), *Thylacinus* (Marsupialia), and *Paleoparadoxia* and *Desmostylus* (Desmostylia)), a consensus on the forelimb posture of which has yet to be achieved, to infer likely forelimb postures, which we compare with previous studies in §4.

2. MATERIAL AND METHODS

(a) Specimens

The maximum possible moment arms of elbow joint extensor, flexor and adductor muscles were measured in dried skeletons and carcasses of 318 extant tetrapod specimens, including 22 lissamphibians (12 genera), five testudines, 44 lepidosauromorphs (25 genera), six crocodylids (four genera), four birds (two genera representing flying and flightless taxa), four monotremes (three genera), 25 marsupials (22 genera), 16 afrotherians, 12 xenarthrans (nine genera), 28 eutherians (24 genera), 38 glires, six basal eurasiatherians, 36 cetartiodactyls (34 genera) and 72 pegasofere (62 genera) (electronic supplementary material, S1). The locomotor category of some taxa [38] but is not considered here, particularly because it is difficult to quantify in many taxa.

We categorized forelimb-based horizontal locomotion on the ground according to basic kinematics of motion. The categories were upright/sagittal (U), sprawling (S) and creeping (C) motions. Uncategorizable, unknown or non-forelimb users were defined as 'X' (electronic supplementary material, table S1). These groups were subdivided into subcategories based on the absence (A), presence (P) or obscurity (X) of scansional (climbing-related) abilities (e.g. group ‘UA’ indicates upright/sagittal with no scansional ability). Animals were categorized as subtype P if scansional behaviour was reported in the literature, but the levels of those abilities were not taken into account because such fine categorization was deemed too arbitrary. The number of locomotor categorical groups was three (U, S and C) in the main category and five (UA, UP, SA, SP and CP) in subcategories; there are no non-scansorial creeping taxa (CA). Next, we considered differences in the groups of muscles (or any tensile forces) that are expected to act at the elbow joint to resist the ground reaction force (GRF) during the stance phase in each category.

In upright/sagittal postures, the GRF mainly flexes the elbow during the stance phase whether the joint angle is small or large (less than 180°), and the extensor muscles (electronic supplementary material, S3 and table S3) resist this with an extensor moment [39–43]. The extensor muscles mainly insert onto the olecranon process, which functions as a lever. The roles of the abductor/adductors are expected to be minimal, because the limb is moving mostly in a sagittal plane (figure 1a). However, we admit that more three-dimensional studies of forelimb dynamics in such 'sagittal' taxa are needed to accurately determine the motions and mechanical roles of muscles. Furthermore, one must be wary of interpreting our qualitative categories too literally as having starkly clear boundaries, because postures may vary widely in extant taxa so categories may be misleading [44]—a point we return to in §4.

During the stance phase in sprawling postures, the GRF is expected to abduct the antebrachium against the humerus around the elbow, so muscles must mainly incur an adduction moment about the elbow joint (figure 1b). Therefore, more sprawling animals are expected to rely more on elbow adductors (electronic supplementary material, table S3). In addition to upright/sagittal and sprawling postures, we considered a locomotor mode that relies on elbow flexors (electronic supplementary material, table S3). An animal is expected to use elbow flexors when they drag their body forward against friction with the ground (figure 1c). We defined this motion as creeping motion, which is typified by sloths [45,46]. Elbow adductors are expected to play little role during this creeping motion, unless the humerus is strongly rotated medially (internally). We also considered vertical locomotion, as opposed to horizontal locomotion in the other postures, to fit into this category; especially for highly scansional taxa. The elbow flexor muscles (electronic
Axes of elbow extension/flexion (OEx/Fl) and abduction/adduction (OAb/Ad) were, respectively, defined as the maximum possible moment arms from bone morphology. The distance from the estimated rotational axis of elbow extension/flexion (OEx/Fl) to the most distant point on the olecranon (ol) was, respectively, defined as the centres of the sigmoid notch (g) or radial condyle (r) in lateral view, and the centre of the radial condyle (c) in cranial view. The distances 'OEx/Fl–ol', 'OEx/Fl–rt', 'OEx/Fl–lsc' and 'OAb/Ad–me' were, respectively, defined as the maximum possible moment arms of elbow extension (Ex), flexors along the brachium (Fl1) and the antebrachium (Fl2), and adductors (Ad). The distance from OEx/Fl to the distal end of the radius was defined as the antebrachial length (A). ab, Antebrachium; E, elbow joint; F, friction; GRF, ground reaction force; h, humerus; lsc, lateral supracondylar crest; m, manus; me, medial epicondyle; ol, olecranon; r, radius; rc, radial condyle; rt, radial tuberosity; S, shoulder joint, uc, ulnar condyle; ul, ulna.

Figure 1. Mechanical models (a–e) of forelimb postures, and measurements taken for each specimen (f–g): (a) Upright/sagittal posture (extensor-dependent), (b) sprawling posture (adductor-dependent), (c) creeping (flexor-dependent against friction), (d) vertical climbing (flexor-dependent), (e) cranial views, and (f) antebrachium in lateral view. Axes of elbow extension/flexion (OEx/Fl) and abduction/adduction (OAb/Ad) were, respectively, defined as the centres of the sigmoid notch (g) or radial condyle (r) in lateral view, and the centre of the radial condyle (c) in cranial view. The distances 'OEx/Fl–ol', 'OEx/Fl–rt', 'OEx/Fl–lsc' and 'OAb/Ad–me' were, respectively, defined as the maximum possible moment arms of elbow extensors (Ex), flexors along the brachium (Fl1) and the antebrachium (Fl2), and adductors (Ad). The distance from OEx/Fl to the distal end of the radius was defined as the antebrachial length (A). ab, Antebrachium; E, elbow joint; F, friction; GRF, ground reaction force; h, humerus; lsc, lateral supracondylar crest; m, manus; me, medial epicondyle; ol, olecranon; r, radius; rc, radial condyle; rt, radial tuberosity; S, shoulder joint, uc, ulnar condyle; ul, ulna.

supplementary material, table S3) are expected to contract when an animal pulls its body upward (figure 1d). The contraction of such muscle is indicated by electromyography [47]. Less scansorial taxa would tend to favour extensor muscle activity about their elbow joints.

Figure 1e–g illustrates how we calculated muscle moment arms from bone morphology. The distance from the estimated rotational axis of elbow extension/flexion (OEx/Fl) to the most distant point on the olecranon (ol) and to the most distant points of lateral supracondylar crest (lsc) and radial tuberosity (rt) (whichever is larger), were, respectively, defined as the maximum possible moment arms of the extensor and flexor muscle groups (electronic supplementary material, S3 and table S3; see also Fujiwara et al. [32]). The distance from the rotational axis of elbow abduction/adduction (OAb/Ad) to the most distant point on the medial epicondyle was defined as the maximum possible moment arm of the elbow adductors (i.e. carpal flexors; figure 1f) and electronic supplementary material, table S3). The distance from the rotational axis of elbow extension/flexion to the distal end of the radius defined the length of the antebrachium (figure 1g). Maximum possible moment arms of the elbow extensor (Ex), flexor (Fl) and adductor (Ad) muscles and antebrachial lengths (A), were measured on the 318 extant and seven fossil specimens (electronic supplementary material, S1). See electronic supplementary material, S3 for details on the measurements and specimens.

(c) Analysis of elbow moment arms in each locomotor category

To test our hypotheses, we examined inter-categorical differences of extensor, flexor and adductor moment arm indices for the main and sub-locomotor categories. Extensor (Ex), flexor (Fl) and adductor (Ad) moment arms were, respectively, divided by the geometric mean (GM) of the three variables (GM = (Ex × Fl × Ad)1/3). This removed some of the influence of body size on these indices. Each moment arm’s length divided by the GM was, respectively, defined as the extensor (Ex/GM), flexor (Fl/GM) and adductor (Ad/GM) indices.

First, we tested if there is a correlation between body size and our locomotor indices. The length of the antebrachium (A) was used as an indicator of body size. We conducted a Spearman’s test between log A and each moment arm index (log (Ex/GM), log (Fl/GM) and log (Ad/GM)) using R v. 2.12.2 (The R Foundation for Statistical Computing: http://CRAN.R-project.org/). The null hypothesis that there is no correlation between the values was rejected if p < 0.05.

Next, differences in the moment arm index distributions (log (Ex/GM), log (Fl/GM) and log (Ad/GM)) among
locomotor categories were tested by a Steel–Dwass test in R software. The test is a pair-wise comparison of one-dimensional distributions between all the pairs of locomotor categories. Significant inter-categorical differences of the distribution were rejected if $p > 0.05$. Finally, the relative values of moment arm indices were compared among locomotor categories by comparing their median values.

(d) Discriminant analysis

In the next step, we estimated the locomotor category for each extinct taxon (electronic supplementary material, S1) based on the distributions of variables from the measurement data for extant taxa. We selected size-dependent and independent variables for the moment arm indices. The size-dependent variables were the log-transformed values of elbow muscle moment arms ($\log (Ex)$, $\log (Fl)$ and $\log (Ad)$). The size-independent variables were dimensionless values calculated by each elbow moment arm divided by the antebrachial length ($A$) ($\log (Ex/A)$, $\log (Fl/A)$ and $\log (Ad/A)$). For both the size-dependent and independent variables, the points of multiple locomotor categories did not distribute normally in a trivariate coordinate space (electronic supplementary material, S4; [48]). Therefore, non-parametric analyses were conducted.

We conducted a non-parametric kernel discriminant analysis for the moment arm indices by using packages ‘ks’ [49] and ‘rgl’ [50] in R software. Discriminant analysis allocates the point to one of the locomotor categories, which maximizes the posterior probability (Bayes’ discriminant rule). The posterior probability of a point $x$ being in group $i$ ($i = C, S, U$ or $CP, SA, SP, UA, UP$) is proportional to a discriminant score for group $i$ ($D_i$), which can be calculated as a product of the prior probability of the group $i$ ($\pi_i$) and kernel density to the group $i$ estimated at the point $x$ ($f_i$) ($D_i = \pi_i \times f_i$) [49]. The larger $D_i$ of a point is in relation with $D_{2i}$, the more the point is located in the densest region of group $i$, but at the sparsest region of group $2$, and the more likely the point is categorized to group $i$ than to $2$. In the first step, the kernel density distributions based on the points for extant taxa were created in trivariate space for both the main (C, S and U) and sub- (CP, SA, SP, UA and UP) categories. An unconstrained smoothed cross validation bandwidth selector was used for the kernel density estimation [49].

The locomotor categories of all the study taxa (both extant and extinct) were estimated based on both size-dependent and independent variables. Each point was categorized to main (C, S and U) and sub- (CP, SA, SP, UA and UP) categories for each variable. All the points were coercively categorized to a certain locomotor ability, even if its discriminant score was significantly lower than the others. Therefore, outliers of the scores (less than 5%) were calculated for each locomotor category, and the outlier points of the estimation were derived (electronic supplementary material, S1).

We checked the accuracy of our discriminant analysis by estimating the locomotor categories of the extant taxa and comparing these estimates against the known categories for each (see electronic supplementary material, S5). The reliability of the discriminant analysis was also tested by a Steel–Dwass test for different distributions of discriminant scores among locomotor categories (see electronic supplementary material, S5). In theory, the size-independent method is applicable to reconstructions of extinct taxa with extreme body sizes. However, we needed to validate the result of each discrimination regardless of the body size in extant taxa. To test this, we conducted a Steel–Dwass test between the results of discriminant scores of normal and extreme body sizes ($\log (A)$) (see details in electronic supplementary material, S6).

Moreover, an error of the discrimination for a point was expected when there was no remarkable difference between the highest and the lower discriminant scores. We defined the ratio between the highest ($D_{1st}$) and the second highest ($D_{2nd}$) discriminant scores as a likelihood ratio ($\log (D_{1st}/D_{2nd})$). This factor was compared between successfully and unsuccessfully discriminated taxa in order to find the minimum-likelihood ratio that made a successful discrimination (electronic supplementary material, S7). We also tested whether the different epiphyseal morphologies known among tetrapod taxa [26] would affect the accuracy of the analysis (electronic supplementary material, S7).

3. RESULTS

(a) Emphases of elbow moment arms in each locomotor category

According to our Spearman’s test between body size (antebrachial length: $A$) and each moment arm index ($\log (Ex/GM)$, $\log (Fl/GM)$ and $\log (Ad/GM)$), a significant correlation was found for one main (U) and one sub- (UA) category of extensor index, in one main (S) and one sub- (UP) category of flexor index, and in two main (S and U) and one sub- (UA) category of adductor index (table 1). The coefficients of determination ($r^2$) were weak ($r^2 < 0.30$) in these six out of 24 locomotor categories, so the implications were inconclusive.

We then compared the distributions and median values of the moment arm indices among the locomotor categories (table 2 and figure 2). The extensor index of category U was significantly larger than those of categories C and S. The flexor index of category C was significantly larger than those of the other main categories S and U. The adductor index of category S was significantly larger than those of the other main categories C and U. For the five subcategories, the extensor indices of categories UA and SA were significantly larger than those of categories UP and SP, respectively. The flexor index of UP was significantly larger than that of UA. The median value of the flexor index of SP was larger than that of SA, but a significant difference of the distributions was not supported (table 2 and figure 2).

(b) Discriminant analyses

Discriminant scores for each locomotor category of our study taxa are listed in electronic supplementary material, table S1-2. According to our Steel–Dwass test between discriminant scores of taxa with normal and extreme body sizes, a significant difference was rejected for the size-independent method (electronic supplementary material, S6). Therefore, the results of our discriminant analysis are not influenced by body size.

For both the size-dependent ($\log (Ex)$, $\log (Fl)$ and $\log (Ad)$) and independent ($\log (Ex/A)$, $\log (Fl/A)$ and $\log (Ad/A)$) variables, significant differences of point distributions among the locomotor categories were revealed by our Steel–Dwass tests (see electronic supplementary materials, S1 and S5). The total error rate in discrimination was approximately 10 per cent for the three main categories and was approximately 20 per cent in
Table 1. Results of Spearman’s and correlation tests between body size as represented by antebrachial length (log A) and each moment arm index (MAI: log (Ex/GM), log (Fl/GM) and log (Ad/GM)), where GM is the geometric mean of elbow extensor (Ex), flexor (Fl) and adductor (Ad) moment arms. Spearman’s rho and p-value, and coefficient of determination ($r^2$) are indicated for each locomotor category (LC).

<table>
<thead>
<tr>
<th>MAI</th>
<th>log Ex/GM</th>
<th>log Fl/GM</th>
<th>log Ad/GM</th>
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<tbody>
<tr>
<td></td>
<td>LC</td>
<td>rho</td>
<td>p-value</td>
</tr>
<tr>
<td></td>
<td>C (=CP)</td>
<td>0.143</td>
<td>0.752*</td>
</tr>
<tr>
<td></td>
<td>S (total)</td>
<td>0.0198</td>
<td>0.872*</td>
</tr>
<tr>
<td></td>
<td>SA</td>
<td>−0.0672</td>
<td>0.769*</td>
</tr>
<tr>
<td></td>
<td>SP</td>
<td>0.00405</td>
<td>0.982*</td>
</tr>
<tr>
<td></td>
<td>U (total)</td>
<td>0.252</td>
<td>2.58E–04</td>
</tr>
<tr>
<td></td>
<td>UA</td>
<td>0.378</td>
<td>6.25E–5</td>
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<tr>
<td></td>
<td>UP</td>
<td>−0.126</td>
<td>0.214*</td>
</tr>
</tbody>
</table>

*Indicates that the correlation between body size (A) and the moment arm index (MAI) cannot be supported ($p > 0.05$).

Table 2. Results of the Steel–Dwass tests for extensor, flexor and adductor indices for three main (C, S and U) or five sub-categories (CP, SA, SP, UA and UP) of locomotion. GM, geometric mean of extensor (Ex), flexor (Fl), and adductor (Ad) moment arms; LC, locomotor categories; MAI, moment arm index; p, p-value.

<table>
<thead>
<tr>
<th>MAI</th>
<th>log Ex/GM</th>
<th>log Fl/GM</th>
<th>log Ad/GM</th>
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<tbody>
<tr>
<td></td>
<td>LC</td>
<td>t</td>
<td>p-value</td>
</tr>
<tr>
<td></td>
<td>C: S</td>
<td>4.66</td>
<td>9.37E–06</td>
</tr>
<tr>
<td></td>
<td>C: U</td>
<td>4.96</td>
<td>2.09E–06</td>
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<tr>
<td></td>
<td>S: U</td>
<td>8.71</td>
<td>2.44E–14</td>
</tr>
<tr>
<td></td>
<td>CP: SA</td>
<td>4.39</td>
<td>1.10E–04</td>
</tr>
<tr>
<td></td>
<td>CP: SP</td>
<td>4.35</td>
<td>1.32E–04</td>
</tr>
<tr>
<td></td>
<td>CP: UA</td>
<td>4.95</td>
<td>6.60E–06</td>
</tr>
<tr>
<td></td>
<td>CP: UP</td>
<td>4.72</td>
<td>2.34E–06</td>
</tr>
<tr>
<td></td>
<td>SA: SP</td>
<td>4.95</td>
<td>7.52E–06</td>
</tr>
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<td></td>
<td>SA: UA</td>
<td>6.49</td>
<td>8.85E–10</td>
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<tr>
<td></td>
<td>SA: UP</td>
<td>0.838</td>
<td>0.919E–01</td>
</tr>
<tr>
<td></td>
<td>SP: UA</td>
<td>9.60</td>
<td>3.79E–14</td>
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<td></td>
<td>SP: UP</td>
<td>5.62</td>
<td>1.93E–07</td>
</tr>
<tr>
<td></td>
<td>UA: UP</td>
<td>10.9</td>
<td>4.81E–14</td>
</tr>
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</table>

*Indicates that the moment arm indices among two locomotor categories were not significantly different ($p > 0.05$).
A regression line for each locomotor category is shown in Figure 2. Correlations between body size (represented by antebbranchial length: $\log A$) and locomotor indices ($\log (Ex/GM)$, $\log (Fl/GM)$ and $\log (Ad/GM)$) in each locomotor category (a–c) and box plots of the indices for each category (d–f). The regression line for each locomotor category is shown in a–c: both asterisks and dotted lines indicate that there is no significant correlation. Upright/sagittal, sprawling and creeping taxa are, respectively, indicated in green, blue and red colours. Scansorial abilities are indicated as A (absent), P (present) and X (obscurity). Fossil taxa are indicated in black: An, Anhanguera; Ds, Desmostylus; Pl, Paleoparadoxia; Pr, Protoceratops; Th, Thylacinus and Tr, Triceratops. Significant differences of distribution were rejected in pairs of SA–UP (subcategory) for the extensor index, S–U (main category), SA–SP, SA–UA (subcategory) for the flexor index, and C–U (main category), CP–SA, CP–UP and SA–SP (subcategory) for the adductor index.
According to the discriminant analyses, *Thylacinus* was categorized as U and UA by our size-dependent and independent indices (figure 3; electronic supplementary materials, S1 and S8). The animal is known as non-scansorial and upright/sagittal [34–36], so the discriminant analysis worked for this extinct taxon.

Two desmostylians, *Paleoparadoxia* and *Desmostylus*, were both categorized as U/UA in the size-dependent analysis, but were, respectively, categorized as U/UA and U/UP in the size-independent analysis (figure 3; electronic supplementary materials, S1 and S8). The estimated posture varied between the two ceratopsians. *Protoceratops* and *Triceratops* were, respectively, categorized as C/UP and U/UA in size-dependent analyses (figure 3; electronic supplementary materials, S1 and S8). *Protoceratops* and *Triceratops* were, respectively, categorized as S/SP and U/UA in our size-independent analyses (figure 3; electronic supplementary materials, S1 and S8). In the pterosaur *Anhanguera*, the estimated forelimb posture was U/UP using size-dependent variables. The antebrachial length was not available for *Anhanguera*, so the posture was not estimated based on size-independent variables (figure 3; electronic supplementary materials, S1 and S8). Among these, one *Paleoparadoxia* specimen (*P. reppeningi*) and *Triceratops* was plotted in the outlier area of the estimated locomotor category in the size-independent analysis (electronic supplementary material, S1). In all extinct taxa, except for the point of *Protoceratops* in the size-dependent method, the likelihood ratio of the discriminant score for three

Figure 3. Three-dimensional discriminant score density plots of (a,b) three main and (c,d) five locomotor sub-categories in both (a,c) size-dependent and (b,d) independent variables. Contours of the density estimations are 50% and 95%. Each colour indicates different locomotor categories. Three main categories: (a,b) C, red; S, green; U, blue. Five subcategories: (c,d) CP, red; SA, yellow; SP, green; UA, blue; UP, purple. Fossil taxa are also plotted on the diagrams: An, *Anhanguera*; Ds, *Desmostylus*; Pl, *Paleoparadoxia*; Pr, *Protoceratops*; Th, *Thylacinus*; Tr, *Triceratops*.
main categories was high and the errors of the results were not expected to be high (electronic supplementary material, S1 and S7).

4. DISCUSSION

Our results for extant taxa bolster our first hypothesis that upright/sagittal (U), sprawling (S) and creeping (C) terrestrial quadrupeds, respectively, emphasize elbow extensor, adductor and flexor moment arms. We also found support for our second hypothesis that there is a trade-off of flexor and extensor moment arms between scansorial (emphasize flexor over extensor: groups SP and UP) and non-scansorial groups (emphasize extensor over flexor: groups SA and UA). The latter result is consistent with other studies [32,51]. We attempted to categorize locomotor abilities only by three parameters from elbow morphology, and our attempt was successful for the discrimination among upright/sagittal, sprawling and creeping postures regardless of the body size (antebrachial length), forelimb/hindlimb body support roles and epiphyseal structure (electronic supplementary material, S6 and S7). Our new indicator is also applicable for determining relationships between morphological variations and locomotor abilities among extant taxa (electronic supplementary material, S1).

Estimation of forelimb postures in extinct taxa using our discriminant analyses relies on an assumption that these animals employ quadrupedal postures on the ground. Regardless of whether the animals were non-forelimb users (e.g. controversial for Anhanguera and other pterosaurs; [52–55]), they will be placed in certain locomotor categories. Although the extinct taxa were categorized as having a certain locomotor ability, users of this method should keep in mind that hypotheses that these animals did not employ terrestrial quadrupedal locomotion (e.g. bipedal or fully aquatic) cannot be rejected solely by using this method. Independent evidence, always important for palaeobiological inferences of function, becomes particularly critical in such cases. In addition, if the discriminant score for the estimated category was not sufficiently larger than those for the other locomotor categories, the result may cause an error, so the users of this method should also compare all the discriminant scores (electronic supplementary material, S7).

Putative trackways of ceratopsid dinosaurs [9] and some pterosaurs [55–57] seem to indicate that they employed upright/sagittal quadrupedal limb orientations, which are consistent with our result. The estimated posture of Triceratops in this study is also consistent with the posture estimated from skeletal morphologies of the antebrachium and manus [17,18] as well as shoulder [15,16], implying that the humerus was kept adducted near the trunk. However, other functional assessments from shoulder morphology are in conflict with this evidence [11,13]; regardless, a posture that does not involve pronounced humeral adduction during the stance phase is expected to rely not on elbow adductors, but mainly on elbow extensors (figure 1). Less problematically, there is no definitive evidence of quadrupedality in desmostylians. Yet our inference that desmostylians were upright and non-scanorial (as well as quadrupedal) is consistent not only with the generally (and uncontroversially) quadrupedal morphology of all known specimens, but also with an estimation based on mechanical modelling of limb joint torques, which inferred that these animals had difficulty adopting a sprawling posture [19].

Our size-dependent method has an advantage over other approaches in its reasonably high accuracy (electronic supplementary material, S5). We consider this method to be generally viable if the sizes of extinct taxa fall into our normal sample size range for extant taxa (147–201 mm in antebrachial length (roughly 1.0–8.5 kg) for creeping taxa; 9.2–74 mm in antebrachial length (roughly 0.04–10 kg) for sprawling taxa and 18–336 mm (roughly 0.1–270 kg) for upright/sagittal taxa). However, taxa with an extremely large body size could have been plotted as outliers of discriminant scores in any locomotor categories just because of their size (e.g. Elephas and Triceratops: electronic supplementary material, S1 and S8). Such outlier points should be cautiously taken into account for determining the forelimb postures in extinct taxa. Our size-independent method, in contrast, has a lower risk for the estimation of posture in extinct animals of extreme sizes. This method assumes that the discriminant scores in taxa with extreme body sizes do not differ from those for a normal range of body sizes. We found that this assumption is statistically valid (electronic supplementary material, S5 and S6).

The estimated forelimb posture of Protoceratops varied depending on what method was used: it was estimated as C/UP in the size-dependent method and S/SP in the size-independent method (electronic supplementary material, S1). The estimation for Protoceratops had insufficient probability to categorize posture using the size-dependent method (figure 3; electronic supplementary material, S7), so we could not conclusively estimate the forelimb posture of this animal in our analyses. Previous studies have variably reconstructed it as upright/sagittal [23,58] or more classically sprawling (e.g. skeleton mounted in American Museum of Natural History [59] and HMNS) by estimating the suitable articular relationships of the pectoral girdle and humerus. Further investigations of other possible indicators of limb orientation, such as one based on shoulder morphologies, or bone bending regimes [1] may help estimate the forelimb posture of Protoceratops. This is important because, in combination with analysis of other taxa such as Triceratops (upright/sagittal in this analysis), it could reveal how ceratopsian forelimb pose and mechanics evolved.

However, one must be cautious about taking our results too literally. Extant taxa can adopt varying postures, e.g. at different speeds or varying individually [44], and some species might adopt a wide range of postures [1]. Our method, like all other methods, is by no means a flawless, unambiguous approach for reconstructing forelimb posture in extinct tetrapods and should always be integrated with all available evidence. However, this quantitative method for qualitatively classifying postures is the first method to focus on elbow mechanics, giving it some advantages over prior approaches, and was reasonably well validated by comparison with a large dataset for extant taxa. We thus conclude that our study concurs with others favouring a more upright/sagittal (and relatively uncontroversially, non-scanorial) forelimb posture and function for Triceratops (and probably for large ceratopsids),
Anhanguera (and likely other pterodactyloids; when quadrapedal), and desmostylian mammals.

We especially thank M. Lowe (UMZC) for his great effort in getting most of the specimens to the collection room in and out for this study. The authors thank M. Manabe, T. Tsujihi (NSM), S. Kawabe, Y. Nakajima (UMUT), K. Tanoue (Fukuoka University) for taking CT-scanned data, L. Tomsett, R. Portela, P. Jenkins (NHM), S. Kawada, N. Kohno (NSM), S. E. Evans (UCL), Y. Matsumoto, M. Watabe, S. Suzuki (HHNS), H. Endo, G. Suwa (UMUT), K. K. P. Lim (ZRC), H. Taru (KPM), T. Anezaki (GMNH), N. Kaneko (GSJ), M. Kawata (University of Tokohoku), W. Anzai, A. Omura (UMUT), and the staff of UMZC for providing specimens and for their great hospitality, D. B. Koyabu (Kyoto University), H. Paxton, H. Haddai, A. King, O. Panagiotopoulou, S. Wilshin and A. W. Conroy (RVC), M. O. Kubo (UMUT) for their helpful advice on our statistical analyses, K. Mori, M. Hosojima (UMUT), V. Allen, and S. Warner (RVC) for helping with dissections, R. Matsumoto (UCL) for collecting literature, J. Molnar (RVC) for helping with laser-scanning, S. E. Pierce (UMZC) and M. Stavrou (RVC) for their helpful advice on forelimb anatomy and mechanics, T. Miyake (Jikei University School of Medicine, Tokyo, Japan), T. Uyeno (NSM), H. Koie (Nihon University, Fujisawa, Japan), Y. Abe, and M. Iwata (Aquamarine Fukushima, Iwaki, Japan) for providing CT-scanned image, and H. Kawahara and Materialise, Co. Ltd. for permitting S.i.F. to use an extra license of their product. We thank Japan Society for Promotion of Science Fellowship and Linnean Society of London for, respectively, funding via grant JSPS (grant no. 22-4730) and an Anne Sleep Award in 2009. J.R.H. thanks the Natural Environment Research Council (UK) for extra funding. We thank reviewers Susannah Maidment and Matthew Bonnan for their constructive criticism.

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