What drove reversions to quadrupedality in ornithischian dinosaurs?: Testing
hypotheses using centre of mass modelling

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Abstract

The exceptionally rare transition to quadrupedalism from bipedal ancestors occurred on three independent occasions in ornithischian dinosaurs. The possible driving forces behind these transitions remain elusive, but several hypotheses – including the development of dermal armour and the expansion of head size and cranial ornamentation – have been proposed to account for this major shift in stance. We modelled the position of the centre of mass (CoM) in several exemplar ornithischian taxa and demonstrate that the anterior shifts in CoM position associated with the development of an enlarged skull ornamented with horns and frills for display/defence may have been one of the drivers promoting ceratopsian quadrupedality. A posterior shift in CoM position coincident with the development of extensive dermal armour in thyreophorans demonstrates this cannot have been a primary causative mechanism for quadrupedality in this clade. Quadrupedalism developed in response to different selective pressures in each ornithischian lineage, indicating different evolutionary pathways to convergent quadrupedal morphology.

Keywords—Ornithischia, quadrupedality, 3D mathematical slicing, centre of mass

Introduction

Ornithischia was a diverse dinosaur clade that dominated the terrestrial herbivorous vertebrate niche throughout much of the Mesozoic. Early forms were small (~1m long) animals (Butler et al. 2008), but they diversified into a variety of small and large quadrupedal and bipedal megaherbivores. All major ornithischian subclades (Thyreophora, Ornithopoda, Marginocephalia) include members that developed a variety of elaborate cranial or dermal structures including hypertrophied osteoderms in thyreophorans, cranial horns and frills in ceratopsians (Marginocephalia), and elaborate nasal crests in hadrosaurids (Ornithopoda), that were likely related to display, defence or intraspecific behaviours (Fig. 1; Ostrom 1962; Galton 1970a; Hopson 1975; Farlow & Dodson 1975; Farlow 1976; Molnar 1977; Coombs 1979; Thulborn 1993).

Quadrupedality evolved at least three times within Ornithischia: once in Thyreophora (in the common ancestor of *Scelidosaurus*, stegosaurs and ankylosaurs), once in Marginocephalia (at some point on the ‘stem lineage’ to ceratopsids), and at least once in Ornithopoda (once in hadrosaurids, and possibly in some non-hadrosaurid iguanodontians; Fig. 1 [Maidment & Barrett 2012, 2014]). The evolution of quadrupedality from a bipedal ancestor is an exceptionally rare transition in the history of tetrapod evolution, having only occurred in the sauropodomorph saurischians (Bonnar 2003; Yates et al. 2010) and the silesaurid dinosauriformes (Nesbitt et al. 2010) outside of Ornithischia. The repeated evolution of quadrupedality from bipedal ancestors within Ornithischia is therefore unprecedented, but the subject has received little attention, and the evolutionary drivers that led to the recurrent adoption of quadrupedality in Ornithischia remain elusive. Determining the possible selection pressures that drove bipedal taxa to revert to a quadrupedal condition is

61 therefore of interest in terms of understanding the full pattern of tetrapod locomotory
62 and biomechanical evolution.

63 Thyreophoran dinosaurs are characterized by an array of postcranial dermal
64 armour extending from the neck to the tip of the tail. Basal members of Thyreophora
65 (*Scutellosaurus* [Colbert 1981]; *Emausaurus* [Haubold 1990]) have numerous small
66 osteoderms on all body regions and these are hypertrophied in more derived
67 thyreophorans. Ankylosaurs possess a variety of large conical, flat, and spike-like
68 osteoderms, and smaller polygonal plates that sometimes fuse to form mosaic-like
69 pavements covering the dorsal surface of the body (as well as osteoderms associated
70 with the skull and mandible), whereas stegosaurs possess plate-like or spinose
71 osteoderms that extend in two parasagittal rows along the back. On the basis of his
72 work on the basal thyreophoran *Scutellosaurus*, Colbert (1981) suggested that
73 primitive thyreophorans might have been facultatively quadrupedal due to the need to
74 provide additional support to resist the weight of this armour.

75 Some ceratopsian dinosaurs possess cranial ornamentation such as a frill
76 (composed of elongated squamosals and parietals) and horns (which are located
77 dorsal to the orbit, on the jugal, and projecting dorsally from the nasal). These
78 features are present incipiently in neoceratopsians (e.g. *Protoceratops* [Brown and
79 Schlaikjer 1940]), but are developed to their greatest extent in the ceratopsids, such as
80 *Chasmosaurus* and *Triceratops* (Hatcher et al. 1907), which possessed some of the
81 largest heads among vertebrates, measured either absolutely or relative to trunk length
82 (Serenio et al. 2007). For example, the ceratopsid *Pentaceratops* has a skull +
83 parietosquamosal frill length that is 118% of trunk length (measured as the distance
84 between the shoulder glenoid and acetabulum). Serenio et al. (2007) suggested that a

head length greater than 40% of trunk length would only be possible in a quadrupedal animal.

We aim to examine quantitatively the effects of previously proposed morphological drivers on ornithischian stance, based on the assumption that any measurable causative mechanism for reversion to quadrupedality must result in an anterior movement of the centre of mass (CoM). We also take the opportunity to model the CoM in a hadrosaurid ornithopod to examine stance in this clade. The stance of iguanodontian ornithopods, and particularly of hadrosaurids, has always been controversial (e.g., review in Norman 1980). Galton (1970b) argued that hadrosaurids were bipedal on the basis of their osteology, while others have presented evidence from trackways (Lockley and Wright 2001), limb proportions (Dilkes 2001) and soft tissues (Sellers et al. 2009) that they may have been at least facultatively quadrupedal. Maidment and Barrett (2014) suggested that hadrosaurids possessed a number of osteological correlates indicative of habitual quadrupedality.

In a bipedal animal, CoM must be located above the hind feet in order for the animal to balance in equilibrium. A quadruped is not constrained in this regard, and the CoM can lie further anteriorly so that body mass is distributed between the fore- and hind limbs. A CoM located anterior to the foot can only occur in an animal that is an obligate quadruped. However, a CoM located over the hind foot does not necessarily indicate bipedality. In contrast, it could occur in a quadrupedal animal that has evolved quadrupedality for reasons other than an anterior shift in CoM, such as a preference for low browse.

Herein, we mathematically model the CoMs of various ornithischian dinosaurs to test the following hypotheses:

- 1) Thyreophorans became quadrupedal because the additional mass of dermal armour forced their CoM to move anteriorly;
- 2) Ceratopsians became quadrupedal because the additional mass of extensive cranial ornamentation forced their CoM to move anteriorly;
- 3) CoM location in hadrosaurids would have allowed them to exploit both bipedal and quadrupedal locomotion.

Methods

Taxon selection. In order to investigate changes in CoM associated with reversions to quadrupedality, basal and derived members of Thyreophora and Ceratopsia were required. A hadrosaurid was also selected to investigate CoM location in this clade. Taxa were chosen based on their phylogenetic position and the completeness of their preserved remains.

Scutellosaurus was chosen as a representative basal thyreophoran.

Scutellosaurus is generally considered to be the basal-most thyreophoran (Maidment et al. 2008; Butler et al. 2009) and is known from a single almost complete skeleton (MNA [Museum of Northern Arizona, Flagstaff, U.S.A.] Pl.175; Colbert 1981), along with fragmentary referred material (Rosenbaum and Padian 2000). Although Colbert (1981) considered *Scutellosaurus* to be a facultative quadruped, it bears no osteological correlates of quadrupedality (Maidment and Barrett 2014). The only other well-known basal thyreophoran, *Scelidosaurus*, was also modelled as a phylogenetic intermediate between *Scutellosaurus* and the derived ankylosaurs and stegosaurs. *Scelidosaurus* is known from a well-preserved and almost complete skeleton (NHMUK R1111; Owen 1861) and several partial skeletons (NHMUK R6407; BRSMG [Bristol City Museum and Art Gallery, U.K.] Ce12785). It is usually

reconstructed as a quadruped (Paul 1997) and has some osteological correlates for quadrupedality (Maidment & Barrett 2014).

Stegosaurus and *Euoplocephalus*, both known from multiple nearly complete specimens, were chosen to represent the two lineages of derived thyreophorans, Stegosauria and Ankylosauria, respectively. Numerous examples of *Stegosaurus* are mounted in museums around the world, and its anatomy is well-documented (Gilmore 1914). *Euoplocephalus* is known from several partial skeletons and an almost complete specimen (NHMUK R5161; Nopcsa 1928; Coombs 1978; Vickaryous et al. 2004). Both *Stegosaurus* and *Euoplocephalus* are universally reconstructed as quadrupedal (Gilmore 1914; Coombs 1978).

The distribution of armour on *Scelidosaurus*, *Stegosaurus* and *Euoplocephalus* is known because several specimens preserve the armour *in situ* (NHMUK R1111; USNM [National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.] 4934; NHMUK R5161); however, the armour of *Scutellosaurus* was not found *in situ*, and so its distribution on the body is conjectural. The reconstruction of the armour of *Scutellosaurus* was based on that of Colbert (1981) with additional information from the position of armour in ankylosaurs and stegosaurs.

The basal ceratopsian *Psittacosaurus* is known from many complete and partially complete skeletons (Osborn 1923; Sereno 2010) and was chosen to represent the basal ceratopsian condition. *Psittacosaurus* lacks morphological indicators of quadrupedality (Maidment and Barrett 2014), although evidence from limb bone scaling suggests that juveniles of this taxon may have been quadrupedal (Zhao et al. 2013). The chasmosaurine ceratopsid *Chasmosaurus* was chosen to represent a derived ceratopsian. Although it is known from numerous crania (Godfrey and Holmes 1995), several with associated postcrania (Maidment and Barrett 2011), no

complete postcranial skeleton is known for *Chasmosaurus*, so body proportions were taken from a complete, articulated postcranium of an indeterminate chasmosaurine (CMN 8547) formerly referred to *Anchiceratops* (Mallon and Holmes 2010).

Ceratopsids are universally considered to be quadrupeds (Dodson et al. 2004).

The lambeosaurine hadrosaurid *Lambeosaurus* was chosen as a representative hadrosaurid. Complete specimens of many hadrosaurid taxa are known (Leidy 1858; Ryan and Evans 2005), but *Lambeosaurus* was chosen because of the accessibility and completeness of the mounted specimen in the ROM (ROM 1218).

More details on the specimens used for reconstruction can be found in the Electronic Supplementary Material (ESM) S1.

Reconstructions. Dorsal and lateral reconstructions of each taxon were produced based on the single most complete specimen of each taxon. Individual postcranial elements were measured, and for specimens that were mounted, neck, trunk and tail lengths were also taken. Where specimens were mounted, photographs were taken in lateral, anterior and, where possible, dorsal view to inform reconstructions. The presence of any reconstructed element was recorded. A variety of literature sources were also used to supplement measurements and photographs (ESM S1). Information on the scaling relationships of missing elements was acquired by examination of other specimens of the same species or closely related taxa.

Hypothesis testing. In order to test the hypotheses outlined above, a series of ‘hybrid’ ornithischian models were also built. These are theoretical models that were devised specifically and solely to test the effect of changing a single variable on the location of the CoM, and it is important to emphasize that we do not consider that these hybrids or animals like them ever actually existed. To test the hypothesis that the addition of dermal armour caused CoM to move anteriorly in thyreophorans,

several hybrids were built. Firstly, the CoM of all thyreophoran models was computed without armour. Secondly, the armour of *Stegosaurus* was placed on *Scutellosaurus* and scaled by femoral length. Finally, the armour of *Euoplocephalus* was placed on *Scutellosaurus* and scaled by femoral length. To test the hypothesis that the development of cranial ornamentation caused anterior movement of the CoM in ceratopsids, the parietosquamosal frill and nasal horn of *Chasmosaurus* were measured, added to the *Psittacosaurus* model, and scaled by femoral length, and compared with the unornamented *Psittacosaurus* model. ESM 2 lists all models and hybrids and the hypotheses they were designed to test.

CoM modelling. CoM estimates were computed by 3D mathematical slicing (Henderson 1999). This method requires the production of dorsal and lateral reconstructions of the taxon of interest, which are combined using custom software to produce a 3D reconstruction (Fig. 2). Some recent studies have used laser scans of mounted skeletons and, in some cases, disarticulated material, to produce 3D reconstructions of dinosaurs for calculations of total mass and CoM (e.g., Bates et al. 2009a, b; Hutchinson et al. 2011; Sellers et al. 2012). The methods are similar in that they produce a virtual 3D reconstruction, and uncertainties in soft tissue reconstruction are common to both methods (Bates et al. 2009a, b; Hutchinson et al. 2011). Previous studies have highlighted the effects of investigator bias on soft tissue reconstruction (Hutchinson et al. 2011), and this was minimized herein because all reconstructions were produced by SCRM. Soft tissue reconstructions were therefore consistent throughout.

The basic tissue density for the axial body and limbs of all the models was set to 1000 g/l. This density incorporates the effect of high density mineralized bone tissue being reduced by pneumatic and fluid filled cavities within bone. The good match

between mass estimates from digital models of living tetrapods (aquatic, terrestrial and flying) and actual body masses using this density (Henderson 2003; 2010) supports the use of this value. Dermal armour and frill and horn densities were set to 2000 g/l based on the density of compact bone. A lung volume was included in all models and situated in the anterodorsal portion of the thoracic region. Lacking direct evidence for lung volumes for ornithischians, and lacking any extant descendants for comparisons, the model lung volumes were set to equal 9.5% of axial body volume. For living tetrapods lung volumes range between 8–10% (Milsom 1975).

Sensitivity analysis. In order to investigate the robusticity of our results to specific reconstruction assumptions, we also built 3D mathematical models of taxa using a different set of body reconstructions (taken from Paul 1997) and calculated CoM location as a percentage of glenoacetabular length. These reconstructions represent an entirely independent dataset, and were built using data from different specimens (see Discussion) and/or different soft tissue assumptions. Comparisons between these models and ours therefore provide an estimate of how robust our calculated CoM locations are to differences in soft tissue reconstruction. No alternative reconstruction of *Scutellosaurus* was available, so this taxon was omitted from the sensitivity analysis.

Results

Total mass, body length, CoM from the tip of the tail, and CoM as a proportion of glenoacetabular distance for the models are given in Table 1. The results of the sensitivity analysis are shown in Table 2.

234 **Centre of mass.** CoM was found to lie anteroventral to the acetabulum in all
 235 models, a result also found by previous CoM studies on dinosaurs using 3D
 236 reconstructions (Bates et al. 2009a, b). The CoM of *Scutellosaurus* (Fig. 3a, b) and
 237 *Psittacosaurus* (Fig. 4a, b) was located dorsal to the pedal digits in the models. The
 238 CoM of *Psittacosaurus* using an alternative reconstruction (Fig. 4c, d) was located in
 239 almost the same position as in our model, being located just 2% of glenoacetabular
 240 distance further anteriorly. The CoM of *Chasmosaurus* was situated a considerable
 241 distance anterior to the acetabulum in our model (Fig. 5a, b; 39% of glenoacetabular
 242 distance) and the same result was recovered using the alternative reconstruction of
 243 Paul (1997; Fig. 5c, d; 41% of glenoacetabular distance). The CoM of
 244 *Euoplocephalus* was also located anterior to the hip joint in our reconstruction and the
 245 alternative reconstruction (Fig. 6). In our reconstruction (Fig. 6a, b) it lies just anterior
 246 to the foot (19% of glenoacetabular distance); however, it is located further anterior of
 247 the acetabulum in the alternative reconstruction (Fig. 6c, d; 32% of glenoacetabular
 248 distance). The CoM of *Stegosaurus* lay dorsal to the foot in both our reconstruction
 249 (Fig. 7a, b; 16% of glenoacetabular distance) and the alternative reconstruction (Fig.
 250 7c, d; 20% of glenoacetabular distance). The same was true for the CoM of
 251 *Scelidosaurus* (Fig. 8; 21% of glenoacetabular distance in our reconstruction; 22% in
 252 the alternative reconstruction) and *Lambeosaurus* (Fig. 9; 28% of glenoacetabular
 253 distance in our reconstruction, 33% in the alternative reconstruction).

254 **Dermal armour and centre of mass.** The CoM of the four thyreophorans was
 255 calculated with and without the addition of dermal armour to the models. In
 256 *Scutellosaurus*, *Stegosaurus* and *Scelidosaurus*, addition of the dermal armour
 257 resulted in small posterior movements of the CoM (10 mm, 3 mm and 85 mm
 258 respectively; Table 1) because the CoM of the armour in these taxa lies posterior to

that of the body (Figs 3a, b; 7a, b; 8a, b). In *Euoplocephalus*, the CoM of the armour was very slightly anterior to the CoM of the body (Fig. 5a, b), resulting in a 4 mm anterior movement of the CoM when the armour was added. The CoM was found to move posteriorly when *Scutellosaurus* was reconstructed with the dermal armour of either *Euoplocephalus* or *Stegosaurus* scaled relative to femoral length (20 mm and 7 mm respectively; Table 1; Fig. 3c–f). In all cases, the addition of dermal armour was found to have an almost negligible impact on the CoM because the total mass of the dermal armour relative to body mass was very low. In our models, the armour of *Euoplocephalus* represented just 3% of body mass, that of *Scelidosaurus* was 5%, *Scutellosaurus* was 7%, and the armour of *Stegosaurus* was only 9% of body mass. The hypothesis that the development of dermal armour caused anterior movement of the CoM can therefore be rejected.

Cranial ornamentation and CoM. The addition of the frill and horns of *Chasmosaurus* to the head of *Psittacosaurus* scaled relative to femoral length resulted in a 6 mm (3% glenoacetabular distance) anterior movement of the CoM (Table 1; Fig. 4e, f). This resulted in the CoM being located slightly anterior to the foot. The removal of the frill and horns so that the back of the skull was scaled to that of *Psittacosaurus* in *Chasmosaurus* resulted, unexpectedly, in a 37 mm (2% of glenoacetabular distance) anterior movement in the CoM (Table 1; Fig. 5e, f). This may be the result of the head mass being concentrated at the anterior end of the neck, providing a long moment arm for the head, rather than being spread more evenly along the length of the neck as would occur due to the posterior elongation of the frill over the neck. The addition of large horns and a cranial frill to the skull of *Psittacosaurus* did result in an anterior shift in the CoM, although the removal of the frill and horns from *Chasmosaurus* did not result in a posterior shift in the CoM.

284

285 **Discussion**

286 Our models cover three orders of magnitude in mass, ranging from
287 *Scutellosaurus* at 2.6 kg (femoral length 8 cm) to *Stegosaurus* at 2704 kg (femoral
288 length 108 cm). A variety of methods have previously been used to examine body
289 mass in dinosaurs. Examples of these methods include limb bone proportions and
290 scaling (Anderson et al. 1985; Campione and Evans 2012), the use of scale models
291 (Colbert 1962; Alexander 1985, Paul 1997), and 3D reconstructions using
292 mathematical (Henderson 1999; Seebacher 2001) or computational (Bates et al.
293 2009a, b; Sellers et al. 2012) models. In general our mass estimates are in accordance
294 with previously published estimates. To our knowledge, no previous mass estimate
295 based on a quantitative technique has been published for *Scutellosaurus*.

296 Our mass estimate for *Scelidosaurus* (323 kg) is somewhat higher than previous
297 estimates (250 kg [Paul 1997]; 64.5 kg [Seebacher 2001]). Seebacher (2001) obtained
298 a mass of just 64.5 kg for *Scelidosaurus* based on an animal 3 m in length using a
299 mathematical modelling approach. Our reconstruction, which is based on NHMUK
300 R1111 (femoral length 39.5 cm) is 3.5 m long but has a mass of 323 kg. This is much
301 closer to the mass estimated for *Scelidosaurus* by Paul (1997) using a 3D
302 reconstruction (250 kg). This discrepancy may be due to Seebacher's (2001) use of a
303 reconstruction of *Scelidosaurus* (Farlow and Brett-Surman 1997), whereas our
304 reconstruction is based on first-hand observation and measurement of individual
305 elements.

306 Seebacher (2001) and Paul (1997) produced higher body mass estimates than
307 those from our model for *Psittacosaurus* (12.1 and 14 kg respectively). Our
308 reconstruction is based on *Psittacosaurus neimongoliensis* whereas Seebacher (2001)

and Paul (1997) based theirs on *Psittacosaurus mongoliensis*, so slight differences in interspecific size and body proportions could be responsible for these body mass differences.

Previous mass estimates for *Euoplocephalus* (2676 kg [Seebacher 2001]; 2300 kg [Paul 1997]) have used NHMUK R5161, the same specimen we used. Seebacher (2001) used a reconstruction (Carpenter 1982) to estimate mass, which is longer-limbed, more slender, and over a metre longer than ours. Paul's (1997) reconstruction is more similar to ours in terms of limb length and rotundity, and our mass estimates are similar.

Previous estimates of mass for *Chasmosaurus* are also slightly greater than ours (1659 kg [Seebacher 2001]; 1500 kg [Paul 1997]). Seebacher's (2001) estimate was based on a reconstruction of a slightly larger animal than ours (body length = 5 m), while Paul's (1997) reconstruction was based on CMN 2280, *Chasmosaurus russelli*, a specimen that preserves only the skull, part of the axial column and forelimbs. Our reconstruction is based on the complete articulated postcranium of CMN 8547, an indeterminate chasmosaurine (Mallon and Holmes 2010) accounting for the small differences in mass estimates.

A variety of mass estimates, derived from a range of methods, have been published for *Stegosaurus*. Colbert (1962) and Alexander (1985) both used scale models and derived the lowest (1780 kg) and one of the highest (3100 kg) mass estimates respectively. Our results are similar to those of recent works based on 3D reconstructions of USNM 4934 (2200 kg [Paul 1997]; 2530 kg [Henderson 1999]; 2610 kg [Seebacher 2001]), the same specimen on which our reconstruction is based. The small differences in mass estimation are therefore likely to be related to subjective soft tissue reconstructions. Anderson et al. (1985) and Campione and

Evans (2012) found the highest mass estimates for *Stegosaurus* (4131 kg and 4950 kg respectively), both based on limb scaling relationships.

Brown et al. (2013) found a mass estimate of 3100 kg for *Lambeosaurus* based on the method of Campione and Evans (2012). This is substantially greater than our mass estimate of the same specimen (1804 kg).

Campione and Evans (2012) found that many of their mass estimates were much higher than those based on life reconstructions. This suggests that either the scaling relationship derived by Campione and Evans (2012) based on extant quadrupedal reptiles and mammals is not applicable to ornithischian dinosaurs, or that life reconstructions are massively underestimating soft tissue density or total amounts of soft tissue. This discrepancy warrants further investigation, but is beyond the scope of this paper and will be investigated elsewhere.

The CoM of *Scutellosaurus* and *Psittacosaurus* was located dorsal to the foot (Figs 3a, b; 4a–d), allowing the animals to move bipedally, although this does not rule out quadrupedal locomotion in either taxon. The CoM of *Chasmosaurus* and *Euoplocephalus* was located anterior of the foot, confirming that they must have walked quadrupedally (Figs 5, 6). The CoM of *Lambeosaurus* (Figs 2, 9) was located dorsal to the foot. Hadrosaurids have often been considered as facultative quadrupeds, able to move both quadrupedally and bipedally (Horner et al. 2004; Sellers et al. 2009) and our CoM estimate is located in a position that would have allowed *Lambeosaurus* to assume both bipedal and quadrupedal styles of locomotion. Recent evidence based on morphology (Maidment et al. in press) and limb-bone scaling (Dilkes 2001; Maidment et al. 2012; Maidment & Barrett 2014) has suggested that hadrosaurids were obligate quadrupeds but the CoM results do not allow us to eliminate either form of locomotion. A previous CoM estimate for the saurolophine

hadrosaurid *Edmontosaurus* found the CoM to lie in a similar position, dorsal to the foot (Bates et al. 2009a).

The CoM of both *Stegosaurus* and *Scelidosaurus* lay dorsal to the foot (Figs 7, 8). Henderson (1999) and Mallison (2014) reconstructed the CoM of *Stegosaurus* and found it to lie just anterior to the foot. Since the method of CoM estimation of Henderson (1999) is the same as ours, differences in the exact location of the CoM are probably related to the differences in the reconstructed musculature in the two models, although our alternative model based on the reconstruction of Paul (1997) finds CoM in a location similar to ours. The CoM of *Stegosaurus* could be interpreted as evidence of bipedality or facultative quadrupedality; however, stegosaurs have never seriously been considered anything but quadrupedal (Owen 1875; Marsh 1877; Gilmore 1914). It has been suggested, however, that stegosaurs could rear on their hind legs, using their tails to balance (the so-called ‘tripodal’ stance [Marsh 1881; Bakker 1978]). A CoM located close to the hips would have allowed them to assume the tripodal posture, and the fact that stegosaurs have a CoM closer to the acetabulum than any other taxon modelled (4% of glenoacetabular distance in our reconstruction) provides some support for this hypothesis. A CoM dorsal to the foot is more reasonably expected in *Scelidosaurus*, a taxon that was presumably close to the transition to quadrupedality from bipedal ancestors in thyreophorans.

The possession of ‘bipedally positioned’ CoMs in quadrupedal thyreophorans suggests that selective pressures other than those related to anterior movement of the CoM caused thyreophorans (or at least stegosaurs) to become quadrupedal. Such selective pressures might include preference for low-browse food stuffs, predator avoidance strategies (keeping the unarmoured ventral surface close to the substrate) or

inter-/intraspecific display behaviours; however, these hypotheses cannot be quantitatively tested using CoM estimations.

The total mass of the dermal armour in the thyreophorans modelled (*Scutellosaurus*, *Scelidosaurus*, *Stegosaurus*, *Euoplocephalus*) was between 3% (*Euoplocephalus*) and 9% (*Stegosaurus*) of total body mass. The CoM of the dermal armour lay posterior to the CoM of the body in *Scutellosaurus*, *Scelidosaurus* and *Stegosaurus*, and very close to the CoM of the body in *Euoplocephalus*. The addition of dermal armour to the body-only reconstructions resulted in small movements of the CoM posteriorly in *Scutellosaurus*, *Scelidosaurus* and *Stegosaurus* and anteriorly in *Euoplocephalus* (Figs 3, 6, 7, 8). Small movements of the CoM posteriorly were also observed in the ‘hybrid’ *Scutellosaurus* models with *Euoplocephalus* and *Stegosaurus* armour, and it was not possible to force *Scutellosaurus* to acquire an anteriorly positioned CoM by the addition of such armour (Fig. 3c–f). It is therefore possible to reject the hypothesis that the development of elaborate plates and hypertrophied spikes in stegosaurs and ankylosaurs caused the CoM to move anteriorly to an extent that might require obligate quadrupedality. Mallison (2014) also found that changes in the arrangement of the dermal armour of the stegosaur *Kentrosaurus* had minimal effect on CoM position.

The original arrangement of osteoderms on *Scutellosaurus* was based on a reconstruction in Colbert (1981), however, the osteoderms were not found in place and the reconstruction is essentially an informed guess. It is worth noting, therefore, that because the total osteoderm mass is only 7% of total body mass in *Scutellosaurus*, changing the arrangement of the armour in this taxon is unlikely to affect CoM position.

407 Sereno et al. (2007) suggested that the large skull size relative to trunk length
408 in ceratopsids may have required them to be quadrupedal, even without the addition
409 of an extensive cranial frill. However, Henderson (1999) suggested that the relatively
410 small contribution made to total body mass by the frill and horns of ceratopsids would
411 have only minor effects on CoM. The addition of a cranial frill and horns to
412 *Psittacosaurus* caused the CoM to move anteriorly by 3% of glenoacetabular distance,
413 but this did result in *Psittacosaurus* gaining a CoM more similar to that of an obligate
414 quadruped than that of a biped (Fig. 4). In order to examine the effect of the frill and
415 horns only, we held the skull size of *Psittacosaurus* constant and only added the frill
416 and horns in proportion to femoral length in our hybrid model. Since skull size is
417 known to increase with positive allometry in ceratopsians (Sereno et al. 2007) it is
418 likely that the addition of a larger skull to the hybrid model would have caused the
419 CoM to move even further anteriorly, reinforcing this result.

420 Association of anterior movement of CoM and the addition of cranial
421 ornamentation provides evidence to support the hypothesis that the development of
422 cranial display and defense structures, in combination with an enlarged skull,
423 provided a selective pressure for the reversion to quadrupedality in ceratopsids. The
424 timing of changes in cranial ornamentation along the ceratopsian stem lineage
425 provides further evidence in support of this hypothesis. The basal ceratopsian
426 *Psittacosaurus* possesses small jugal horns and only a slight elongation of the
427 posterior skull. Its skull/trunk length ratio is 30-39% (Sereno et al. 2007). In
428 *Archaeoceratops*, a basal neoceratopsian, elongation of the back of the skull is
429 increased to form an incipient frill (You and Dodson 2004). These taxa are generally
430 considered to be bipedal (Sereno 1990; Maidment and Barrett 2014). In the
431 neoceratopsian *Leptoceratops*, an incipient frill is present, while the more derived

neoceratopsian *Protoceratops* possesses a fully developed although small frill (You and Dodson 2004), and its skull/trunk length ratio is 41% (not including frill; Sereno et al. 2007). Maidment and Barrett (2014) found that *Leptoceratops* possessed one of five osteological correlates for quadrupedality, while *Protoceratops* possessed two of the five characters used in that study as indicators of quadrupedality. Indeed, Maidment and Barrett (2014) found that quadrupedal characters were acquired in a stepwise fashion along the ceratopsian stem lineage. Sereno et al. (2007) found that skull/trunk length ratios gradually increase along the ceratopsian stem lineage to a maximum of 63% (without frill) in the quadrupedal ceratopsid *Pentaceratops*. The gradual development of cranial ornamentation and large skull size along the ceratopsian stem lineage appears to correlate with the gradual acquisition of quadrupedal characteristics. Based on current evidence, we therefore accept the hypothesis that the structures in ceratopsians resulted in, or at least contributed to, a reversion to quadrupedality.

Despite the convergent acquisition of quadrupedality and the musculoskeletal features associated with it, the selective pressures that led to its evolution in ornithischian dinosaurs were likely to have been different in each clade. The evolutionary driving forces that caused the development of quadrupedality in Ornithopoda and Thyreophora remain elusive, but may have been related to a particular feeding strategy such as a preference for low browse, or changes in gut dimensions and complexity associated with megaherbivory. These hypotheses, however, are difficult to test either qualitatively or quantitatively due to ambiguities in the reconstructions of the relevant soft tissues.

Acknowledgements

SCRM was funded by Natural Environment Research Council grant number NE/G001898/1 awarded to PMB during the course of this work. Thanks to K. T. Bates (University of Liverpool) for discussion. The manuscript was greatly improved by the comments of two anonymous reviewers.

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Figures

Fig. 1 Ornithischian relationships

Fig. 2 Three-dimensional mesh model of *Lambeosaurus* in **a**, dorsal; and **b**, lateral view showing lung volume (dark grey shaded area) and centre of mass (black cross). Similar models were generated for each taxon and hybrid. Scale bar equals 1 m.

Fig. 3 Dorsal (**a**, **c**, **e**) and lateral (**b**, **d**, **f**) outlines of *Scutellosaurus* models showing centre of mass. **a–b**, *Scutellosaurus* model; **c–d**, *Scutellosaurus* reconstructed with the

dermal armour of *Euoplocephalus*; **e–f**, *Scutellosaurus* reconstructed with the dermal
armour of *Stegosaurus*. See text for details of reconstruction methods. **Dermal**
armour CoM, centre of mass of dermal armour only; **Body CoM**, centre of mass of
the body and dermal armour. Scale bars equal to 25 cm.

Fig. 4 Dorsal (**a, c, e**) and lateral (**b, d, f**) outlines of *Psittacosaurus* models showing
centre of mass. **a–b**, *Psittacosaurus* model; **c–d**, alternative reconstruction of
Psittacosaurus from Paul (1997); **e–f**, *Psittacosaurus* reconstructed with the frill and
horns of *Chasmosaurus*. See text for details of reconstruction methods. **Body CoM**,
centre of mass. Scale bars equal to 25 cm.

Fig. 5 Dorsal (a, c, e) and lateral (b, d, f) outlines of *Chasmosaurus* models showing centre of mass. **a–b**, *Chasmosaurus* model; **c–d**, alternative reconstruction of *Chasmosaurus* from Paul (1997); **e–f**, *Chasmosaurus* reconstructed with no frill and horns as in *Psittacosaurus*. See text for details of reconstruction methods. **Body CoM**, centre of mass. Scale bars equal to 100 cm.

Fig. 6 Dorsal (a, c) and lateral (b, d) outlines of *Euoplocephalus* models showing centre of mass. a–b, *Euoplocephalus* model; c–d, alternative reconstruction of *Euoplocephalus* from Paul (1997). See text for details of reconstruction methods.

Dermal armour CoM, centre of mass of dermal armour; **Body CoM**, centre of mass of body plus dermal armour. Scale bars equal to 100 cm.

Fig. 7 Dorsal (a, c) and lateral (b, d) outlines of *Stegosaurus* models showing centre of mass. a–b, *Stegosaurus* model; c–d, alternative reconstruction of *Stegosaurus* from Paul (1997). See text for details of reconstruction methods. **Dermal armour CoM**, centre of mass of dermal armour; **Body CoM**, centre of mass of body plus dermal armour. Scale bars equal to 100 cm.

Fig. 8 Dorsal (a, c) and lateral (b, d) outlines of *Scelidosaurus* models showing centre of mass. **a–b**, *Scelidosaurus* model; **c–d**, alternative reconstruction of *Scelidosaurus* from Paul (1997). See text for details of reconstruction methods. **Dermal armour CoM**, centre of mass of dermal armour; **Body CoM**, centre of mass of body plus dermal armour. Scale bars equal to 50 cm.

Fig. 9 Dorsal (a, c) and lateral (b, d) outlines of *Lambeosaurus* models showing centre of mass. **a–b**, *Lambeosaurus* model; **c–d**, alternative reconstruction of *Lambeosaurus* from Paul (1997). See text for details of reconstruction methods. **Body CoM**, centre of mass. Scale bars equal to 100 cm.

Tables

Table One. Results of the centre of mass modelling. Highlighted in bold are those animals whose CoM position indicates obligate quadrupedality. **CoM**, centre of mass; **CoM % GAD**, centre of mass as a percentage of gleno-acetabular distance.

Model	Body length (m)	Total mass (kg)	CoM (m from end of tail)	CoM % GAD
<i>Chasmosaurus</i>	4.48	1595	2.10	39
<i>Chasmosaurus_Psittaco_frill</i>	4.48	1623	2.14	41
<i>Psittacosaurus</i>	1	8	0.57	28
<i>Psittacosaurus_Chasmo_frill</i>	1	9	0.57	31
<i>Lambeosaurus</i>	6.85	1804	4.37	28
<i>Scutellosaurus</i>	1.09	3	0.74	12
<i>Scutellosaurus_no_armour</i>	1.09	2	0.75	17
<i>Scutellosaurus_Euoplo_armour</i>	1.09	3	0.73	8
<i>Scutellosaurus_Stego_armour</i>	1.09	3	0.75	14
<i>Scelidosaurus</i>	3.52	323	1.99	21
<i>Scelidosaurus_no_armour</i>	3.52	307	1.99	21
<i>Euoplocephalus</i>	5.06	2131	2.84	19
<i>Euoplocephalus_no_armour</i>	5.06	2063	2.84	18
<i>Stegosaurus</i>	5.21	2704	2.92	4
<i>Stegosaurus_no_armour</i>	5.21	2448	3.00	11

Table Two. Results of the sensitivity analysis in comparison with the original results. **CoM**, centre of mass; **CoM % GAD**, location of the CoM as a percentage of glenoacetabular length measured from the acetabulum; **% change in CoM**, Difference in CoM location expressed as a percentage of glenoacetabular length when the results of the sensitivity analysis are compared with the results from our reconstructions. Positive numbers indicate an anterior movement of the CoM relative to our original CoM locations.

Model	Body length (m)	Total mass (kg)	CoM % GAD	% change in CoM
<i>Psittacosaurus</i>	1.66	20.3	30	2
<i>Chasmosaurus</i>	4.38	927	41	3
<i>Scelidosaurus</i>	3.08	114	22	1
<i>Euoplocephalus</i>	6.19	1966	33	14
<i>Stegosaurus</i>	5.74	1821	20	16
<i>Lambeosaurus</i>	8.21	2372	33	4

What drove reversions to quadrupedality in ornithischian dinosaurs?: Testing hypotheses using centre of mass modelling

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Supplementary Information Table S1 – Specimens and literature used for ornithischian dinosaur reconstructions

Taxon	Primary Specimen	Secondary specimens	Literature sources	Notes
<i>Scutellosaurus lawleri</i>	MNA Pl.175		Colbert (1981); Sereno (1991)	Skull size scaled as in <i>Lesothosaurus</i> ; armour placement based on ankylosaurs and stegosaurs
<i>Scelidosaurus harrisonii</i>	NHMUK R1111	Photograph of complete specimen in private collection		
<i>Stegosaurus armatus</i>	USNM 4934	SMA DS-RCR-2003-02	Gilmore (1914)	Size of armour does not include hypothetical horny covering; skull reconstruction by SCRM
<i>Euoplocephalus tutus</i>	NHMUK R5161	ROM 784 (<i>Dyoplosaurus</i>); AMNH 5214 (<i>Ankylosaurus</i>)	Nopcsa (1928); Coombs (1979)	Body shape and armour based on NHMUK R5161; skull size based on <i>Ankylosaurus</i> and scaled relative to femoral length; tail length based on <i>Dyoplosaurus</i>

<i>Lambeosaurus lambei</i>	ROM 1218	ROM 845 (<i>Corythosaurus</i>); TMP 1966.04.01 (<i>Lambeosaurus magnacristatus</i>)	Evans & Reisz (2007)	
<i>Psittacosaurus neimongoliensis</i>	IVPP V120888	IVPP V738 (<i>Psittacosaurus sinensis</i>)		Skull of IVPP V120888 incompletely preserved so size was obtained from IVPP V738 and scaled relative to femoral length
<i>Chasmosaurus belli</i>	ROM 843	CMN 8547 (Chamosaurinae indet.)	Mallon & Holmes (2010)	Skull and limb proportions based on ROM 843; overall body shape informed by CMN 8547

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Supplementary Information Table S2 – Models and hypotheses

Model name	Body length (cm)	Hypothesis to be tested
<i>Scutellosaurus</i>	109	centre of mass
<i>Euoplocephalus</i>	506	centre of mass
<i>Stegosaurus</i>	521	centre of mass
<i>Scelidosaurus</i>	352	centre of mass
<i>Lambeosaurus</i>	685	centre of mass
<i>Psittacosaurus</i>	100	centre of mass
<i>Chasmosaurus</i>	448	centre of mass
<i>Scutellosaurus</i> _no_armour	109	Dermal armour causes centre of mass to move forward
<i>Scutellosaurus</i> _Euoplo_armour	109	Dermal armour causes centre of mass to move forward
<i>Scutellosaurus</i> _Stego_armour	109	Dermal armour causes centre of mass to move forward

<i>Euoplocephalus_no_armour</i>	506	Dermal armour causes centre of mass to move forward
<i>Stegosaurus_no_armour</i>	521	Dermal armour causes centre of mass to move forward
<i>Scelidosaurus_no_armour</i>	352	Dermal armour causes centre of mass to move forward
<i>Psittacosaurus_Chasmo_frigill</i>	100	Development of frill and horns causes centre of mass to move forward
<i>Chasmosaurus_Psittaco_frigill</i>	448	Development of frill and horns causes centre of mass to move forward