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1	Muscle moment arm analyses applied to vertebrate paleontology: a case study using
2	Stegosaurus stenops Marsh, 1887
3	
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20	RH: BRASSEY ET AL.—MUSCLE MOMENT ARMS OF STEGOSAURUS

21 ABSTRACT—The moment arm of a muscle defines its leverage around a given joint. 22 In a clinical setting, the quantification of muscle moment arms is an important means 23 of establishing the 'healthy' functioning of a muscle and in identifying and treating 24 musculoskeletal abnormalities. Elsewhere in modern animal taxa, moment arm 25 studies aim to illuminate adaptions of the musculoskeletal system towards particular 26 locomotor or feeding behaviors. In the absence of kinematic data, paleontologists 27 have likewise relied upon estimated muscle moment arms as a means of 28 reconstructing musculoskeletal function and biomechanical performance in fossil 29 species. With the application of 'virtual paleontological' techniques, it is possible to 30 generate increasingly detailed musculoskeletal models of extinct taxa. However, the 31 steps taken to derive such models of complex systems are seldom reported in detail. 32 Here we present a case study for calculating three-dimensional muscle moment arms 33 using Stegosaurus stenops Marsh, 1887 to highlight both the potential and the 34 limitations of this approach in vertebrate paleontology. We find the technique to be 35 mostly insensitive to choices in muscle modeling parameters (particularly relative to 36 other sources of uncertainty in paleontological studies), although exceptions do exist. 37 Of more concern is the current lack of consensus on what functional signals, if any, 38 are contained within moment arm data derived from extant species. Until a correlation 39 between muscle moment arm and function can be broadly identified across a range of 40 modern taxa, the interpretation of moment arms calculated for extinct taxa should be 41 approached with caution.

INTRODUCTION

44	Biomechanics is the application of mechanical principles to biological
45	systems. An understanding of how mechanical principles act to facilitate or constrain
46	biological form is essential for our understanding of adaptation and the causal link
47	between phenotype and evolutionary success (Alexander, 2003; Taylor and Thomas,
48	2014). At the level of the individual, the fundamental processes of locomotion,
49	feeding, breathing, and reproduction are strongly dictated by the geometric
50	arrangement of muscle and bone. More broadly, studies of predation, competitive
51	exclusion, adaptive radiation, and convergent evolution may all be considered in the
52	light of the musculoskeletal system.
53	Here, we focus on one particular aspect of functional anatomy, muscle
54	moment arms, or the leverage of muscles around a joint. As a geometric property,
55	moment arms can be straightforward to calculate, and have therefore been widely
56	applied to fossil taxa to elucidate evolutionary trends in biomechanical performance
57	within and between extinct lineages, and higher-level biomechanical parameters such
58	as active muscle volume and estimated energy expenditure. With the recent growth in
59	'virtual paleontology' (Sutton et al., 2014), increasingly advanced modeling
60	techniques are now employed to estimate muscle moment arms. Using a new 3D
61	digital reconstruction of Stegosaurus stenops (Brassey et al., 2015) as a worked
62	example, we describe in detail the steps taken when calculating muscle moment arms
63	in fossil taxa. In particular, we highlight the relative sensitivity/insensitivity of this
64	approach to modeling parameters. Additionally, we discuss what functional signals, if
65	any, are present in the muscle moment arms of extant taxa, and the degree to which
66	these signals may be discernable in fossil taxa.

67

68 Muscle Moment Arms in Extant Taxa

69 In biomechanics, musculoskeletal function is strongly dictated by the 70 geometry of the muscle-tendon units of the body, and the most basic descriptor of 71 muscle geometry is muscle moment arm. Torque (or moment) is the tendency for an 72 applied force to rotate an object around an axis, and is calculated as the cross product 73 of force and the lever-arm (herein 'moment arm') of the force system (Gregory, 74 2006). The moment arm is defined as the perpendicular distance from said axis to the 75 line of action of the force. In the context of biomechanics, a muscle moment arm can 76 be thought of as the leverage of a given muscle-tendon unit around a joint and as a 77 means of transforming muscle force into joint rotation. As such, moment arms are 78 crucial for understanding how muscles produce limb movement. In this simplified 79 lever system, larger moment arms produce larger joint moments as:

80

$$81 \qquad M_{\text{joint}} = MA \times F_{\text{mus}} \tag{1}$$

82

where M_{joint} is the joint moment, MA is the moment arm, and F_{mus} is the muscle force. However, larger moment arms are also associated with a decrease in muscle contraction velocity as:

86

87 $\omega = \tan^{-1}(\Delta L_{\text{mus}}/\text{MA})/t$ (2)

88

89 where ω is the angular velocity of the joint, ΔL_{mus} is the change in the length of the 90 muscle, and *t* is time (Channon et al., 2010). Muscle moment arms may therefore

91 distinguish between limbs optimized for high rotational velocity versus those 92 optimized for high torque (Stern, 1974; but see below for confounding factors). 93 Within human clinical and sports sciences, the quantification of 'healthy' 94 muscle moment arms is essential for the treatment of movement abnormalities and in 95 the planning of orthopedic surgeries (Arnold et al., 2000). Therefore considerable 96 effort has been invested in developing techniques for reliably estimating muscle 97 moment arms. For cadaveric material, muscle moment arm can be calculated 98 according to the classic 'geometric' definition (the shortest perpendicular distance 99 from the joint center of rotation to the muscle-tendon unit's line of action) using an 100 idealized origin-insertion model, assuming each muscle is represented as a straight 101 line between origin and insertion (Karlsson and Peterson, 1992; Hughes et al., 1998; 102 see Fig. 1).

103 However, moment arm often varies with joint angle (An et al., 1984), and 104 hence muscle dynamics vary throughout the gait cycle (Williams et al., 2008). 105 Consequently, a more informative metric is the relationship between joint angle and 106 instantaneous muscle moment arm. The tendon-travel method (Spoor and van 107 Leeuwen, 1992; Otis et al., 1994) plots joint angle against tendon displacement and 108 fits linear or second/third order polynomial models to the relationship. The equations 109 can then be differentiated to give either a constant value for moment arm (as in the 110 case of linear regression) or the relationship between joint angle and moment arm (in 111 the case of polynomial equations). The tendon-travel method benefits from 112 minimizing the uncertainty associated with locating the joint center and has been 113 applied extensively to both human and non-human modern taxa (Favre et al., 2008; 114 Channon et al., 2010; Crook et al., 2010; Astley and Roberts, 2012). However, 115 concerns have been raised regarding the application of tendon-travel to the calculation

116 of moment arms. Sustaita et al. (2015) found considerable disagreement between 117 moment arms calculated using the 'geometric' definition and those calculated via 118 tendon-travel, most likely due to dynamic changes in the travel path of tendons during 119 phalangeal joint excursion causing increased tendon travel without a concomitant 120 increase in a given in-lever. Additionally, Hutchinson et al. (2014) highlighted the 121 issue of kinematic 'cross-talk', in which the joint coordinate system is misaligned 122 with the axis about which movement is assumed to occur (for example, the flexion-123 extension axis may deviate from the mediolateral anatomical direction: Piazza and 124 Cavanagh, 2000). Thus, physical manipulation of the joint within one plane of 125 movement will inevitably produce some motion about the others, introducing 126 additional error into tendon-travel estimates.

127 Traditionally applied, both methods for estimating moment arms assume the joint to be operating solely within the plane of movement under investigation (i.e., 128 129 ignoring the 'cross-talk' described above), and involve labor-intensive dissection. 130 Increasingly, however, 3D medical imaging techniques, such as computed 131 tomography (CT), magnetic resonance imaging (MRI), and ultrasound, are being 132 employed to carry out in-vivo subject-specific quantification of muscle moment arms 133 (Sammarco et al., 1973; Kumar, 1988; Juul-Kristensen et al., 2000; Maganaris, 2004), 134 either for the purpose of surgical planning and clinical decision-making or for ex-vivo 135 quantification based on cadaveric material. These approaches avoid invasive surgeries 136 and allow joint movement to be quantified in 3D. However, calculating muscle 137 moment arms for the wide variety of limb postures assumed during habitual 138 locomotion requires extensive imaging of the patient. Therefore a combination of 139 patient-specific 3D imaging and generic computer-based musculoskeletal modeling

has become common practice in clinical biomechanics (Arnold et al., 2000 andreferences therein).

142

143 Muscle Moment Arms Applied to the Fossil Record

Within the disciplines of paleontology and physical anthropology, bone 144 145 morphology is often the only source of information upon which to base 146 reconstructions of the behavior and phylogenetic relationships of extinct species. 147 Other information on bone material properties (elastic moduli, density) and muscle 148 architecture (fiber length, pennation angle) are either lost entirely or preserved only 149 under exceptional conditions (McNamara et al., 2010). When required for 150 biomechanical modeling approaches, such as finite element analysis (FEA) or 151 multibody dynamic analysis (MBDA), these properties must therefore be estimated 152 with reference to the extant phylogenetic bracket (EPB: Witmer, 1995a) or explicitly 153 excluded from the analysis. 154 Although soft tissues are rarely preserved in the fossil record, musculoskeletal 155 reconstructions of extinct taxa are frequently attempted (e.g., fish: Anderson and 156 Westneat, 2009; early tetrapods: Neenan et al., 2014; amphibians: Witzmann and 157 Schoch, 2013; dinosaurs: Maidment and Barrett, 2011, 2012; pterosaurs: Costa et al., 158 2013; mammals: Gill et al., 2014; birds: Tambussi et al., 2012; hominins: Nagano et 159 al., 2005; D'Anastasio et al., 2013). Furthermore, the qualitative discussion of muscle 160 moment arms is a long-established practice in vertebrate paleontology (Morton, 1924; 161 Simpson and Elftman, 1928), and the calculation of muscle moment arms has been 162 applied to the fossil record to address biomechanical questions at several levels:

163 1. The functioning of individual muscle-tendon units. For example, determining the
164 function of a particular muscle (i.e., flexor vs. extensor) around a given joint in an
165 individual (e.g., Bates et al., 2012a).

166 2. The functioning of musculoskeletal groups. For example, using the sum of muscle
167 moment arms around a joint to infer limb pose in an individual (e.g., Hutchinson et
168 al., 2005).

3. The functioning of muscle-tendon units, or musculoskeletal groups, across multiple
individuals. For example, using muscle moment arms to infer changes in locomotor
ability, feeding or other behaviors within a lineage (e.g., Bargo, 2001).

172 In the absence of soft tissues, muscle moment arms may be calculated from 173 dry skeletal/fossil remains on the basis of estimated muscle attachment sites, simple 174 2D trigonometry, and/or more complex 3D computer models. Early studies tended to 175 follow an idealized 2D origin-insertion method (e.g., DeMar and Barghusen, 1972; 176 McHenry, 1975; Emerson and Radinsky, 1980) in which each muscle is simplified to 177 one line of action, and a single value for a moment arm is calculated geometrically on 178 the basis of skeletal landmarks identifying joint centers and muscle insertions (see 179 Fig. 1). However, following the development of computer-based musculoskeletal 180 modeling within the clinical sciences, paleontologists have adopted this technique to 181 generate detailed 3D models of fossil myology including complex joints, muscle 182 geometry, and travel paths for the purpose of moment arm estimation (e.g., 183 Hutchinson et al., 2005; Chapman et al., 2010; Bates and Schachner, 2011; Bates et 184 al., 2012a, b; Maidment et al., 2014a; Costa et al., 2013). Both approaches have merit, 185 and both are still commonly applied to calculate the muscle moment arms of extinct 186 taxa.

187 Van Der Helm and Veenbaas (1991) identified two phases in assessing the 188 mechanical behavior of a system: 1) deriving an adequate model of the system and; 2) 189 using the model to calculate forces, stresses, and motions. In the case of the 190 musculoskeletal system, once a model has been created, the calculation of muscle moment arms, muscle force, joint torque, etc., is relatively straightforward and has the 191 192 potential to generate a vast quantity of data very quickly. In some cases, however, 193 only the results of the analyses are discussed in detail, whereas the steps taken to 194 derive a simplified model of a fossil from such a complex system may be poorly 195 described or absent entirely.

196 Elsewhere, considered reviews of paleontological FEA have highlighted the 197 sensitivity of model results to input parameters and cautioned against their over-198 interpretation (Rayfield, 2007; Bright, 2014), reflecting a growing concern within the 199 field over the exponential growth in the number of fossil biomechanics studies with 200 comparatively little validation on extant taxa (Anderson et al., 2011; Brassey, in 201 press). Here we contribute to this discussion by reviewing the procedure for 202 calculating muscle moment arms using 3D musculoskeletal models of fossil species, 203 highlighting the steps that involve user subjectivity and potential sources of 204 uncertainty in model parameters. Whilst the growth in graphics-based computational 205 models has made it possible to create increasingly complex and arguably more 206 'realistic' biomechanical models of fossil taxa, this has been at a cost. Much of the 207 literature surrounding musculoskeletal models of fossil species is an impenetrable 208 'black-box' to non-specialists (Anderson et al., 2011) as methodologies are often 209 sparse in detail or relegated to supplementary materials (although see Domalain et al., 210 2016; Lautenschlager, 2016). Furthermore, the sensitivity of model results to input

parameters are not always fully explored (although see Hutchinson et al. [2005] and
Bates et al. [2012a] for sensitivity analyses on fossil muscle reconstructions).

213 Here we present a workflow for the generation of a musculoskeletal model of 214 a specific fossil individual and the subsequent calculation of muscle moment arms. 215 We aim to improve transparency with regard to model creation, whilst emphasizing 216 the potential utility of this approach and drawing attention to its limitations. Previous 217 studies have addressed these issues in the context of clinical human anatomy (Hicks et 218 al., 2014 and references therein), but we highlight additional issues that are solely the 219 concern of those working on fossil material. Furthermore, we consider which 220 functional signals (if any) are discernable within the muscle moment arm data of 221 extant taxa, and therefore what we might reasonably expect to find from an equivalent 222 paleontological study.

223 The capacity of a given muscle to generate torque around a joint is a function 224 of both its force-generating capability (as defined by physiological cross-sectional 225 area) and its moment arm. Multibody dynamic analyses employing forward- or 226 inverse-dynamic simulations of locomotion (Sellers and Manning, 2007; Sellers et al., 227 2009, 2013), biting (Bates and Falkingham, 2012; Lautenschlager et al., 2016) and 228 head and neck movements (Snively et al., 2013) in fossil species are also reliant upon 229 estimates of both muscle architecture and muscle moment arms. The following 230 discussion is therefore highly relevant to those creating musculoskeletal models for 231 the purpose of MBDA and FEA on extinct species.

232

MODEL CONSTRUCTION

234

233

235	The specimen used as an example herein is a sub-adult individual of the
236	ornithischian dinosaur Stegosaurus stenops Marsh, 1887 (NHMUK [Natural History
237	Museum, London, U.K.] PV R36730), collected from the Upper Jurassic Morrison
238	Formation of Wyoming, U.S.A. This specimen is the most complete Stegosaurus
239	found to date, with over 80% of the body represented (Brassey et al., 2015; Maidment
240	et al., 2015). The specimen was digitized as disarticulated elements using
241	photogrammetric protocols described elsewhere (Falkingham, 2012; Mallison and
242	Wings, 2014) and the freely available photogrammetry software 'VisualSFM'
243	(http://ccwu.me/vsfm) and 'Meshlab' (http://meshlab.sourceforge.net) and the
244	reconstructed articulated skeleton was posed in 3DsMax
245	(www.autodesk.com/3dsmax) (see Fig. 2). Details regarding the extent of
246	missing/repaired elements and degree of taphonomic damage are reported elsewhere
247	(Maidment et al., 2015). Likewise, the procedure for rearticulating the digital model is
248	documented in Brassey et al. (2015).
249	Muscle moment arm analysis was carried out in 'Gaitsym'
250	(http://www.animalsimulation.org; Sellers and Manning, 2007). Whilst we take a 3D
251	graphics-based computational approach to calculating moment arms of the
252	appendicular skeleton, much of our discussion is also applicable to the classic 2D
253	origin-insertion method frequently employed by paleontologists and to
254	musculoskeletal reconstructions of the skull.
255	The procedure for model creation is described in detail below. Briefly,
256	muscles were reconstructed on the basis of stegosaurian limb myology, as
257	reconstructed by Maidment and Barrett (2012), including 13 muscles in the forelimb
258	and 19 in the hind limb. In addition, pairs of antagonistic puppet-string 'driver'
259	muscles were attached for the purpose of driving the limbs from maximal theoretical

260 flexion to maximum theoretical extension (see Fig. 2 and 'Joint Ranges of Motion', 261 below, for more detail). Alternatively, pre-existing muscles within the model can be 262 used for this purpose, assuming the geometry of the muscle is such that the maximum 263 flexion/extension can be achieved when the muscle is activated. Whichever 264 mechanism is used to drive the limb through flexion-extension (either by the puppet-265 string muscles, or by firing off the pre-existing muscles intrinsic to the model), joint 266 limits are predetermined (see below) and will remain the same, as will the resulting 267 moment arms.

268 Moment arms were calculated according to the classic geometric definition 269 (shortest perpendicular distance from joint center to muscle line of action) as opposed 270 to the tendon travel method, although both will result in the same answer using the 3D 271 modeling approach presented herein. As the model comprised several bi-articular 272 muscles (muscles that travel across two joints), joints in the limb other than the one 273 under investigation were locked in all planes of movement during the analysis, as is 274 common practice in paleontology and modern cadaveric experiments (Channon et al., 275 2010). Pairs of driver muscles were activated in sequence (each activation lasting 0.5 276 seconds) to drive the limb segment through its full range of motion from its original 277 neutral posture whilst instantaneous moment arms were calculated for every muscle at 278 a default interval of 0.0001 seconds. Joint angle and moment arms were exported to 279 'R' (R Core Team, 2016) and plotted using a cubic smoothing spline (smooth.spline 280 function within the 'stats' package).

281

282 Articulation of the Skeleton

Every mechanical model begins with at least two rigid bodies (in this case, bones) connected by a kinematic constraint (in this case, a joint). When generating a

musculoskeletal model of an extant individual, skeletal geometry is often derived
from a CT or MRI scan of the intact body and the articulation of the skeleton is
therefore relatively well constrained. In the case of fossil taxa, however, the skeleton
may be digitized as disarticulated elements (as in the case of *Stegosaurus* presented
here) or as a museum-mounted specimen (Maidment et al., 2014). In either scenario,
the absence of associated soft tissues requires subjective decisions to be made
regarding the rearticulation of the skeleton.

292 Although the preservation of calcified cartilage in fossil long bones has been 293 widely reported (Holliday et al., 2010 and references therein), the non-ossified 294 epiphyseal joint cartilage (chondroepiphysis) that would have capped the ends of 295 bones is rarely fossilized (Chinsamy-Turan, 2005). In extant archosaurs, removal of 296 the chondroepiphysis accounts for a 5–9% decrease in long bone length in the limbs 297 of Alligator mississippiensis and 0-10% in a range of modern birds (Holliday et al., 298 2010). Previous studies of fossil muscle moment arms have attempted to correct for 299 this missing cartilage. In a study on the hind limbs of *Tyrannosaurus rex*, Hutchinson 300 et al. (2005) added 7.5% to the length of the femur, 5% to that the tibia, and 10% to 301 metatarsus length on the basis of an undescribed set of cartilage measurements from 302 extant taxa. In other studies limb bones are clearly spaced apart, yet no specific 303 reference is made to the size of spacing, nor how this value was calculated (e.g., Bates 304 et al., 2012a, b).

Failure to account for missing articular cartilage has the effect of shortening the effective segment length and bringing muscle origin and insertion points closer together. As an example, Figure 3 illustrates the effect of incorporating articular cartilage on moment arm values for the M. iliofibularis (IFB) measured around the knee during knee flexion. IFB was modelled as travelling in a straight path from

310 origin to insertion without passing through via points or around cylinders (see Muscle 311 Paths, below). For a discussion of the process of estimating joint center locations, see 312 Joint Centers, below. The effect of missing articular cartilage on calculated moment 313 arms varies with joint angle (Fig. 3) with the discrepancy between models with and 314 without cartilage increasing with knee flexion. When accounting for an additional 315 (worst-case scenario) 10% of long bone length as cartilage (Fig. 3C), the maximum 316 value calculated for IFB moment arm is 26% greater than when cartilage is ignored. 317 However, if the joint center is shifted distally to maintain an equal distance between 318 muscle insertion and center of rotation when adding cartilage (Fig. 3D), this 319 discrepancy is considerably reduced. In modern taxa, the extent to which joint center 320 locations differ between those calculated in-vivo, versus those based on dry articular 321 surfaces missing cartilage, is unknown (see later section 'Joint Centers'). 322 Given that high variability has been documented in long bone cartilage 323 thickness among extant birds (within Galliformes, cartilage accounts for 10% of 324 femoral length in Gallus gallus and 1% in Coturnix japonica: Holliday et al., 2010) it 325 is reasonable to predict that such disparity might also have characterized extinct 326 clades. When generating muscle moment arm data across a comparative sample of 327 fossil taxa, for example, the dinosaurian clades Ornithischia (Maidment et al., 2014a) 328 or Allosauroidea (Bates et al., 2012b), it is prudent to consider that interspecific 329 variability in cartilage thickness will overlie any hypothesized functional signal in 330 muscle moment arms, and may affect the interpretation of the dataset. In extant 331 mammals, a significant negative allometric relationship exists between body mass and 332 femoral condyle cartilage thickness (Malda et al., 2013). A similar pattern has also 333 been identified in ontogenetic samples of Alligator and Numida, in which smaller 334 individuals possess a relatively greater thickness of chondroepiphysis to total bone

length (Bonnan et al., 2010). Should this relationship prove consistent across modern
birds or reptiles, it would prove useful in constraining hind limb joint spacing in
comparative samples of fossil archosaur taxa.

338 Likewise, the loss of intervertebral fibrocartilagenous disks or synovial 339 capsules from between adjacent vertebrae in extinct taxa has the effect of shortening 340 the length of the reconstructed vertebral column. This effect has previously been 341 discussed in the context of estimated neck flexibility and range of motion (Mallison, 342 2010a; Cobley et al., 2013; Taylor and Wedel, 2013) and as a potential source of 343 uncertainty in volumetric mass estimates (Brassey et al., 2015). Additionally, for 344 muscles originating from the tail (e.g., M. caudofemoralis longus in archosaurs) or thorax (e.g., M. latissimus dorsi and M. trapezius in tetrapods), the incorporation of 345 346 additional spacing to account for intervertebral soft tissues will also impact calculated 347 muscle moment arms in a similar manner to epiphyseal cartilage, as discussed above. 348 Furthermore, placement of the scapula relative to the ribcage has a knock-on effect on 349 the location of the shoulder joint relative to the thorax. Whilst mounted skeletons are 350 often characterized by the scapula immediately overlying the ribs, the volume of soft 351 tissue separating the skeletal elements has not been quantified in extant taxa. 352 In addition to joint spacing, the joint morphology of extinct taxa can be

altered, both due to the removal of cartilage and other soft tissues though the process of fossilization (Bonnan et al., 2010), and due to subsequent taphonomic deformation and weathering. This can increase uncertainty with regards to the orientation and positioning of skeletal elements, and further hamper efforts during rearticulation. In the case of *Stegosaurus* (NHMUK PV R36730), for example, the degree of mediolateral flaring of the pubis and ischium is open to interpretation.

359 In ornithischian dinosaurs, the prepubis is an anterior extension of the pubis 360 arising from its proximal margin and extending anterior to the acetabulum. This 361 process acts as an origin for the M. ambiens (AMB), which subsequently inserts onto 362 the cnemial crest of the tibia (Maidment and Barrett, 2011). When reconstructing the 363 Stegosaurus model, the pubis and ischium were rearticulated with the ventral surface 364 of the ilium to form the borders of an open acetabulum using the orientations of their 365 articular surfaces as a guide. However, the angles at which the paired pubes and ischia 366 extend with respect to the midline are uncertain. Whilst the paired pubes must be in 367 contact distally, the contact between the iliac articulation of the pubis and the pubic 368 peduncle of the ilium is less well constrained by osteology. Figure 4 illustrates the 369 effect of varying the angle of the pubis relative to the midline on AMB flexion-370 extension (FlexExt), abduction-adduction (AbdAdd), and long-axis rotation (LAR) 371 moment arms calculated at the hip during hip flexion-extension. The pubis was 372 modeled in two orientations: a) with the long axes of the pubes aligned parallel to the 373 iliac blades (Fig. 4A), which are themselves extremely flared in the mediolateral 374 direction, with their distal ends meeting at a ventral midline symphysis; and b) with 375 the long axes of the pubes rotated medially from this initial position, with distal ends 376 meeting in a symphysis but with less extreme flaring (Fig. 4B). 377 Predictably, rotating the pubis medially does not impact upon the flexion-378 extension moment arm of AMB, and the functioning of the muscle remains consistent 379 as a flexor. Likewise, AbdAdd moment arms for both model configurations suggest

380 AMB functions as a hip abductor as the origin as path of the muscle remains lateral to

the hip joint throughout the range of motion. When the pubis is rotated medially,

average AbdAdd moment arm does decrease from 0.23 to 0.14 m, however, due to the

383 muscle path shifting closer to the joint center. Interestingly LAR moment arms in the

flared pubis model suggest a lateral rotation function at values of hip flexion between 385 35–60° (Fig. 4A), whereas AMB acts as a medial rotator throughout most of the range of motion in the medial pubis model, switching to lateral rotation only at very high values of flexion (>50°) and representing a small change in predicted muscle function between the two models.

Uncertainty with regards to skeletal articulation therefore has the potential to affect not only the magnitude of calculated muscle moment arms, but also the inferred function of the muscle unit itself. This highlights the importance of having a strong grounding in both the osteology and myology of the study taxa and in conducting sensitivity analyses, not only to quantify uncertainty in muscle attachment sites, as has previously been the case (Hutchinson et al., 2005; Bates et al., 2012a), but also to investigate the effects of uncertainty in skeletal articulation.

396 Finally, the neutral stance in which the model is posed must be clearly stated 397 in order to facilitate comparisons between species and across studies. For some 398 muscles, moment arm values calculated with respect to a given joint axis are highly 399 sensitive to the joint angle about one or both of the other axes (O'Neill et al., 2013), 400 as highlighted by the issue of 'cross talk' when estimating extant moment arms via the 401 tendon-travel method (Hutchinson et al., 2014; see Introduction). For the estimation 402 of hind limb muscle moment arms in dinosaurs, a standard neutral hip posture of 0° 403 extension, 10° abduction, and 0° long axis rotation has been broadly agreed upon 404 (Hutchinson et al., 2005; Bates and Schachner, 2011; Bates et al., 2012a; Maidment et 405 al., 2014a), a convention that we follow herein. Comparatively little work has been 406 carried out on the moment arms of forelimb muscles in extinct taxa using 3D 407 musculoskeletal models (although geometric 'dry-bone' analyses do exist: Fujiwara 408 and Hutchinson, 2012; Martín-Serra et al., 2014). We therefore assume a neutral

shoulder posture of 30° retraction, 10° abduction, and 0° long axis rotation, following
this earlier work.

411 Undoubtedly, the selection of a 'neutral posture' does introduce a degree of 412 uncertainty and places unnecessary emphasis on reconstructing the standing posture 413 of individual taxa. When undertaking a comparison between several species of 414 differing bone morphology, the degree of osteological rotation around the long axis of 415 the bone, or extent of valgus, may vary. In such an instance, identifying an 416 'equivalent' starting point for a moment arm analysis may prove problematic. An alternative way forward may be to follow the protocol used in biplanar X-ray imaging 417 418 studies (M. F. Bonnan, pers. comm., January 2017), in which the bones may be posed 419 in a flat plane or a folded position (Bonnan et al., 2016). Such reference postures 420 might be anatomically unfeasible, but are more easily replicated across a wide range 421 of taxa of diverse morphology and would provide a more consistent starting point for 422 comparative muscle moment arm studies.

423

424 Joint Ranges of Motion

425 Muscle moment arm can change as a function of joint angle (An et al., 1984) 426 and it is common practice to report moment arm values calculated as a limb is moved 427 through its full range of motion (ROM) in a particular plane. In Figure 4, for example, 428 the hip joint is moved from full flexion (-60°) to full extension (60°), assuming a 429 neutral posture of 0° in which the femur is held perpendicular to the ground in the sagittal plane. It is important to emphasize that the selection of the joint ROM is 430 431 entirely under the control of the user. That is, whilst it is possible to calculate a value 432 for muscle moment arm for absolutely any joint angle (including angles at which the

433 limb would be entirely disarticulated), it is at the discretion of the user to constrain the434 ROM to within probable biomechanical limits.

435 For example, Maidment et al. (2014a) compared hind limb muscle moment 436 arms calculated for a diverse sample of ornithischian dinosaurs across a hip flexion-437 extension ROM of -60° to 60°. Whilst this approach of comparing species across a 438 fixed ROM simplifies comparisons, it does raise a teleological issue. The 439 biomechanical feasibility of each individual achieving such a ROM in-vivo is not 440 taken into account, and on the basis of osteological and myological reconstructions it 441 is considered highly unlikely that some species (including this specimen of 442 Stegosaurus) could have attained the lower-most values for hip flexion (see Fig. 5). 443 The value of plotting muscle moment arms calculated at unrealistic joint angles is 444 therefore questionable.

445 An alternative approach is to investigate feasible joint ROM on a specimen-446 by-specimen basis, either through physical rearticulation of the skeleton or casts 447 thereof (Johnson and Ostrom, 1995; Senter and Robins, 2005; Taylor and Senter, 448 2010) or through manipulation of 3D digital models (Mallison, 2010a, b; Pierce et al., 449 2012). However previous studies have found ROM at the joints to be strongly affected 450 by the presence/absence of soft tissues and cartilage around limb (Hutson and Hutson, 451 2012) and intervertebral joints (Taylor and Wedel, 2013; Cobley et al., 2013), and 452 accounting for the removal of extrinsic (integument, muscles, capsular ligaments) and 453 intrinsic (cartilage) soft tissues from the fossil skeleton is not straightforward. Within 454 the shoulder and elbow of Alligator, for example, the removal of extrinsic soft tissues 455 acts to increase ROM, whilst subsequent removal of articular cartilage acts to 456 decrease ROM, resulting in a counter-intuitive net decrease in ROM from an intact to 457 entirely skeletonized limb (Hutson and Hutson, 2012, 2013). In contrast, within the

458 neck of the ostrich, removal of both extrinsic and intrinsic soft tissues acts to increase 459 ROM (Cobley et al., 2013). A growing body of work is quantifying joint ROM both 460 in non-human mammals (Ren et al., 2008; Bonnan et al., 2016) and within the context 461 of the dinosaur EPB, although the total number of studies remains limited. In light of 462 this paucity of modern data, the conservative approach of Maidment et al. (2014a), 463 where all taxa are modelled with the same broad ROM, may be preferable. However, 464 the requirement for anatomically realistic ROM data remains an issue for MBDA of 465 locomotion, feeding, etc.

466 Furthermore, assessments of possible joint ROM tend to focus solely on bone-467 to-bone contact within the fossil limb, such as joint impingement and dislocation. For 468 example, moment arm papers dealing with hind limb muscles in extinct taxa often 469 model the bones of the pelvis and hind limb only (Hutchinson et al., 2005; Bates et 470 al., 2012a, b; Maidment et al., 2014a, b). Potential collisions with the head, arms, and 471 torso are ignored. Yet, as illustrated in Figure 5, the positioning of the ribcage can act 472 as a further constraint on joint ROM, as the extent of hip flexion is limited by the 473 potential for the femur to collide with the posterior dorsal ribs (assuming 10° 474 abduction and zero long axis rotation). However, this approach is considerably more 475 time consuming (as digital models of the thoracic vertebrae and dorsal ribs are also 476 required) and places further onus upon accurate rearticulation of the trunk, which is 477 itself subject to various assumptions (e.g., the potential range of movement between 478 the rib and its vertebral articulations, the exact geometry of the articulations, and the 479 effects on these of missing soft tissues). In our Stegosaurus model, for example, the 480 characteristic triangular ribcage present in the skeletal mounts of the American 481 Museum of Natural History and Senckenberg Museum stegosaurs is reconstructed by 482 sweeping the distal ends of the ribs anteriorly (Fig. 5). Yet ribs are frequently

483 damaged, taphonomically deformed (e.g., Maidment et al., 2015), or absent entirely, 484 and the extent to which this represents an accurate skeletal rearticulation is unclear. 485 Whilst the incorporation of additional body parts, such as the tail or torso, into a 486 musculoskeletal model may further constrain limb ROM, this must be balanced 487 against a concurrent increase in uncertainty regarding model articulation and also the 488 concomitant reduction in analytical sample size, which becomes limited perforce to 489 those specimens that are relatively complete. On the rare occasions when trackways 490 can be assigned confidently to fossil taxa, their gauge, stride length, and other track 491 features may also inform potential posture and limb range of motion (e.g., Alexander, 492 1989; Henderson, 2006; Hatala et al., 2016; but see Falkingham, 2014).

493

494 Muscle Definitions

495 Muscle Anatomy—Following the articulation of rigid bodies, the next stage 496 in building our biomechanical model involves reconstruction of the overlying 497 musculature. As highlighted above, it is possible to output moment arm values for an 498 array of nonsensical musculoskeletal arrangements, but we emphasize and advocate 499 the importance of grounding fossil biomechanical studies within a comprehensive 500 understanding of the anatomy of the study taxa. In the case of fossil myologies, 501 accurate reconstructions require the assimilation of two sources of information (Fox, 502 1964): 1) evidence of muscle attachment sites on bone surfaces, including scarring, 503 ridges, trochanters, and fossae; and 2) phylogenetic inference of muscle 504 presence/absence based of the anatomy of closely related extant taxa (Witmer, 505 1995a). 506 The use of osteological correlates in soft tissue reconstruction is well

507 established in vertebrate paleontology. Muscle scarring can indicate the location and,

508 to a limited extent, the size of a muscle attachment, and has been applied to broad 509 interspecific samples of taxa to trace the evolution of cranial (Witmer, 1995b; 510 Holliday, 2009) and postcranial musculature (Hutchinson, 2001a, b; Maidment and 511 Barrett, 2012). Muscles inserting via tendons or aponeuroses tend to leave more 512 distinct scars than those inserting via fleshy attachments (Bryant and Seymour, 1990), 513 yet those without well-developed scars may still be reconstructed with a reasonable 514 level of confidence (Hutchinson and Carrano, 2002) particularly when placed within a 515 phylogenetic context (see below). The correspondence between the location of 516 attaching muscles and resulting scars has been validated in extant taxa, in both the 517 skull (Hieronymus, 2006) and postcrania (Hutchinson, 2002; Meers, 2003), although 518 recent research has cautioned against the interpretation of scar morphology as 519 representative of original muscle size and/or action (Zumwalt, 2006). 520 Application of the EPB approach can further constrain soft tissue inferences 521 (Bryant and Russell, 1992; Witmer, 1995a). At its most straightforward, the EPB 522 places fossil taxa within the phylogenetic context of their closest related extant taxa, 523 with any condition present in both extant taxa being inferred as present in their last 524 common ancestor and in all of its descendants. For the purpose of estimating moment 525 arms, the EPB also has the advantage of permitting the reconstruction of muscles that 526 lack distinct attachment scarring. Furthermore, application of the EPB to soft tissue 527 restoration involves a 'hierarchy of inferences' and reconstructions are assigned to 528 levels I, II, or III depending upon the degree of speculation involved (Witmer, 1995a). 529 This categorization therefore allows the degree of uncertainty in reconstructed 530 myology to be recorded and communicated. Depending on the taxa of interest, 531 however, the EPB can be relatively broad and encompass modern taxa that may be 532 too functionally divergent from the fossil species to provide a basis for useful

comparisons (for example, extant amphibious crocodiles form part of the EPB for
extinct flying pterosaurs). This highlights the importance of grounding fossil muscle
reconstructions in a detailed understanding of the complexity and variability that
characterizes modern taxa, and the value of traditional anatomical descriptions as a
necessary precursor to further functional analyses.

538 To Clump or To Split?—Every biomechanical model represents a trade-off 539 between realism, precision, and generality, and in the case of musculoskeletal models, 540 this trade-off is particularly evident in myological reconstructions. The detail required 541 of a musculoskeletal model is a function of the question under investigation. In some 542 instances, all muscles acting around a particular joint are reconstructed in order that 543 the sum total moment arm may be estimated and limb posture inferred (Hutchinson et 544 al., 2005; Payne et al., 2006; Maidment et al., 2014a). In other instances, when the 545 question under consideration seeks to address an aspect of biomechanical 546 performance across a large comparative sample, only 'major muscles' may be 547 reconstructed. Biomechanical models of the masticatory system of fossil mammals, 548 for example, often include only the major jaw adductors, the M. temporalis and M. 549 masseter, in moment arm calculations (Iuliis et al., 2001; Bargo, 2001; Vizcaíno and 550 Iuliis, 2003; Cassini and Vizcaíno, 2012). In such instances, the decision regarding 551 which muscles to include is often made on the basis of reconstructed muscle volume 552 (i.e., smaller muscles are more likely to be excluded). 553 Kappelman (1988) took the approach of grouping a suite of muscles together 554 as a functional unit on the basis of their shared travel path around a joint. When 555 estimating the moment arm of extensor muscles crossing the knee in bovids, for

example, Kappelman (1988) considered all members of the Mm. quadriceps femoralis

557 group collectively as having a shared moment arm, as they all converge on the

558 patellar tendon and pass over the surface of the patella at an equal distance from the 559 joint center. A similar approach has also been taken when modelling the Mm. 560 quadriceps femoralis group around the human knee (Herzog and Read, 1993). 561 Likewise, when joint surfaces are modelled as cylinders in multibody dynamic 562 packages, such as Gaitsym and OpenSim (http://opensim.stanford.edu/: Delp et al., 563 2007), the minimum value for the moment arms of all muscles passing around the 564 joint will be constrained as the radius of the cylinder and hence will be equal (see 565 Geometric Shapes, below). This incorporation of isolated muscles into functional 566 groups is particularly important when musculoskeletal models are to be used as the 567 basis for forward dynamic modelling of movement. In this scenario, the addition of 568 each extra muscle increases the dimensionality of the optimal control search space 569 and causes a huge increase in terms of the cost of the simulation (Sellers et al., 2013), 570 and recent fossil gait simulation studies have therefore restricted themselves to 571 modeling generic 'knee flexors' and 'hip extensors', for example (Sellers et al., 2009). 572 In extant taxa, however, the separate heads of a single muscle have 573 occasionally been found to possess very different moment arms around the same joint 574 (e.g., equine M. biceps femoris and M. gastrocnemius: Crook et al., 2010). Different 575 subunits of a single muscle may therefore be recruited for a different function during 576 activation (Ackland et al., 2008). The corollary of grouping muscles by function, 577 therefore, is that it may be necessary to model a single muscle as two separate 578 functional units, particularly when osteological evidence suggests the presence of two 579 distinct heads. For example, Bates et al. (2012a) modeled two aspects of the M. 580 iliofemoralis (cranial and caudal), corresponding to the M. iliotrochantericus caudalis 581 and M. iliofemoralis externus, respectively, in extant birds. Even if both heads are

found to have similar moment arms, modelling them as separate muscle-tendon units
allows for potential functional differentiation in future forward dynamic analyses.
Ultimately, the decision to group or to split muscles on the basis of function
reflects a compromise between modelling the intricacy we know to characterize
modern musculoskeletal systems, and the computing time and degree of uncertainty
we must accept if we attempt to include such complexity into our models of extinct
taxa.

589 Muscle Origins and Insertions—While some muscles are characterized by possessing discrete 'heads' as discussed above, others are large and fan-shaped with 590 591 broad attachment sites lacking distinct segregations. Single lines of action spanning 592 from origin to insertion cannot adequately describe the geometry of such muscles, and 593 multiple lines of action with independent origins and insertions may need to be 594 designated a priori (van der Helm and Veenbaas, 1991). Travel paths originating at 595 opposing positional extremes within a given muscle are expected to pass across the 596 joint at different locations, and therefore possess different values of muscle moment 597 arm.

598 When subdividing fan-shaped muscles, the criteria for selecting the number 599 and location of multiple lines of action are not always made clear, and may be related 600 to position ('superficial' vs. 'deep'), perceived function, or selected in order to 601 capture differing fiber directions within the muscle. The practice of partitioning 602 muscles with large attachment sites is common in human biomechanical modelling 603 (Delp et al., 1990; van der Helm and Veenbaas, 1991; Holzbaur et al., 2005; 604 Chadwick et al., 2009; Arnold et al., 2010; Webb et al., 2012) and is increasingly 605 applied to other extant taxa, particularly in MBDA of skull function (Wroe et al., 606 2007, 2013; Gröning et al., 2013; Watson et al., 2014). Modern studies benefit from

the incorporation of dissection data and MRI-based imaging of in-situ 3D muscle

608 geometry when subdividing muscles for this purpose. In contrast, the representation

of large muscles in paleontological models ranges from single lines of action (with the

origin located at the centroid of the attachment site: Ravosa, 1996), to separate bodies

611 representing the two extremes in attachment location (typically anterior-most vs.

612 posterior-most positions, or preacetabular vs. postacetabular: Hutchinson et al., 2005;

Bates et al., 2012a; Maidment et al., 2014a), to several lines of action (McHenry et al.,

614 2007; D'Anastasio et al., 2013; Gill et al., 2014).

615 To illustrate this point, we model the M. latissimus dorsi (LAT) of 616 Stegosaurus, a large fan-shaped dorsolateral muscle located posterior to the shoulder 617 joint that is responsible for humeral retraction (Meers, 2003; Dilkes et al., 2012). The 618 scapula is considered fixed relative to the trunk, and the shoulder is modelled as a 619 simple hinge joint permitting only flexion-extension. LAT is simplified into five lines 620 of action, originating from the neural spines and transverse processes of dorsal 621 vertebrae 3–7, travelling posterior to the shoulder joint and attaching at a common 622 insertion point on the posterior shaft of the humerus ventral to the head (Fig. 6). 623 Tendon length is, of course, another unknown parameter in model construction. If the 624 tendon of LAT was long, and the fibers of LAT merged onto the tendon prior to 625 passing around the shoulder joint, the LAT can be considered to have effectively a 626 single moment arm. However, assuming the tendon was short, LAT would have had 627 numerous lines of action around the joint, and therefore a range of moment arm 628 values. Travel paths were modified by via points located on the rib tubercula, lateral 629 margins of the dorsal ribs and the lateral surface of the scapula blade to prevent 630 intersection with the skeleton (see Muscle Paths, below).

631 Figure 6A (solid line) illustrates the variation in LAT moment arm with 632 humeral protraction-retraction. At maximum humeral protraction, LAT moment arm 633 values are low and decrease from the most posterior muscle line of action to the 634 anterior-most. At maximum humeral retraction, LAT moment arms are considerably 635 higher. As a percentage of LAT moment arm, divergence between anterior- and 636 posterior-most muscle lines of action is greatest at full humeral protraction, and at a 637 minimum at 40° retraction. Crucially however, the interpreted function of the muscle 638 remains consistent amongst these different lines of action. Whilst incorporating 639 multiple lines of action for a given muscle into a model will more adequately 640 represent the action of a muscle attaching over a large area of the bony surface (van 641 der Helm and Veenbaas, 1991), a single centroid-based muscle path appears sufficient 642 for describing the change in LAT moment arm with joint angle in this particular fossil 643 taxon. Comparisons of single muscle moment arms across taxa and between studies 644 therefore remain valid, but should be accompanied by a description of how the muscle 645 origin centroid was determined to improve the repeatability of the technique. 646 In many instances, muscle moment arm estimates may be more sensitive to 647 shifts in muscle insertion than origin. As in the case of the LAT (Fig. 6B-E), muscle 648 insertions are often closer to the joint center of interest than muscle origins. Shifting 649 the position of a muscle insertion by a given distance will therefore displace the 650 muscle line of action from the joint center further than an equal shift in the position of 651 muscle origin (O'Neill et al., 2013). In terms of myological reconstructions, the 652 insertion of the LAT on the posterior surface of the humerus has a particularly clear 653 osteological correlate in Stegosaurus (Maidment et al., 2015:fig. 67). Yet whilst the 654 LAT insertion on the latissimus tubercle is well constrained and small in size relative 655 to that of other pectoral muscles, the scar does extend up to 100 mm proximodistally.

656 In Figure 6D–E, the insertion of LAT has been shifted 50 mm to its proximal-657 most position on the humerus and Figure 6A (dashed line) illustrates the effect that 658 this change has upon calculated moment arms. The impact of shifting LAT insertion 659 site is negligible at full humeral protraction, and variation introduced through the 660 positioning of muscle lines-of-action at the origin contributes more to variation in 661 LAT moment arms. With increased humeral retraction, however, variability in 662 moment arms due to insertion site position comes to dominate over variation due to 663 muscle origin.

664 For the purpose of muscle moment arm estimation, this suggests that a shift 665 towards concentrating on improving the identification of muscle insertion locations 666 would be particularly beneficial (Hutchinson et al., 2014). Exceptions will exist, 667 however, in which the joint center is located closer to muscle origin than insertion (as 668 in the case of Stegosaurus, with the origins and insertions of the M. adductor group 669 and M. iliotibialis muscles around the hip). This highlights the idiosyncratic nature of 670 muscle modelling and emphasizes the need for a muscle-by-muscle approach to 671 sensitivity analyses; the same parameters that might strongly affect the moment arm 672 of one muscle may have little or no effect on neighboring muscles acting around the same joint. 673

674

675 Joint Definitions

Joint Centers—Given the geometric definition of a muscle moment arm as the perpendicular distance from joint center to the muscle-tendon unit line of action, it is crucial to accurately determine the position of the joint center when conducting moment arm analyses. Calculated moment arms have been found to vary considerably with estimated joint center in clinical human studies, and in some cases can result in a

shift in predicted function from flexion to extension (Herzog and Read, 1993). Delp
and Maloney (1993) estimated that a 20 mm shift in the position of the human hip
center may result in a change in percentage moment arms of between 0–38%,
dependent upon the direction of shift and the axes about which the moment arms are
measured.

686 Consequently, there is a considerable body of research on methods for 687 accurately determining joint centers in modern taxa, which may be broadly 688 subdivided into geometric and kinematic techniques. Kinematic joint centres are 689 calculated on the basis of instantaneous helical axes, in which the motion of an object 690 can be broken down into a rotation about and a translation along its rotational axis. 691 Kinematic joint centers can be estimated in-vivo or in-vitro via the tracking of 692 anatomical landmarks through the limb range-of-motion using motion capture 693 (Sholukha et al., 2013) or biplanar fluoroscopy (Pillet et al., 2014). 694 Geometric joint centers are calculated on the basis of fitting simple geometric 695 shapes to joint surfaces, derived from 3D coordinate measurement systems such as 696 microscribes or computed tomographic (CT)/magnetic resonance imaging (MRI) data. 697 Geometric joint centers are considered fixed throughout the range-of-motion, thus 698 ignoring possible translation of one element relative to another (see Joint Type, 699 below). In clinical human trials, joint centers calculated using kinematic and 700 geometric techniques are in broad agreement (e.g., glenohumeral joint: Veeger, 2000; 701 femoroacetabular joint: Klein Horsman et al., 2007; femorotibial joint: Eckhoff et al., 702 2003). As such, this technique can be considered applicable to disarticulated 703 skeletons, including those of extinct taxa, for which kinematic data cannot be 704 collected.

705 Within the paleontological literature, methodological descriptions of the 706 process of determining geometric joint centers range from detailed (Hutchinson et al., 707 2005; Fujiwara and Hutchinson, 2012) to sparse (Sellers et al., 2013) or entirely 708 absent (Sellers et al., 2009; Maidment et al., 2014b). Typically, the femoroacetabular 709 joint is identified by fitting circles and spheres to the acetabulum and femoral head 710 respectively, and subsequently aligning their centroids (Hutchinson et al., 2005; Costa 711 et al., 2013). The center of the elbow has been similarly defined as the center of the 712 radial condyle and sigmoid notch on the humerus and radius/ulna respectively, 713 calculated through the process of geometric shape fitting (Fujiwara and Hutchinson, 714 2012). Likewise, the position of the knee joint centre has been estimated by fitting 715 circles to the medial and lateral condyles, and taking the midpoint of the axis joining 716 the centers of both circles (Hutchinson et al., 2005).

717 As discussed above, the loss of articular cartilage will undoubtedly affect the 718 position of the joint center calculated through the process of shape fitting. However, 719 given the lack of data on the thickness and distribution of cartilage in extant species, it 720 is difficult to account for in extinct taxa. Taphonomic distortion of the epiphyses may 721 also impact accurate identification of joint centers. Figure 7 demonstrates the process 722 of fitting circles to the medial and lateral femoral condyles of Stegosaurus stenops. 723 Figure 7A shows the considerable extent of taphonomic warping present in the distal 724 femoral condyles, in which the condylar long axes have been rotated away from the 725 anteroposterior axis of the femur mediolaterally. First, vertices were manually 726 selected in Meshlab along a line trending anteroposteriorly across the ventral surface 727 of both condyles (Fig. 7B), hence ignoring any taphonomic distortion. Selected 728 vertices were projected onto a sagittal plane cutting through the femur, and best-fit 729 circles were fitted to the coordinates (Fig. 7D-E.) using the 'circle fit' function from

730 MATLAB File Exchange (Bucher, 2004). The center of the knee joint was 731 subsequently calculated as the midpoint of the line connecting the centers of both 732 medial and lateral femoral circles. This process was repeated by selecting vertices 733 describing the main curvature of the condyles, thus taking the rotation of condylar 734 long axes into account (Fig. 7C), and fitting best-fit circles to the data (Fig. 7F–G). 735 When accounting for deformation, the condylar surfaces approximate a circle 736 more closely than when vertices are selected in a strict anteroposterior plane (Fig. 737 7D-E vs. Fig. 7F-G), the radii of the fitted circles increase considerably (medial 738 condyle radius increases 21%; lateral condyle radius increases 38%), and the 739 calculated position of the joint center shifts by 12.7 mm. The effect of this upon 740 calculated moment arms around the knee is discussed below. Given the sensitivity of 741 estimated joint centers to the manual selection of surface vertices, and to the presence 742 of taphonomic deformation, it is therefore essential that the process of calculating 743 joint centers be explicitly stated in the study methodology. 744 Furthermore, the Stegosaurus specimen presented here comprises a near-745 complete skeleton, within which the extent of taphonomic deformation can be 746 accurately assessed and compared against other documented Stegosaurus individuals. 747 In contrast, when material is highly fragmentary or of uncertain taxonomic affinity, 748 the degree to which underlying morphology represents 'normal' or 'taphonomic' 749 processes may be less clear. There is a well-established body of literature on the 750 technique of fossil 'retrodeformation' to account for taphonomic effects, and its 751 subsequent impact upon functional analyses. Thus far, these studies have generally 752 focused upon skull morphology, however (Lautenschlager et al., 2014; Cuff and 753 Rayfield, 2015; but see Motani, 1997). Future research should concentrate on the 754 postcranial skeleton, in particular the geometry of long bone epiphyses, to elucidate

the effects of fossilization and potential deformation upon interpreted skeletalfunction.

757 Joint Type—As outlined above, the geometric method of calculating joint 758 center does not require kinematic data and is solely based upon the surface contours 759 of the joint. This approach does, however, assume that the joint center remains fixed 760 relative to the two bodies. Yet in reality, many joints are characterized by some 761 degree of sliding (translation) in addition to pure rotation. Classically, movement in 762 the knee joint has been found to comprise both rolling and sliding (Iwaki et al., 2002), 763 with the condyles of the tibia sliding towards the extensor surface of the femur during 764 knee flexion (Johnson et al., 2008). Translation at the knee joint has been incorporated 765 into musculoskeletal models of modern humans (Steele et al., 2012) and chimpanzees 766 (O'Neill et al., 2013) but has not, to the authors' knowledge, been investigated in 767 fossil species.

768 Likewise, the glenohumeral joint of the shoulder is typically considered as a 769 simplified ball-and-socket joint with minimal translation (Veeger and van der Helm, 770 2007). However, movement at the shoulder is a function of mobility at both the 771 glenohumeral joint and the scapulothoracic gliding plane, and the medial border of the 772 scapula remains in contact with, and translates/rotates relative to, the thoracic wall. 773 The contribution of scapula motion to total arm elevation ('scapulohumeral rhythm') 774 is relatively well known in modern humans (Inman et al., 1944; Bolsterlee et al., 775 2014), and a musculoskeletal model of the forelimb of Japanese macaques has 776 incorporated scapula movement as a triaxial gimbal joint (Ogihara et al., 2009; 777 although this model has thus far only been used in studies of bipedalism). However, 778 this only provides a first approximation of the wide range of possible scapula motions, 779 and again, we know of no paleontological musculoskeletal model in which

780 translation/rotation of the scapula is included. Similarly, biomechanical models of 781 feeding in fossil taxa often assume a simplified hinge for the jaw joint (e.g., Bates and 782 Falkingham, 2012; Wroe et al., 2013; Lautenschlager et al., 2015; but see Snively et 783 al., 2015) despite some degree of translation and/or long-axis rotation being present in 784 both mammal (Noble, 1973; Terhune et al., 2011) and reptile (Jones et al., 2012) jaws. 785 Currently kinematic data on joint translation in non-human species are 786 extremely sparse and, as a result, any attempt to incorporate movement of the joint 787 center into models of fossil species would be speculative. Furthermore, the 788 importance of incorporating translation into joint mobility will vary across taxonomic 789 groups (e.g., between mammals and archosaurs). In contrast, the calculation of a fixed 790 center of rotation based solely on joint geometry is comparatively simple, repeatable 791 and widely applicable across a broad range of paleontological specimens. Ultimately, 792 the degree of complexity incorporated into fossil reconstructions should be a function 793 of the question being considered. If the goal of a study is to generate the most 794 'accurate' model of a particular fossil joint, then an argument can be made for 795 incorporating as much detail as possible on joint mechanics. If, however, the goal is to 796 make broad comparisons of muscle function across a large sample of taxa, assuming a 797 fixed joint center may be more feasible.

When ignoring the role of translation, musculoskeletal joints are typically modelled as fixed hinge joints with one degree of rotational freedom (as in the case of the elbow, knee, and jaw) or ball-and-socket joints with three degrees of rotational freedom (in the shoulder and hip). When assigning joint limits (i.e., the range of motion through which the limb may move), maximum and minimum joint angles are straightforward when assigned to hinge joints operating solely within one plane. In contrast, setting joint limits upon ball-and-socket joints can be considerably more

805 difficult. At the simplest level, Euler angles can be used to represent motion by three 806 rotations about three different axes. Independent limits can be specified on each Euler 807 angle, however the resulting range of motion has been shown to predict in-vivo 808 motion ranges poorly (Baerlocher and Boulic, 2001). Furthermore, Euler angles are 809 not particularly intuitive (two angles that appear intuitively close to each other may 810 not necessarily have similar Euler angles) and can be difficult to set at sensible values 811 (Sellers, 2014). For the purpose of calculating muscle moment arms in simple 812 anatomical planes, it may be more straightforward to define three orthogonal hinge 813 axes and restrict joint movement to one axis in turn, as opposed to defining true ball-814 and-socket joints, and this also avoids the potential for gimbal lock.

815

816 Muscle Paths

817 At the simplest level, a muscle can be modelled as a straight line travelling 818 from origin to insertion (Fig. 1), and it is in this manner that early studies of muscle 819 moment arm (then more commonly referred to as 'lever arm') in fossils were 820 conducted (Miller, 1915; Fisher, 1945; Maynard Smith and Savage, 1956). An 821 advantage of this 'dry-bone' approach is that no assumptions regarding the travel path 822 of the muscle are required, and calculations are based solely upon muscle scarring and 823 estimated joint centers. Furthermore, the data collection process involves 824 straightforward measurements of bone geometry and sample sizes can therefore be 825 large. Recently, a study used a similar idealized origin-insertion model to calculate 826 muscle moment arms around the elbow in a large dataset (n = 318) of extant and 827 extinct tetrapods (Fujiwara and Hutchinson, 2012). Similar sample sizes are currently 828 unachievable when calculating moment arms on the basis of articulated 3D digital 829 models.

830 However, many studies seek to quantify changes in muscle moment arms with 831 joint angle, and must therefore accommodate complex muscle geometries and muscle 832 paths that shift as the limb moves through its range of motion. In the case of a 3D 833 reconstruction of *Homo neanderthalensis* hamstring muscle paths were modelled as 834 straight lines and did not intersect with the skeleton throughout the range of knee 835 flexion angles considered (Chapman et al., 2010). In most instances, however, the 836 path from origin to insertion is not linear (Gröning et al., 2013). Muscles must 837 therefore be wrapped around objects, or constrained to travel through predetermined 838 points, in order to prevent intersection with the skeleton or unrealistic 'bow-stringing' 839 away from the bone surface (Murray, 1995). This is referred to as the 'centroid 840 approach' (Garner and Pandy, 2000) in which a muscle path is represented as a 841 curving line connecting cross-sectional centroids along the muscle's length. 842 Figure 8A illustrates the problem of muscle paths intersecting with the 843 skeleton. The M. iliotibialis 1 (ILT1) was reconstructed as travelling in a straight line 844 from its origin on the dorsal ilium to its insertion on the cnemial crest on the tibia. 845 With knee flexion, ILT1 implausibly intersects the skeleton and migrates caudally to 846 the joint centre of rotation, shifting the interpreted muscle function from knee 847 extensor to knee flexor. This highlights the utility of multibody dynamic software 848 packages with graphical user interfaces (GUIs) that allow the user to visualize the 849 model and resulting simulations. It is crucial that the user manually inspects the travel 850 path of each muscle as the limb is moved through its full range of motion in order to 851 detect any potential issues with muscle wrapping or joint impingements. A concern 852 when running numerical musculoskeletal simulations without accompanying 853 visualizations is the ease with which models can be created, and properties assigned, that would otherwise immediately appear unfeasible if the data were viewed as an 854
855 articulated skeleton. The process of visually inspecting muscle paths is time 856 consuming, but essential in order to achieve meaningful values for estimated moment 857 arms. In addition, when musculoskeletal models are to be used for MBDA, muscle 858 wrapping has been found to have a notable effect on force generation and the 859 inclusion of complex wrapping (as opposed to straight line origin-insertion) can bring 860 force estimates closer in line with in-vivo measured values (Gröning et al., 2013). 861 The specific options available for modifying the path of a muscle vary 862 between software packages (e.g., Gaitsym vs. OpenSim; see later discussion). 863 Regardless, a compromise will always exist between anatomical accuracy and muscle 864 paths that can be achieved feasibly within the constraints of the modeling software. 865 Two broad categories for describing changes in muscle path have been used: via 866 points and geometric shapes.

867 Via Points—Via points constrain the muscle to pass frictionlessly through a 868 specific point in space as defined by Cartesian coordinates, acting as retinacula (Delp 869 et al., 1990). By assigning several via points, complicated muscle paths can 870 effectively be divided into a series of straight-line segments. Figure 8B–C illustrates 871 the path of the M. ischiotrochantericus (ISTR) from its origin on the medial surface of 872 the ischium to its insertion on the proximolateral femur. In this instance, three via 873 points (one on the posterodorsal margin of the ischium and two on the lateral margin 874 of the femur) were necessary to prevent the ISTR from intersecting the skeleton 875 throughout the limb's full range of motion.

Via points are problematic for a number of reasons, however. By constraining the muscle to pass through a given xyz location, the muscle is prevented from sliding across the bony surface. Furthermore, the moment arm of a muscle around a given joint will be entirely determined by the location of via points fixed immediately to

880 either side of that joint. In other words, when via points are used to subdivide a complicated muscle path into a series of straight line segments, the calculated moment 881 882 arm is that of the segment running across the joint in question, as opposed to a 883 reconstructed muscle running the entire anatomical distance from origin to insertion. 884 Osteological evidence of muscle scarring at origin and insertion sites may not, 885 therefore, contribute directly to the calculated moment arms. Instead, the positioning 886 of via points (which are byproducts of the modeling approach) can heavily influence 887 estimated moment arms.

888 When defining via points, it is necessary to specify the body segment to which 889 they will remain fixed during limb movement. In some instances, when a via point 890 replicates the behavior of a retinaculum located on the bony surface, for example, the 891 appropriate body segment is clear. In other scenarios, via points may be a fixed point 892 in space, some distance from the skeleton (Bates et al., 2012a:fig. 2G around the knee 893 joint of Lesothosaurus diagnosticus; Maidment et al., 2014a:fig. 2A-H around the 894 knee joint of several ornithischian dinosaurs). In the aforementioned studies, only 895 muscle moment arms around the hip are calculated. Figure 9 illustrates the behavior 896 of IFB when via points are employed in a similar manner to modify the muscle path 897 around the knee during knee flexion.

Two IFB muscles are included here, both originating and inserting at the same location as described in Figure 9, and both passing through the same via point located posterior to the knee joint center. The two IFB models differ in the body segment to which the via point is fixed; one remaining fixed relative to the femur (IFB_f), and the other fixed to the tibia (IFB_t). With knee flexion, the paths of IFB_f and IFB_t diverge (Fig. 9). When remaining fixed relative to the femur during joint rotation, the IFB_f

904 impinges on the posterior surface of the tibia, whilst the IFB_t via point remains
905 stationary relative to the tibia and intersects the posterior surface of the femur.

906 The knee is a fairly straightforward case in which a clear biomechanical 907 argument could be made for the femur being the most appropriate body segment upon 908 which to attach the IFB via point, due to the likely location of the knee joint center 909 within the distal femoral condyles. In other cases, however, such as the neck, spine, 910 and ribcage, the decision as to which rigid body segment to kinematically link the via 911 point can be more ambiguous. Additionally, Sellers (2014) raises concerns regarding 912 the unrealistic behavior of via points at extreme values of joint rotation (as in Fig. 9), 913 and Garner and Pandy (2000) highlight the potential for discontinuities in moment 914 arms to occur when calculated across joints with more than one degree of freedom.

915 Geometric Shapes—As an alternative to via points, 'obstacle set' wrapping 916 (Garner and Pandy, 2000) seeks to represent anatomical features (such as bony 917 surfaces and underlying soft tissues) as simple geometric shapes including spheres, 918 cylinders, and toroids. Coordinates describing the surface contours of a joint may be 919 collected from CT/MRI, or via the use of a digitizing probe or microscribe on 920 cadaveric or dry skeletal material. Shapes may then be fitted to the bony landmarks 921 using an optimization process (Van der Helm et al., 1992) or via simple best-fitting of 922 circles as illustrated in Figure 7.

In contrast to via points, geometric shapes do not constrain a muscle to pass through a specific xyz position in space, and instead allow the muscle to slide across the surface of the object. Within the paleontological literature, cylinders are most often deployed at the epiphyses of long bones to replicate the wrapping path of muscles around the condyles (Hutchinson et al., 2005; Sellers et al., 2013). Typically, the axis of a cylinder is constrained to pass through the joint center, with the long axis

929 of the cylinder aligned mediolaterally. The radius of the object can then be set to 930 approximate the contours of the joint surface. Alternatively, geometric shapes can be 931 used to wrap around other bony features distant from the joint surface. For example, 932 Klein Horsman et al. (2007) used cylinders to replicate the wrapping of the M. 933 iliopsoas around the pubic bone in a musculoskeletal model of the human lower 934 extremity. Figure 10 illustrates the use of cylinders to wrap the M. 935 puboischiofemoralis internus (anterior and posterior) around the prepubis of 936 Stegosaurus, without which the muscles intersect with the skeleton implausibly. In 937 this instance, the cylinder is not constrained to an anatomical axis and is instead 938 aligned to a particular bony feature.

939 When using cylinders to approximate joint contours, the appropriate joint 940 center and cylinder radius may be calculated via the process of circle fitting to the 941 condylar surface (as outlined above). If taphonomic damage has occurred simple 942 geometric shapes may be used to reconstruct the former extent of underlying bony or 943 soft tissues. The impact that such retrodeformation may have upon estimated moment 944 arms will vary on a muscle-by-muscle basis. In Figure 11 we reconstruct the path of 945 the M. flexor tibialis externus (FTE) in Stegosaurus. Figure 11B illustrates the 946 original model, in which no attempt has been made to correct for the occurrence of 947 taphonomic deformation. Medial and lateral condyle cylinder radii and joint center 948 were calculated as outlined in Figure 7B, D-E. Alternatively, Figure 11C illustrates 949 the path of FTE when wrapped around a modified joint center with cylinders 950 accounting for the effect of deformation, as detailed in Figure 7C, F–G. As seen in 951 Figure 11A, calculated moment arms for FTE are relatively insensitive to the presence 952 of taphonomic damage at the condyles. Beyond 5° of knee flexion, the path of FTE no

953 longer wraps around the knee joint cylinder, and any discrepancy between models is954 entirely due to a small shift in the joint center of rotation.

955 By contrast, when both muscle origin and insertion are located close to the 956 joint of interest, the muscle path may wrap around the fitted joint cylinder throughout 957 most of the joint's range of motion. In Stegosaurus, the M. femorotibialis lateralis 958 (FMTL) originates on the lateral femoral shaft and attaches to the cnemial crest of the 959 tibia (Fig. 12B). As illustrated in Figure 12A, the moment arm of FMTL remains constant through the entire range of motion of the knee as the path of the muscle 960 961 remains tightly wrapped around the knee joint cylinder. Furthermore, the value of the 962 moment arm is exactly equal to the radius of the object around which it is wrapped. 963 The phenomenon of constant muscle moment has been noted previously (Hutchinson 964 et al., 2005), highlighting the sensitivity of calculated moment arms to the estimated 965 size of the joint cylinders. In the case of the FMTL, accounting for deformation of the 966 femoral condyles results in a 28% increase in calculated moment arm throughout the 967 full range of motion at the knee.

968 Muscles modeled as wrapping around cylinders do appear to behave better (in 969 terms of avoiding skeletal impingement or unrealistic travel paths) than those 970 modeled with via points, particularly at extreme joint angles. A recent 971 musculoskeletal model of an extinct sauropod (Sellers et al., 2013) avoided the use of 972 via points altogether, opting instead for simplified geometric wrapping surfaces at the 973 joints. Regardless of the particular path modifier chosen, muscle function is often 974 assumed a priori when determining the path of a muscle. For example, when 975 wrapping a muscle around a cylinder, the direction of wrapping must be manually 976 assigned. In Figure 11B, the FTE has been explicitly modeled as travelling posterior 977 to the joint center and the associated wrapping cylinder, and its function has therefore

been constrained as a knee flexor. Therefore, whilst the general aim of many fossil
moment arm studies is to investigate muscle 'function', it must be recognized that the
broad function of many muscles (i.e., flexor vs. extensor) has already been
predetermined by virtue of the wrapping parameters chosen, and the EPB-based
myology upon which the model is based.

983 Finally, the layering of neighboring soft tissues such as muscle and tendon 984 may also be taken into consideration when defining individual muscle paths and 985 wrapping. Several studies calculating muscle moment arms have attempted to account 986 for this effect, with inferior muscles wrapping closer to joint surfaces than those lying 987 superior (Hutchinson et al., 2005). However, estimates of the likely thickness of 988 underlying muscle and tendon in fossils should be based on modern dissection data, of 989 which little has been published outside the clinical literature. Additionally, our current 990 models cannot account for shortening and thickening during contraction in 991 surrounding soft tissues and any potential effect that this may have upon calculated 992 moment arms. As such, it would be prudent to restrict modeling to individual muscle-993 tendon units in isolation from other neighboring soft tissues, in order to minimize 994 subjectivity and improve repeatability in model creation.

Biarticular Muscles—Several of the muscles included in the present model
are biarticular (i.e., span more than one joint). In common with most modern
cadaveric analyses of muscle moment arms (e.g., Channon et al., 2010), here we fix
the additional joint whilst manipulating the joint of interest through its range of
motion. Elsewhere, calculated muscle moment arms around the ankle have been
shown to be relatively insensitive to knee flexion (Holokwa and O'Neill, 2013). This
suggests that the simplification of fixing additional joints may not unduly affect

1002 calculated moment arms around joints of interest, although further data from living1003 taxa are required to confirm this.

1004 It must also be recognised that a biarticular muscle moment arm around one 1005 joint will be sensitive to the wrapping parameters of a neighbouring joint. Moment 1006 arms calculated around the knee, for example, are determined in part by the position 1007 of the hip wrapping surface, which is itself a function of the hip joint center location 1008 and wrapping geometry. Uncertainty in one joint can therefore permeate calculations 1009 of moment arms around neighbouring joints. In the case of biarticular muscles, 1010 sensitivity analyses may therefore benefit from incorporating uncertainty in both 1011 joints.

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1013 INTER- AND INTRASPECIFIC VARIATION IN MUSCLE MOMENT ARMS1014

1015 Making Interspecific Comparisons between Fossil Taxa

1016 The foregoing discussion considers how the muscle moment arms of a single 1017 fossil individual may be calculated. Yet absolute values for the moment arms of a 1018 single individual are rarely of interest. Rather, comparative studies of numerous fossil 1019 species may be undertaken in order to quantify changes in muscle function within or 1020 between lineages, or higher order biomechanical variables assessed via forward 1021 dynamics approaches. When comparing a linear metric such as muscle moment arm 1022 between species, geometric similarity would predict absolutely larger animals to 1023 possess larger moment arm values. Therefore, in order to tease functional signals and 1024 overall body size signals apart, it is necessary to normalize muscle moment arm 1025 values.

1026 Osteometric scaling is a well-established practice in the human clinical 1027 literature (Sommer et al., 1982; Duda et al., 1996), and facilitates inter-specimen 1028 comparisons of muscle attachment sites. In comparative studies across modern taxa, 1029 limb muscle moment arms have been scaled by segment length (that is, moment arms 1030 calculated around the hip and knee are normalized to femur length, whilst those 1031 around the ankle are normalized to tibia length) (Payne et al., 2006; Crook et al., 1032 2010). This methodology has been applied to hind limb muscle moment arms 1033 calculated for comparative samples of dinosaur taxa (Bates et al., 2012b; Maidment et 1034 al., 2014a). Likewise the moment arms of jaw muscles acting around the 1035 temporomandibular joint have been normalized to mandible length in extant (Smith 1036 and Redford, 1990) and extinct (Vizcaíno and Iuliis, 2003) species. 1037 The motivation behind normalizing muscle moment arms by segment length is 1038 often to control for 'body size'. By removing size-related signals from moment arm 1039 data, any functional signals of interest will become more apparent. When dividing 1040 muscle moment arms calculated around the hip by femoral length, for example, there 1041 is an assumption that femoral length is strongly correlated to overall 'body size' and 1042 does not itself contain a functional signal. Yet this is not the case. Several independent 1043 studies have found long bone length is often a less accurate predictor of body mass in 1044 modern vertebrates relative to cross-sectional properties (Damuth and MacFadden, 1045 1990; Campione and Evans, 2012), and segment length may contain a strong

1046 functional signal (Brassey et al., 2013). The elongated zeugopodium of modern

1047 wading birds is an extreme example.

When attempting to remove 'body size' from an analysis of moment arms, a metric known to be highly correlated with body mass in modern species (such as stylopodial circumference or diameter: Campione and Evans, 2012; Brassey et al.,

1051 2013) could be applied to normalize the data. Figure 13 illustrates the effect of 1052 normalizing moment arm values calculated for the M. caudofemoralis longus (CFL) 1053 around the hip in Stegosaurus and Kentrosaurus aethiopicus (see Maidment et al., 1054 2014a for model details), a smaller Late Jurassic stegosaurian. By normalizing CFL 1055 moment arms by linear dimensions of the femur, values for the two species are 1056 brought into closer agreement. Whilst the rank order of the two species does not 1057 change (Stegosaurus consistently has larger values for CFL moment arm than 1058 Kentrosaurus), the extent of the divergence between the two species does differ 1059 depending upon the normalizing metric applied. Peak CFL moment arms in 1060 Stegosaurus are 19% greater than those of Kentrosaurus when normalizing to femur 1061 length, compared to 38% when normalizing to anteroposterior diameter (Fig. 13B vs. 1062 Fig. 13D).

1063 However, this approach still requires a judgment to be made regarding which 1064 skeletal metric should be preferred. Alternatively, an osteometric scaling approach 1065 based on procrustes superimposition of skeletal elements could be applied to remove the effects of translation, rotation, and scaling, and quantify the impact of changes in 1066 1067 bone geometry and attachment sites on muscle moment arms. A geometric mean of 1068 several skeletal variables could also be used. In reality, however, the occurrence of 1069 taphonomic damage and weathering may preclude the application of a particular 1070 metric to a given group of fossils, and normalization of a dataset should be considered on a case-by-case basis. To facilitate future comparisons, the process of moment arm 1071 1072 normalization should be explicitly described in the methodology. In addition, the 1073 potential for the normalization process to change the rank order of calculated moment 1074 arms within the sample should be recognized.

1075

1076 Intraspecific Variation in Moment Arms

In addition to interspecific differences, evidence from the clinical literature 1077 1078 suggests that within-species variation in muscle moment arms can also be 1079 considerable. In human adults, the relationship between moment arm and joint angle 1080 typically describes an overall similar curve between individuals, whilst possessing 1081 different absolute values (in the knee: Herzog and Read, 1993; and elbow: Murray et 1082 al., 2002). Much of the difference in absolute values is attributed to intraspecific 1083 variation in total body size. Yet, despite performing osteometric scaling on the basis 1084 of markers and reference points, Duda et al. (1996) still found considerable 1085 differences in the position of femoral muscle attachment centroids across a sample of 1086 humans, resulting in moment arm standard deviations of up to 65% of the mean in 1087 some muscles. Therefore, even when accounting for changes in overall body size, 1088 intraspecific variation in muscle attachment sites is likely to be present in calculated 1089 muscle moment arms. 1090 Outside of humans, few data exist for extant taxa regarding within-species 1091 variation in attachment sites and muscle moment arms (but see Smith et al., 2007). 1092 Within the body of available data, confounding epigenetic factors confuse matters 1093 further, including adaptations in response to exercise regimes in captive zoo animals 1094 and domesticated species. Ontogeny also has an impact on moment arms, with 1095 muscles shifting their location relative to one another, and to the joint they act around, 1096 with age (Carrier, 1983; Young, 2005; Singleton, 2015). The moment arms calculated 1097 herein for a subadult *Stegosaurus* specimen, for example, may not be directly 1098 comparable to those of a mature individual of the same species, or to adult specimens

1099 of closely related taxa.

1100 Intraspecific variation is rarely considered in paleontological musculoskeletal 1101 reconstructions, however, due either to lack of specimens or constraints associated 1102 with the time-consuming process of model creation. Yet given the substantial 1103 inconsistency in muscle attachment positions (and hence moment arms) in modern 1104 humans, further research into the relative magnitudes of inter- and intraspecific 1105 variability in moment arms across modern comparative samples may be necessary. If 1106 between-species variation in moment arms is found to dwarf that within-species, then 1107 we may have more confidence in attributing patterns in calculated moment arms of 1108 fossil species to functional shifts within lineages.

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1110 VERIFICATION AND VALIDATION OF MUSCLE MOMENT ARM MODELS

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1112 The discussion provided above outlines the process of generating 1113 musculoskeletal models for fossil taxa from which muscle moment arms may then be 1114 calculated. Yet, in addition to creating an accurate 3D representation of a fossil skeleton and associated musculature, it is important to verify and validate model 1115 1116 results. In their review of computational modeling of the neuromusculoskeletal 1117 system, Hicks et al. (2014) considered the best practices for verifying and validating biomechanical models of muscles and movement. These authors emphasized the 1118 1119 difference between verifying MDBA software ('are we solving the equations 1120 correctly?') and validating model results ('are we solving the correct equations?'). 1121 1122 Verification 1123 For users, the process of verifying whether or not MBDA software is

1124 implementing algorithms correctly has been mostly completed. When employing

1125 well-established software modules (either commercial or open source), most source code has been independently verified by an extensive user community. Commercial 1126 1127 packages such as SIMM (Delp et al., 1990), Adams (MSC Software Corp.), and 1128 AnyBody (AnyBody Technology) have already been successfully applied to a wide 1129 spectrum of biomechanical problems, including non-human extant taxa (frog: Kargo 1130 and Rome, 2002; horse,:Brown et al., 2003; tuatara: Curtis et al., 2010; rat: Wehner et 1131 al., 2010; rabbit: Watson et al., 2014; pigs: Basafa et al., 2014) and occasionally 1132 fossils (Hutchinson et al., 2005; Snively et al., 2013). 1133 The above-mentioned software packages do not, however, provide full access 1134 to the source code. OpenSim (Delp et al., 2007) and GaitSym (Sellers, 2014) are 1135 open-source alternatives. OpenSim uses SimBody as its physics engine, and has been 1136 applied in numerous non-human studies, including the macaque forelimb 1137 (Schaffelhofer et al., 2015), and chimpanzee (O'Neill et al., 2013), sheep (Lerner et 1138 al., 2015), and rat (Johnson, 2009) hind limbs. Likewise, Gaitsym is open-source and 1139 uses the Open Dynamics Engine (ODE) physics library to perform most rigid body 1140 dynamics calculations. Gaitsym (and its precursors) have been applied to MBDA of

both extant (human: Sellers et al., 2010; chimpanzee: Sellers et al., 2013) and extinct

1142 (hominoid: Nagano et al., 2005; Sellers et al., 2005; dinosaur: Sellers and Manning,

1143 2007; Bates et al., 2012a, b; Maidment et al., 2014a) taxa.

1144 A recent study comparing the results of MDBA run using various physics 1145 engines (including ODE, Bullet, and Simbody) reassuringly found only minor

1146 differences in performance when applied to a simple walking task (Peters and Hsu,

1147 2014). However, as far as we are aware, a straightforward comparison of moment arm

1148 values calculated for equivalent musculoskeletal models across different MBDA

software packages has yet to be attempted. Such a comparison could potentially prove

1150 interesting, as current MBDA packages differ considerably in the muscle wrapping parameters available to users. For example, while muscles may be modelled as 1151 1152 wrapping around toroids in OpenSim, GaitSym only allows muscle wrapping around 1153 cylinders. Models created in one package may not, therefore, be directly imported and 1154 verified in another. Finally, 3D moment arm calculations are essentially simple 1155 trigonometry problems, and may be verified using back-of-the-envelope calculations. 1156 Moment arm values calculated from detailed 3D musculoskeletal models employing 1157 complex muscle-wrapping should therefore be verified using this simplified approach 1158 to ensure that both techniques converge on similar results.

1159

1160 Validation

1161 Validating the outputs of musculoskeletal models for extinct species is 1162 obviously impossible. Therefore, for a biomechanical reconstruction technique to be 1163 considered reliable when employed in paleontology, its validity can only be 1164 approximated by applying it to relevant extant taxa (Hutchinson, 2011). When 1165 attempting to validate techniques for calculating muscle moment arms and inferring 1166 muscle function, we can ask the following questions related to modern taxa: 1) do 1167 muscle moment arms calculated using musculoskeletal models agree with 1168 experimental values?; and 2) do calculated muscle moment arms contain an obvious 1169 functional signal? 1170 How do Muscle Moment Arms Calculated using Musculoskeletal Models 1171 Compare with those Measured Experimentally?—Within clinical biomechanics, 1172 there exists a substantial body of research comparing moment arm estimates derived

1173 from mathematical models to those estimated experimentally, due to the considerable

advantages associated with avoiding invasive procedures or dissections. Numerous

1175 studies have found human moment arm estimates calculated from 3D computer 1176 models to fall consistently within the range of empirical data, for both 'simple' hinge 1177 joints such as the elbow (Murray et al., 1998) and more 'complex' joints including the 1178 knee (Arnold et al., 2000; Gatti et al., 2007). In non-human studies, a similar pattern 1179 is present in the hip and knee joints of frogs (Kargo and Rome, 2002) and 1180 chimpanzees (O'Neill et al., 2013), and the distal forelimb of horses (Brown et al., 1181 2003), in which moment arms estimated from 3D musculoskeletal models have been 1182 found to be well-matched to those calculated experimentally, typically via the tendon-1183 travel method. In some situations, it has been suggested that 3D modeling may be 1184 preferable to the tendon-travel method, due to the potential for muscle lines-of-action 1185 to be altered through the process of excising surrounding soft tissues during dissection 1186 (Hutchinson et al., 2015). Thus, the broad agreement between experimental and 1187 model results in extant taxa supports musculoskeletal modeling as a valid approach to 1188 calculating muscle moment arms in extinct taxa assuming a reliable myological 1189 reconstruction is available. The modern studies cited above rely upon detailed 1190 dissection data to inform the model-making process, something that is obviously 1191 unobtainable for fossil taxa. Whilst the agreement between techniques gives us 1192 confidence in 3D models as a means of calculating moment arms, musculoskeletal 1193 modeling is still subject to the phenomenon of 'Garbage In, Garbage Out' (GIGO), 1194 and the value of the moment arms output is directly a function of the quality of the 1195 myology upon which the model is based.

Functional Signals in the Muscle Moment Arms of Extant Species—For a given property to be informative when applied to the fossil record, it must be first understood in extant taxa. In the case of muscle moment arms, values derived from fossil species are rarely of interest in and of themselves, but are instead used as a

1200 proxy for musculoskeletal function. Yet, as highlighted by Gans and De Vree 1201 (1987:76): "It remains necessary to check whether sites at which muscles are placed 1202 differ interspecifically and whether the functional [...] implications of these 1203 differences match possible differences in role. If they do not, it is likely that the 1204 character state reflects phylogeny more than function". Whilst dissection-based 1205 myological descriptions have a rich history in the field of modern comparative 1206 anatomy, and muscle moment arms are increasingly reported, the relationship 1207 between gross muscle architecture and muscle function across broad comparative 1208 datasets remains less than clear.

1209 In some instances, the calculated muscle moment arms of extant taxa may 1210 contain a functional signal. Rat hind limb muscle moment arms have been found to 1211 vary considerably throughout the physiological limb range of motion, yet peak and 1212 remain relatively constant within the range of motion domain occupied during 1213 locomotion (Johnson et al., 2008), implying moment arms may be indicative of 1214 dynamic limb posture. A caveat is that most rodent locomotion studies, such as 1215 Johnson et al. (2008), rely upon skin markers for their kinematics, which may poorly 1216 reflect the behavior of the underlying joints (Bauman and Chang, 2010). Likewise, the 1217 hardness of food items has been shown to influence mandible shape, and hence the 1218 mechanical advantage (ratio of the inlever and outlever) of several masticatory 1219 muscles in laboratory mice (Anderson et al., 2014), implying jaw muscle moment 1220 arms may correlate to dietary preference. Yet elsewhere, the moment arms of ostrich 1221 hind limb antigravity muscles calculated via 3D modeling were not found to peak at 1222 angles corresponding to mid-stance of walking and running during gait trials 1223 (Hutchinson et al., 2015), suggesting that there may not be a straightforward 1224 relationship between limb posture during stance phase and moment arms.

1225 Additionally, the functional characteristics of muscle architecture can be 1226 studied on three levels (Gans and De Vree, 1987): 1) muscles within the organism; 2) 1227 fibers within the muscle; and 3) sarcomeres within the fibers. While paleontologists 1228 are restricted to the reconstruction of gross myology, there is mounting evidence that 1229 organisms primarily adapt their musculature to prevailing biomechanical conditions 1230 by changing intrinsic muscle properties. An increase in muscle moments within the 1231 limbs of sprinting racehorses relative to endurance horses has been attributed to 1232 increased muscle volume and physiological cross-sectional area rather than moment 1233 arm, for example (Crook et al., 2010). Similarly, modern gibbons have been found to 1234 employ a variety of compromises between fiber length and moment arm in order to 1235 achieve diverse biomechanical objectives (torque vs. control) within the hind limb 1236 (Channon et al., 2010), and adaptation to different feeding strategies in feline jaw 1237 muscles has been identified primarily in muscle fiber length (Hartstone-Rose et al., 1238 2012).

1239 In reality, the potential for a muscle to produce a moment is a function of both 1240 its moment arm and its ability to generate force, which is itself influenced by muscle 1241 size and internal organization. It may, therefore, be the 'totality' of the muscle 1242 architecture that is under the influence of selection (Gans and De Vree, 1987), without 1243 a well-defined relationship between one particular variable (such as moment arm) and 1244 a given function. Until a correlation between moment arm and function can be 1245 broadly identified across a range of modern taxa, the interpretation of moment arms 1246 calculated for extinct taxa should be approached with caution (Maidment et al., 1247 2014a). 1248

SUMMARY

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1251 In the preceding discussion, we outline the process of generating a 1252 musculoskeletal model for the purpose of muscle moment arm calculations in fossil 1253 specimens. In doing so, we highlight the model parameters to which calculated 1254 moment arms are particularly sensitive or robust. As a field, paleontology is 1255 increasingly engaging with methods of specimen digitization and musculoskeletal 1256 simulation and it is tempting to create ever more detailed and sophisticated models of 1257 extinct species. It is crucial, however, that our desire to generate 'realistic' models of 1258 fossil taxa does not outstrip the extent to which we may make reasonable inferences 1259 regarding the individual, and that we avoid becoming so 'seduced' by a technique that 1260 we might end up with models we no longer understand (Anderson et al., 2011). 1261 It is beneficial, therefore, to refer back to the hierarchy of biomechanical 1262 questions outlined in the Introduction, to which muscle moment arm analyses are 1263 frequently applied. When utilizing musculoskeletal models to predict the role of an

1264 individual muscle around a joint (e.g., flexor vs. extensor), we might reasonably have 1265 confidence in the interpretation of muscle moment arms, as uncertainty in factors such 1266 as wrapping cylinder radii or joint center location are unlikely to change the 1267 fundamental action of a muscle. Variation in such parameters will impact upon 1268 moment arm magnitudes, however, and thus may change the rank order of individuals 1269 within a broad interspecific sample and fundamentally affect the interpretation of a 1270 dataset. Consequently, it is currently unclear whether moment arm analyses may be 1271 appropriately applied to test broader evolutionary hypotheses regarding changes in 1272 biomechanical function between lineages. Furthermore, the functional signal 1273 contained within the moment arms of extant species can often be contradictory. Until 1274 the methodology outlined above for the calculation of muscle moment arms can be

shown to reliably illuminate aspects of biomechanical function in extant taxa,

paleontological studies of moment arms are being held at an "impasse" (Hutchinson etal., 2015:1).

1278 Looking to the future, it is worth considering how we wish to use muscle 1279 moment arm data when applied to the fossil record. Is it important to understand the 1280 mechanical signal contained within muscle moment arm data? Or can muscle moment 1281 arms be used in a purely statistical sense, as a correlate for another parameter of 1282 interest? And, if the latter is the case, are complex models and simulations required to 1283 capture this data? 3D musculoskeletal models are still labor intensive, and their usage 1284 necessarily restricts sample sizes. If the aim of analysis is simply to 'bin' extinct 1285 species into disparate categories, such as 'cursorial vs. digging', or 'upright vs. 1286 sprawling', discriminant analyses on modern datasets of 2D moment arms may be 1287 more appropriate. Such analyses may be based on straightforward linear osteological 1288 measurements (Fujiwara and Hutchinson, 2012), facilitating the collection of large 1289 modern datasets without the need for extensive dissections or complex 3D muscle 1290 wrapping paths in our models. Statistical analyses such as these would also allow 1291 confidence limits to be ascribed to any predictions of potential function.

1292 Alternatively, if 3D musculoskeletal models are favored, muscle moment arms 1293 may simply be a 'means to an end' for calculating other meaningful biomechanical 1294 parameters using powerful tools such as FEA, inverse- or forward MBDA. In this 1295 instance, muscle moment arms do still function as statistical correlates for the 1296 maximum moment-generating capacity of muscles. Such analyses can provide 1297 important insights into the functioning of muscle groups during locomotion, and may 1298 even generate gaits de novo. These studies do, however, require additional 1299 assumptions regarding the physiological cross-sectional area of muscles, fiber and

1300	tendon lengths, and muscle activation patterns. Fundamentally, the quality of the
1301	fossil and the existence of modern analogues with associated anatomical data should
1302	dictate the complexity of the question being addressed, and by virtue the detail
1303	required within the model.
1304	Moving forward, it is also essential that moment arm analyses pass the
1305	fundamental test of reproducibility. Previous paleontological studies have claimed
1306	that comparisons between musculoskeletal models may be easily made, as the 3D
1307	moment arm technique is quantifiable and repeatable (Maidment et al., 2014a).
1308	However, the extent to which moment arm calculations are reproducible has rarely
1309	been confirmed (although see Bates et al., 2012a). In addition to inter-observer
1310	variation in the interpretation and implementation of a given myology, variation in
1311	wrapping parameters between MBDA software packages makes repetition of results
1312	across studies challenging. Future studies should seek to standardize the reporting of
1313	musculoskeletal model parameters, in order to facilitate data sharing and model
1314	reproducibility.
1315	
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1323	
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FIGURE 1. Schematic of human M. triceps moment arm calculation illustrating the
2D origin-insertion method. Moment arm is calculated as the perpendicular distance
from the muscle line of action to the joint center [Intended for column width].

1877



1878

1881

- 1879 FIGURE 2. A 3D articulated model of *Stegosaurus stenops* in right lateral view. Red
- 1880 lines represent a pair of antagonistic 'driver' muscles attaching to the midshaft of the
- 1882 the femur to extreme hip flexion and hip extension respectively. [Intended for column

anterior and posterior surface of the femoral midshaft, used for driving the position of

1883 width].





FIGURE 3. Quantifying the effect of articular cartilage on M. iliofibularis (IFB) 1886 1887 moment arms measured around the knee. A, solid line represents IFB moment arm 1888 without articular cartilage separating the distal condyles of the femur and proximal 1889 surface of the tibia, as illustrated in **B**; dotted line represents moment arm of IFB 1890 calculated with an additional 10% of length added to the femur and tibia (of which 1891 half is located at the knee) while joint center remains unchanged, as illustrated in C; 1892 dashed line represented IFB moment arm calculated with 10% additional cartilage and 1893 joint center shifted distally, as illustrated in D. [Intended for 2/3 page width]. 1894



1896 FIGURE 4. Quantifying the effect of the positioning of the pubis on M. ambiens

1897 (AMB) moment arms measured around the hip. Positive values for moment arms

1898 imply hip extension, hip adduction, and lateral femoral rotation for FlexExt, AbdAdd,

and LAR respectively. Solid lines represent AMB FlexExt, dashed lines represent

- 1900 AMB AbdAdd, and dotted lines represent AMB LAR. Path of AMB marked in red on
- 1901 skeletal model. A, illustrates the pubis orientated parallel to the iliac blades; B,
- 1902 illustrates pubis rotated medially from this position. [Intended for column width].
- 1903



FIGURE 5. Determining range of motion in the hip. A, hip flexion of 60° results in collision between the femur and last dorsal ribs whereas; B, hip flexion of 50° could have been achieved without contact between the hind limb and torso. This reflects the bony limits to range of motion, whilst the physiological limb postures achievable may have been more limited. [Intended for column width].



1912

1913 FIGURE 6. A, variation in M. latissimus dorsi (LAT) moment arm with humeral

1914 protraction-retraction for five lines of action. A negative joint angle is protraction,

1915 while a positive joint angle is retraction. A positive moment arm indicates shoulder

1916 retractor leverage. Solid lines, centroidal insertion of LAT on posterior surface of the

1917 humerus, as illustrated in B–C. Dashed lines, LAT insertion shifted to most proximal

1918 extent, as illustrated in **D–E**. [Intended for 2/3 page width].





1921

FIGURE 7. The calculation of knee joint center via circle fitting to the medial and
lateral condyles. A, ventral view of the distal femoral condyles displaying taphonomic
distortion; B, markers indicate the vertices at which coordinate data was collected for

anteroposterior

anteroposterior

the medial condyle along a line running anteroposteriorly; C, coordinate data
collected from vertices located along a line describing the long-axis of the distorted
medial condyle; D–E, circles fitted to the medial and lateral condyles respectively,
based on vertices sampled in a strict anteroposterior plane; F–G, circles fitted to
medial and lateral condyles when accounting for warping of the condylar long axis.
Colored dots indicate centroid of circle. [Intended for 2/3 page width].



1933 FIGURE 8. A, M. iliotibialis 1 intersects the surface of the femur when the knee is1934 flexed if modeled as travelling in a straight line from origin to insertion; B–C, travel

1935 path of M. ischiotrochantericus defined by a series of straight line segments separated

1936 by fixed via points. [Intended for column width].

1937



1938

1939 FIGURE 9. Muscle paths of the M. iliofibularis (IFB) from knee extension (left) to

1940 full flexion (right). IFB_f, via point fixed relative to femur; IFB_t, via point fixed relative

to tibia. The path of IFB is strongly affected by the body segment to which the via

1942 point is fixed. Both muscle paths intersect the skeleton at high values for knee flexion,

1943 highlighting the importance of visually inspecting models throughout the entire limb

1944 range of motion. [Intended for page width].





1947 FIGURE 10. Muscle paths of the M. puboischiofemoralis internus (anterior and

1948 posterior) in *Stegosaurus stenops*. A, muscle paths intersect implausibly with the

1949 prepubis with increased femoral flexion when modelled as simple origin-insertion

1950 straight paths. **B**, muscle paths wrap around a cylinder positioned correspond to the

1951 surface contours of the prepubis, preventing intersection with the skeleton. [Intended

1952 for 2/3 page width].



FIGURE 11. Calculation of moment arms for the M. flexor tibialis externus (FTE) in *Stegosaurus stenops*. A, variation in FTE moment arm with knee flexion. Positive
values for moment arm indicate leverage for knee flexion. B, original model in which
calculated joint center and cylinder radius is based upon deformed distal femoral
condyles. C, modified model in which joint center and cylinder radius is altered to
account for taphonomic damage, as outlined in Figure 7. [Intended for column width].



Knee joint flexion angle (degrees)



1963 FIGURE 12. Calculation of M. femorotibialis lateralis (FMTL) moment arm in

1964 Stegosaurus stenops. Positive values for moment arm indicate leverage for knee

1965 extension. A, FMTL moment arm is constant throughout the entire range of motion of

1966 the knee; **B**, the path of FMTL is tightly constrained to wrap around the knee joint

1967 cylinder. Dashed line, moment arm around deformed condyles; solid line, moment

arm calculated around retrodeformed condyles (as outlined in 'Joint Centers' section).

1969 [Intended for column width].



1971

FIGURE 13. Moment arms calculated for M. caudofemoralis longus (CFL) around
the hip in *Stegosaurus stenops* (solid line) and *Kentrosaurus aethiopicus* (dashed
line). Positive values for moment arm indicate leverage for hip extension. A, moment
arm values without normalization; B, moment arm normalized to femur length; C,
moment arms normalized to mediolateral (ML) diameter; D, moment arm normalized

1977 to anteroposterior (AP) diameter. [Intended for 2/3 page width].