Osteological correlates for quadrupedality in ornithischian dinosaurs

SUSANNAH C.R. MAIDMENT and PAUL M. BARRETT

The evolution of quadrupedality from bipedal ancestors is an exceptionally rare transition in tetrapod evolution, but it has occurred several times within the herbivorous dinosaur clade Ornithischia. Stegosauria, Ankylosauria, and Ceratopsidae are all uncontroversially quadrupedal, while basal ornithischians and basal ornithopods are uncontroversially bipedal. However, stance in iguanodontian ornithopods, including the hadrosaurs, and in non-ceratopsid ceratopsians is debated because robust osteological correlates of quadrupedality have not been identified. We examine a suite of characteristics that have been previously proposed as osteological correlates for bipedality or quadrupedality in dinosaurs. These include both discrete anatomical features, which we assess as correlates for quadrupedality using character optimization onto a composite cladogram, and proportional ratios, which we assess as correlates by reconstructing nodal ancestral states using squared-change parsimony, followed by optimization. We also examine the correlation of these features with body size. An anterolateral process on the proximal ulna, hoof-shaped manual unguals, a transversely broadened ilium, a reduced fourth trochanter and a femur longer than the tibia are found to be robust correlates of quadrupedality in ornithischian dinosaurs. Along the ceratopsid "stem" lineage, quadrupedal characters were acquired in a stepwise fashion, with forelimb characters developing prior to changes in the hind limb. In contrast, iguanodontid ornithopods display a mosaic of character states, indicating varying degrees of facultative quadrupedality that probably arose for a variety of different reasons. Hadrosaurs are found to possess all character states associated with quadrupedality and were probably predominantly quadrupedal. In general, quadrupedal ornithischians do not appear to have been constrained by their bipedal ancestry to a particular order of character acquisition.

Key words: Dinosauria, Ornithischia, osteological correlate, quadrupedality.

Susannah C.R. Maidment [s.maidment@imperial.ac.uk], Department of Earth Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom; current address: Department of Earth Science and Engineering, Imperial College, South Kensington Campus, London SW7 2AZ, UK;
Paul M. Barrett [p.barrett@nhm.ac.uk], Department of Earth Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

Introduction

During the entire history of tetrapod evolution, a reversion to quadrupedality from primitively bipedal ancestors has occurred only among the ornithodiran archosaurs (Fig. 1), making it one of the rarest locomotory transitions. Within the herbivorous dinosaur clade Ornithischia, reversions to quadrupedality have occurred on several occasions. While basal ornithischians and the basal-most members of all ornithischian lineages are considered to have been unequivocally bipedal (Galton 1971; Sereno 1991; Senter 2007), eurypodan thyreophorans (stegosaurs and ankylosaurs) and ceratopsids were clearly obligate quadrupeds (e.g., Galton and Upchurch 2004; Dodson et al. 2004) that evolved quadrupedality independently of each other (Figs. 1, 2).

However, debate continues over the stance of iguanodontian ornithopods, which has been controversial since their initial discovery nearly 200 years ago (e.g., review in Norman 1980). Although early workers debated the quadrupedal or bipedal nature of iguanodontians (e.g., Leidy 1858; Cope 1869; Huxley 1870; Dollo 1905), the mounting of *Iguanodon bernissartensis* in the tripodal "kangaroo stance" in the Royal Institute of Natural Sciences, Belgium (Dollo 1883) and the discovery of bipedal dinosaur trackways (e.g., Beckles 1862) led to an early consensus that these dinosaurs were bipedal. Subsequently, Gilmore (1909) and Norman (1980, 1986) both suggested that iguanodontids adopted both bipedal and
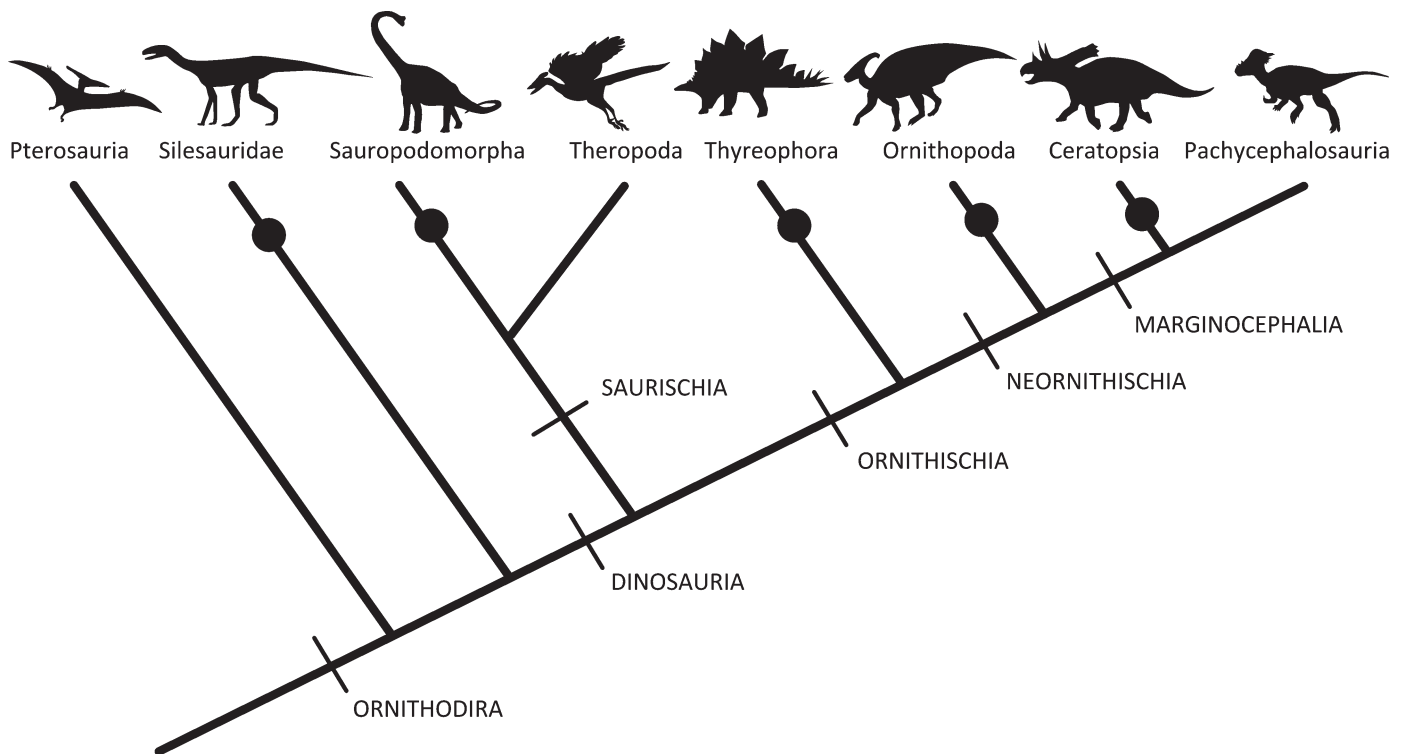
Fig. 1. Simplified relationships of ornithodiran archosaurs showing major clades discussed in the text. Circles on branches indicate clades where secondary quadrupedality has evolved.

quadrupedal stances (facultative quadrupedality), but Galton (1970) argued that hadrosaurs were bipedal. Lockley and Wright (2001) provided evidence for quadrupedality in some Cretaceous ornithopods from numerous quadrupedal ornithopod trackways, and Dilkes (2001) suggested that juvenile hadrosaurs were bipedal but that they adopted a quadrupedal mode of life in adulthood. Carpenter and Wilson (2008) have recently argued that the basal iguanodontian *Uteodon aphanoecetes* was quadrupedal, while Maidment et al. (2012) provided osteological evidence suggesting that hadrosaurs predominantly used their forelimbs for locomotion.

One reason that the determination of stance in iguanodontians is so controversial is that there are no universally agreed osteological correlates of quadrupedality in ornithischians, even though previous workers (Colbert 1964; Galton 1970; Norman 1980; Bonnan 2003; Yates and Kitching 2003; Chinnery 2004; Yates et al. 2010; Maidment et al. 2012) have proposed various characteristics that they considered to be indicative of either bipedality or quadrupedality, but the utility of these features as robust osteological correlates of quadrupedality has never been tested.

Here, we assess the validity of the osteological correlates that have been proposed as indicative of quadrupedality using phylogenetic optimization of discrete osteological characters and ancestral state reconstruction and optimization of continuous characters, including characters dealing with single elements and those comprising ratios between multiple elements. Following the existing consensus, we assume that ceratopsids and eurypodan thyreophorans were obligate quadrupeds, and that basal ornithischians and basal ornitho-

pods ("hypsilophodontids") were bipedal. Finally, we use the resulting character distributions to examine stance in basal thyreophorans, basal ceratopsians and iguanodontians.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; NHMUK, Natural History Museum, London, UK; ROM, Royal Ontario Museum, Toronto, Canada; UALVP, University of Alberta, Calgary, Canada; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Previously-proposed osteological correlates for quadrupedality

Most earlier work has focused on the transition from bipedality in basal saurischians and basal sauropodomorphs to the obligate quadrupedality of eusauropods, via a number of taxa that show the gradual acquisition of "quadrupedal" features (e.g., Bonnan 2003; Yates and Kitching 2003; Yates et al. 2010). Table 1 shows the previously proposed osteological correlates for quadrupedality and the character states used to assess their robustness herein.

Fig. 2. Composite cladogram of ornithischians sampled in this study. → Relationships based on Butler et al. (2008), Brown et al. (2011), Maidment (2010), Farke et al. (2011), McDonald et al. (2010), Prieto-Marquez (2010), Sampson et al. (2010), Sereno (2010), Xu et al. (2010), and Thompson et al. (2012).
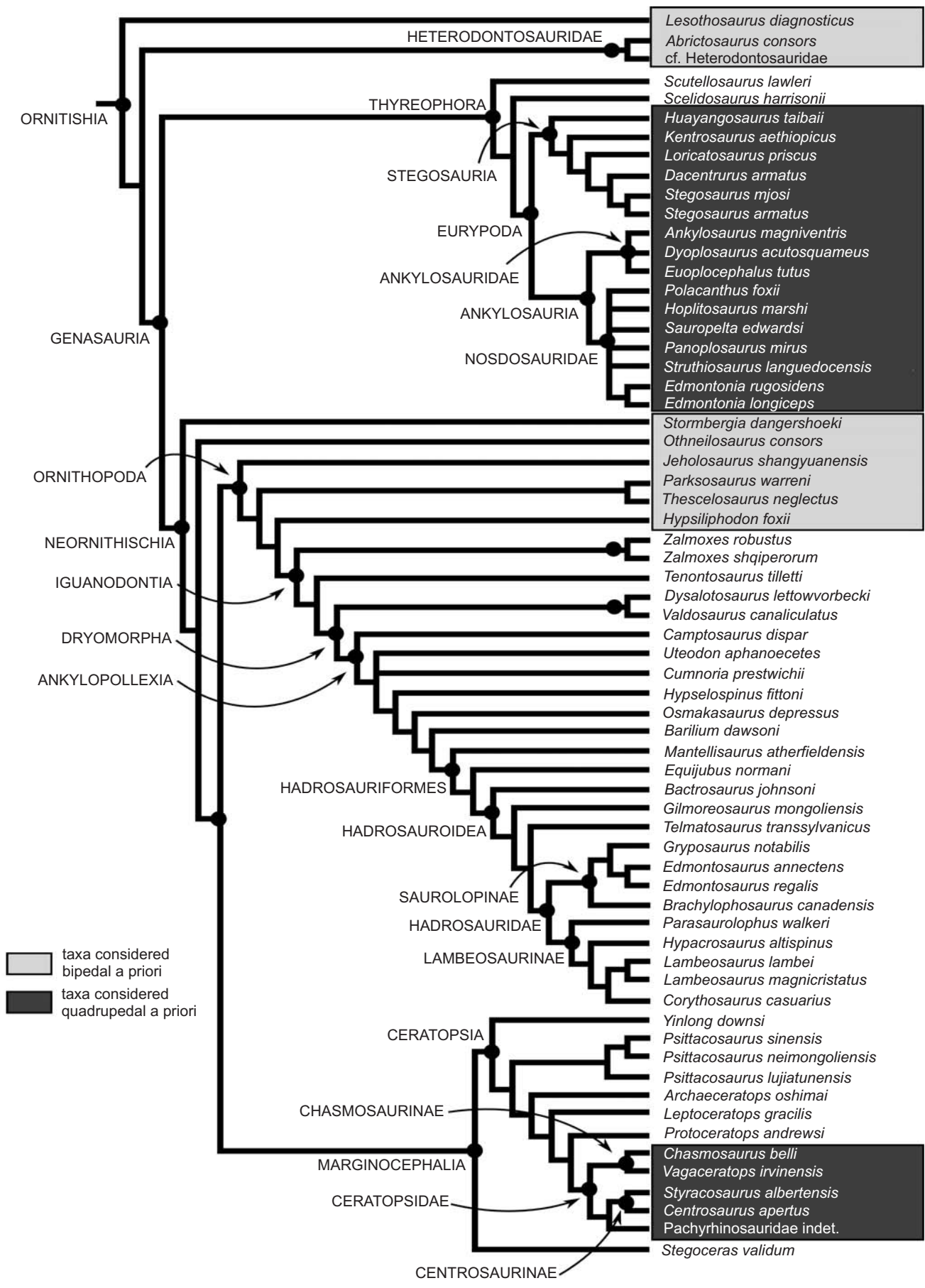
Table 1. Previously proposed osteological correlates for quadrupedality that are assessed herein.

Osteological correlate	Proposed by	Character
Manus of bipeds longer relative to forelimb than in quadrupeds	Colbert (1964); Galton (1970)	metacarpal 3/forelimb length ratio; continuous character
Lower part of forelimb elongate relative to upper part in bipeds but shorter in quadrupeds	Galton (1970)	radius/humerus length ratio; continuous character
Anterolateral process of ulna absent in bipeds but present in quadrupeds	Bonnan (2003); Yates and Kitching (2003); Yates et al. (2010)	lateral process of ulna absent (0); present (1); discrete character
Hoof-like manual unguals present on manus	Galton (1970)	hoof-like manual unguals absent (0); present (1); discrete character
Forelimb shorter relative to hind limb in bipeds than in quadrupeds	Galton (1970); Yates and Kitching (2003); Chinnery (2004); Yates et al. (2010)	forelimb/hind limb length ratio; continuous character
Tibia longer than femur in bipeds but shorter than femur in quadrupeds	Colbert (1964); Galton (1970)	tibia longer than or equal to femur length (0); femur longer than tibia (1); discrete character
Larger fourth trochanter present in bipeds than in quadrupeds	Galton (1970); Yates and Kitching (2003)	fourth trochanter pendant (0); prominent crest but not pendant (1); reduced to a rugose ridge or absent (2); discrete multistate character
Femur bowed in lateral view in bipeds but not in quadrupeds	Chinnery (2004); Yates et al. (2010)	femur, in lateral view: bowed (0); straight (1); discrete character
Pes longer relative to hind limb in bipeds than in quadrupeds	Colbert (1964); Galton (1970); Yates and Kitching (2003)	metatarsal 3/hind limb length ratio; continuous character
Ilium broader in quadrupeds than in bipeds	new character	maximum width of ilium/iliac blade length ratio; continuous character

Several previously proposed osteological correlates were not assessed. Galton (1970) suggested that there were proportional differences between bipeds and quadrupeds, with bipeds having proportionally longer tails relative to trunk length. This character is difficult to implement, however, because apart from hadrosaurids, few ornithischians are preserved well enough for the total trunk and tail lengths to be measured. Galton (1970: 469) also suggested that the lattice of ossified tendons possessed by hadrosaurs strengthened the vertebral column, and was "...undoubtedly an adaptation for bipedal posture...". Since a latticework of ossified tendons is unknown outside Hadrosauroidea (Horner et al. 2004), but bipedality was the basal condition for Ornithischia, this character is clearly not required for bipedal locomotion. Norman (1986) suggested that the fusion of the scapula and coracoid was a feature commonly observed in quadrupeds. However, this characteristic varies intraspecifically and is probably related to ontogeny (SCRM, personal observations 2004–2010), so is not a robust character for assessing quadrupedalism. Norman (1986) also suggested that quadrupeds possessed more robust sternals than bipeds. However, sternal elements are unknown in basal ornithischians (Norman et al. 2004a) and basal thyreophorans (Norman et al. 2004b). Only one element tentatively identified as a sternal has ever been found associated with a stegosaur (Galton and Upchurch 2004; SCRM personal observations 2003–2007), and sternals are poorly known in ankylosaurs (Vickaryous et al. 2004). As the morphology of the sternals is therefore unknown in most ornithischians, this character is not useful for assessing stance.

Yates and Kitching (2003) and Yates et al. (2010) identified two features as indicators of quadrupedalism in sauropodomorphs. Yates and Kitching (2003) suggested that a facet on the distal radius for articulation with the ulna was present in quadrupeds but not in bipeds. However, such a feature is present on a wide variety of ornithischians, including basal ornithopods (e.g., *Hypsilophodon*, NHMUK R196), basal iguanodontids (e.g., *Camptosaurus*, USNM 4282), thyreophorans (e.g., *Euoplocephalus*, AMNH 5337; *Stegosaurus* USNM 4937), ceratopsians (e.g., *Protoceratops*, AMNH 6424; *Chasmosaurus*, ROM 839) and hadrosaurs (e.g., *Brachylophosaurus*, CMN 8893). Yates et al. (2010) further suggested that the lesser trochanter was rotated to be visible in lateral view in quadrupedal sauropodomorphs, but in ornithischians the lesser trochanter is visible in lateral view in all taxa examined (Supplementary Online Material available at http://app.pan.pl/SOM/app59-Maidment_Barrett_SOM.pdf : SOM 1: table S1). As these characters are widespread in both bipedal and quadrupedal ornithischians, they do not constitute osteological correlates for quadrupedality in this clade, although they may still represent robust correlates for quadrupedalism in Sauropodomorpha.

While examining the appendicular elements of a wide range of ornithischian dinosaurs (SOM 1: table S1), it was noted that iliac width varied considerably between clades. The dorsal margin of the ilium is folded laterally in eurypodan thyreophorans, so that the broadest surface of the ilium faces ventrally rather than laterally (Coombs 1978a) and a similar situation occurs in ceratopsids. Some iguanodontian ornithopods and hadrosaurs also bear a variably developed laterally everted dorsal margin of the ilium (sometimes termed the "antitrochanter"). This relative width of the ilium is therefore proposed as a potential new osteological correlate for quadrupedality herein, and is assessed alongside the previously proposed correlates.

Material and methods

The appendicular elements of specimens from 59 species of ornithischian dinosaurs, representing members of all clades, were examined first-hand (SOM 1: table S1) and measured using a tape measure for elements over 200 mm, and callipers for elements smaller than 200 mm (for measurements see SOM 2). In order to limit investigator bias, only measurement data collected first-hand was used. The measurements of left and right elements for a specimen were averaged. Deformed specimens were disregarded. Any specimen less than 50% the size of the largest individual of the same species was removed from the dataset to limit scaling differences that may have occurred through ontogeny. Where more than one specimen for a species was measured, species values were averaged. Additional information on the presence/absence of discrete characters was supplemented using the literature.

Optimization.—In order to optimize characters, a composite cladogram of ornithischians was built (Fig. 2). General relationships between ornithischian clades follow Butler et al. (2008). Relationships within more exclusive clades are taken from the following works, which represent the most recently published and complete phylogenies containing the taxa we sampled: Ankylosauria, Thompson et al. (2012); Stegosauria, Maidment (2010); non-iguanodontid ornithopods ("hypsilophodontids"), Brown et al. (2011); non-hadrosaurid iguanodontids, McDonald et al. (2010); Hadrosauridae, Prieto-Marquez (2010); non-ceratopsid ceratopsians, Sereno (2010); Xu et al. (2010); Centrosaurinae, Farke et al. (2011); Chasmosaurinae, Sampson et al. (2010). These phylogenies are generally complementary and taxa do not overlap between them. *Lesothosaurus diagnosticus* is generally considered to be the most completely known basal ornithischian (e.g., Thulborn 1971; Sereno 1991, 1999) and so is commonly used as the basal ornithischian outgroup in phylogenetic analyses of ornithischian clades (e.g., Maidment et al. 2008; McDonald et al. 2010; Thompson et al. 2012). In recent phylogenetic analyses that include a range of basal ornithischian taxa, however, *Lesothosaurus* has proven unstable. Butler et al. (2008) resolved it as a basal thyreophoran, while Butler et al. (2010) found it to be the most basal neornithischian. This instability is to be expected in a taxon that possesses few unique character states but shares numerous plesiomorphies with several other ornithischian lineages, representing what amounts to an "ancestral" condition. The phylogenetic relationships of Heterodontosauridae are also controversial (see Butler et al. 2008 for a review). On the basis of current evidence, we consider that *Lesothosaurus* represents the most basal well-known ornithischian, and this is reflected in its basal placement in our composite cladogram, in what we believe represents a consensus view.

Taxa were placed in one of three groups a priori (Fig. 2). Stegosaurs, ankylosaurs, and ceratopsids were designated as unambiguously quadrupedal. Uncontroversial bipeds include the basal ornithischians *Lesothosaurus* and *Abrictosaurus* and non-iguanodontian ornithopods (commonly referred to as "hypsilophodontids"). Stance in all of the other taxa considered was designated as unknown. Although taxa placed in our uncontroversial quadrupedal and uncontroversial bipedal groups have never been seriously considered to have had any other stance, we admit that there is some circularity in our methods. Their stance was originally determined because of their osteology, possibly including some of the features we assess as correlates herein. However, we consider that the consistency of the sets of osteological characteristics that allow these taxa to be confidently placed in one group or the other is such that our method is validated. Furthermore, the presence of a centre of mass anterior to the hips, only possible in an obligate quadruped, has been confirmed using mathematical modelling in ceratopsids (Henderson 1999), validating their placement in the uncontroversial quadrupedal group. It is not possible to appeal to characteristics present in extant animals for which stance is known, because both extant bipeds and quadrupeds have quadrupedal ancestors, whereas bipedal and quadrupedal dinosaurs had bipedal ancestors. The bauplan of bipedal dinosaurs is very different from that of extant bipeds. For example, dinosaurs possessed a muscular tail along which the femoral extensor musculature originated. Extant mammalian bipeds do not possess a muscular tail, and the locomotor musculature is arranged differently.

Discrete characters (Table 1) were optimized onto the composite cladogram (Fig. 2) using MacClade v.4.06 (Maddison and Maddison 2003). Branch lengths were equal throughout. Unambiguous optimization was used because it is the most conservative approach and does not assume a model for transformations, and because our composite phylogeny contains soft polytomies, which are problematic for ACCTRAN or DELTRAN optimization (Maddison and Maddison 2003).

The ancestral states of continuous characters were reconstructed and optimized using squared-change parsimony (Maddison 1991) implemented in MacClade v.4.06. In order to reconstruct character states at ancestral nodes, the dataset must be complete and the tree must be either fully resolved or contain only hard polytomies. The composite phylogeny was therefore pruned to leave only those taxa for which we had data for each character. The resulting trees did not possess any soft polytomies for any of the characters, with the exception of the pruned tree for iliac width/iliac blade length. In this tree, two soft polytomies (within Ankylosauridae and between *Cumnoria* and *Uteodon*) were present, and were resolved using all possible solutions. Using different solutions to resolve the polytomies resulted in no change to the overall optimization patterns, however.

Body size.—Taxa in the "bipedal" category are much smaller than those in the "quadrupedal" category, and there is no overlap in femoral length between these two groups: the femoral length of the bipeds ranges from 77 mm (in *Abrictosaurus*) to 265 mm (in *Parksosaurus*), while the femoral length

of the quadrupeds ranges from 535 mm (in *Dyoplosaurus*) to 1250 mm (in *Dacentrurus*). The "unknown" group of taxa, however, overlaps in femoral length with both bipeds and quadrupeds, with femoral lengths ranging from 63.1 mm (in *Psittacosaurus lujiatunensis*) to 1252.5 mm (in *Edmontosaurus regalis*). Because of the lack of overlap between bipedal and quadrupedal size ranges (at least in terms of femoral length), it is extremely difficult to tease apart the possible effects of body size on the presence/absence or relative development of the osteological correlates for quadrupedality.

Body size is sometimes considered to be causative factor in the evolution of ornithischian quadrupedalism, presumably because many quadrupedal ornithischians are at the larger end of the size spectrum occupied by the clade (Hutchinson 2005). However, there is no a priori reason to consider size a causative mechanism in the evolution of quadrupedality (Maidment and Barrett 2012). Geometrically scaling the smallest, bipedal ornithischians to the size of the largest quadrupedal ornithischians has no effect on centre of mass because the mass distribution around the hips would remain the same. Although mass increases with the cube of length, large animals are able to retain similar bone safety factors as small animals using reorientation of the limbs to become more columnar and changes in bone curvature (Biewener 1989; Carrano 2001). Size increase alone cannot therefore account for the evolution of quadrupedality in ornithischians, and it is reasonable to conclude that osteological changes associated with the evolution of quadrupedalism would not necessarily correlate with size. However, because of the lack of overlap in size between the bipedal and quadrupedal groups used in this study, it is possible that some of the previously proposed osteological correlates for quadrupedality are actually associated with large size, and these characters would display the same distribution on the composite cladogram as characters associated with quadrupedality.

In order to assess the impact of body size on the osteological correlates, continuous character states were regressed against measures of body size. For the forelimb characters, femoral length was used as a measure of body size, while for hind limb characters, humeral length was used as a measure of body size. The character forelimb length/ hind limb length ratio was regressed both against femoral and humeral length. Although it is expected that some degree of autocorrelation would occur because humerus length contributes to forelimb length, while femur length contributes to hind limb length, this is unavoidable because few ornithischian specimens are complete enough to use measures of body size such as body length, and mass estimations in any extinct taxon are problematic due to unknown soft tissue parameters (e.g., Alexander 1985; Henderson 1999; Bates et al. 2009a, b; Campione and Evans 2012; Sellers et al. 2012).

Femur and humerus lengths were log-transformed, and regressions were carried out in PAST (v. 2.09; http://folk.uio.no/ohammer/past; Hammer et al. 2001). Reduced major axis (RMA) regression was used because error is present in both the X and Y variables. A p value of less than 0.05 was considered to represent a statistically significant correlation between the X and Y variables.

The influence of body size on the qualitative characters were addressed by plotting the absence/presence data against femoral length. The degree of size overlap of the taxa with the "absent" character state and those with the "present" character state was calculated as a percentage of the femoral length range of the sample.

Results

Manus/forelimb length ratio.—A short manus relative to forelimb length was considered to be characteristic of quadrupeds by Colbert (1964) and Galton (1970). The complete manus is rarely preserved in ornithischians, so this character was assessed by reconstructing ancestral states and optimizing the metacarpal 3 length/radius+humerus length ratio as a continuous character in order to maximize sample sizes (Table 2; SOM 1: fig. S1). If correct, a high ratio would be expected in bipeds and a low ratio in quadrupeds. The ancestral value of the metacarpal 3/forelimb ratio for the base of Ornithischia is 0.14. The reconstructed ratio for the basal node in Stegosauria is decreased from the primitive ornithischian value to 0.113, but that for ankylosaurs remains at 0.14. The ancestrally reconstructed ratio is slightly increased in centrosaurines (0.159) and chasmosaurines (0.153), though the value for the ceratopsid node (0.148) is intermediate between those for the primitive ornithischian and chasmosaurine/centrosaurine nodes. Reconstructed values for nodes among non-hadrosaurid ornithopods and non-ceratopsid ceratopsians are similar to or lower than that at the base of Ornithischia (0.11–0.14), while much higher values are observed at the base of Hadrosauridae (0.172) and within both hadrosaurid clades (0.19–0.22). Metacarpal 3 is not consistently more elongate in bipeds than it is in quadrupeds, so this character is rejected as an osteological correlate for ornithischian quadrupedality. In contrast, elongation of the manus appears to be a feature unique to Hadrosauridae and may be an autapomorphy of the clade. Some elongation of the manus also occurs in ceratopsids, although not to the same degree as in hadrosaurs.

Radius/humerus length ratio.—Galton (1970) suggested that quadrupeds had shorter forelimb epipodials relative to propodial length than bipeds. This feature was assessed by reconstructing ancestral states and optimizing the radius length/humerus length ratios (Table 2; SOM 1: fig. S2). Bipeds would be expected to have higher ratios, while quadrupeds would have lower ratios if correct. The ancestral reconstructed value for this ratio at the base of Ornithischia was 0.631. Bipedal ornithischians had ratios ranging from 0.61 (*Lesothosaurus*) to 0.78 (*Hypsilophodon*). Basal nodes within Stegosauria and Ankylosauria have ratios that are slightly higher than the basal ornithischian condition (0.66 and 0.637 respectively), as does the node uniting these two

Table 2. Reconstructed ancestral states for continuous characters using squared-change parsimony. Abbreviations: Fore/hind, forelimb length/hind limb length ratio; IW/IBL, iliac width/iliac blade length ratio; MC3/fore, metacarpal 3 length/forelimb length ratio; MT3/hind, metatarsal 3 length/hind limb length ratio; R/H, radius length/humerus length ratio.

Node	MC3/Fore	R/H	Fore/hind	MT3/hind	IW/IBL
Ornithischia	0.14	0.63	0.48	0.26	0.09
Heterodontosauridae+Genasauria	0.15	0.65	0.50	0.25	0.13
Heterodontosauridae					0.07
Genasauria	0.13	0.66	0.55	0.21	0.22
Thyreophora				0.18	0.43
Eurypoda	0.13	0.65	0.62	0.13	0.65
Stegosauria	0.11	0.66			0.86
Stegosaurus+Dacentrurus					0.77
Stegosaurus		0.67	0.59		0.72
Ankylosauria	0.14	0.64			0.65
Ankylosauridae					0.66
Euoplocephalus+Ankylosaurus					0.85
Nodosauridae		0.64		0.13	0.66
Struthiosaurus+Edmontonia					0.61
Cerapoda					0.12
Othnielosaurus+Neornithischia				0.21	0.08
Neornithischia	0.13	0.67	0.53	0.22	0.08
Ornithopoda	0.12	0.73		0.23	0.05
Iguanodontia+*Hypsilophodon+Parksosaurus*				0.22	0.05
Iguanodontia+*Hypsilophodon*					0.05
Iguanodontia	0.13	0.75	0.58		0.05
Dryomorpha				0.23	0.07
Ankylopollexia	0.14	0.72	0.56	0.21	0.08
Hadrosauriformes+*Barilium+Hypselospinus+Cumnoria+Uteodon*		0.75	0.59		0.13
Hadrosauriformes+*Barilium+Hypselospinus+Cumnoria*					0.08
Hadrosauriformes+*Barilium+Hypselospinus*					0.08
Hadrosauriformes+*Barilium*					0.08
Hadrosauriformes				0.20	0.12
Hadrosauroidea					0.19
Hadrosauridae	0.17	0.91	0.58	0.19	0.20
Saurolophinae	0.19	1.00		0.18	
Gryposaurus+Edmontosaurus	0.21	0.94	0.57	0.17	
Lambeosaurinae	0.19	0.96			
Hypacrosaurus+Lambeosaurus+Corythosaurus	0.20	1.09	0.57	0.19	
Lambeosaurus+Corythosaurus	0.21	1.13	0.57	0.18	0.21
Lambeosaurus				0.17	
Marginocephalia		0.61	0.45	0.22	0.09
Ceratopsia	0.13	0.58	0.50		0.08
Ceratopsidae+*Protoceratops+Leptoceratops+Archaeoceratops+Psittacosaurus*	0.13	0.62	0.59	0.21	0.07
Psittacosaurus	0.13	0.64	0.62	0.23	0.05
P. sinensis+P. neimongoliensis				0.23	0.04
Ceratopsidae+*Protoceratops+Leptoceratops+Archaeoceratops*					0.07
Ceratopsidae+*Protoceratops+Leptoceratops*	0.13	0.63	0.64	0.19	
Ceratopsidae+*Protoceratops*	0.13	0.61	66.00		0.12
Ceratopsidae	0.15	0.54	0.67		0.25
Chasmosaurinae	0.15	0.53	0.70		
Centrosaurinae	0.16	0.48		0.14	0.29
Styracosaurus+Centrosaurus		0.57	0.64		

clades (Eurypoda: 0.61), but all of these values are within the range occupied by bipedal taxa. The basal margino-cephalian nodal value was slightly lower than the basal ornithischian nodal value (0.609) and the basal ceratopsian nodal value was lower still (0.581). However, along the ceratopsian lineage leading to ceratopsids, radius/humerus length ratios increased slightly to overlap and lie partially within the range displayed by bipedal taxa (reconstructed values for taxa and nodes from 0.612–0.67). This trend reverses at the base of Ceratopsidae, which has a lower reconstructed value (0.539) than the basal ceratopsian condition, which is reduced further in Centrosaurinae (0.476) and Chasmosaurinae (0.53). Non-hadrosaurid ornithopod taxa and nodes along the hadrosaurid "stem" lineage have values (0.63–0.80) that are higher than that for the basal ornithischian node, but that lie within or above the range displayed by unambiguous bipeds. Hadrosaurids possessed high ratios and high ancestrally reconstructed nodal values, with a basal value of 0.96 (this value effectively retained at the base of Lambeosaurinae, 0.964) and a nodal value for saurolophines of 1.004.

Uncontroversial bipeds do not possess higher radius/humerus length ratios than uncontroversial quadrupeds, so this character can be rejected as a correlate for ornithischian quadrupedality. The possession of very high ratios is unique to hadrosaurs and may be autapomorphic for the clade. Elongate lower limbs may be an adaptation to quadrupedalism unique to hadrosaurs, enabling the forelimbs to touch the ground. The possession of low ratios is found only in ceratopsids.

Anterolateral process on the ulna.—Bonnan (2003), Yates and Kitching (2003) and Yates et al. (2010) suggested that an anteriorly directed lateral process of the ulna indicated quadrupedality. This feature was optimized as a discrete character (Fig. 3). An anterolateral process on the ulna is optimized as being absent in all unambiguous bipeds, but is present in eurypodan thyreophorans and ceratopsids. The feature also optimizes as being present in all ornithopods more derived than *Zalmoxes*, with reversals in *Dysalotosaurus* and *Uteodon* among ornithopods. It is also present in the neoceratopsian *Protoceratops*. The anterolateral process on the ulna is present in quadrupeds but not in bipeds, and therefore appears to be a potentially robust correlate for ornithischian quadrupedality based on optimization alone.

In our sample there is only a 9% overlap in the total femoral length range between taxa in which the ulna anterolateral process in present and those in which it is absent (Fig. 4A). There therefore appears to be some correlation with large size and the presence of the anterolateral process on the ulna, based on our sample.
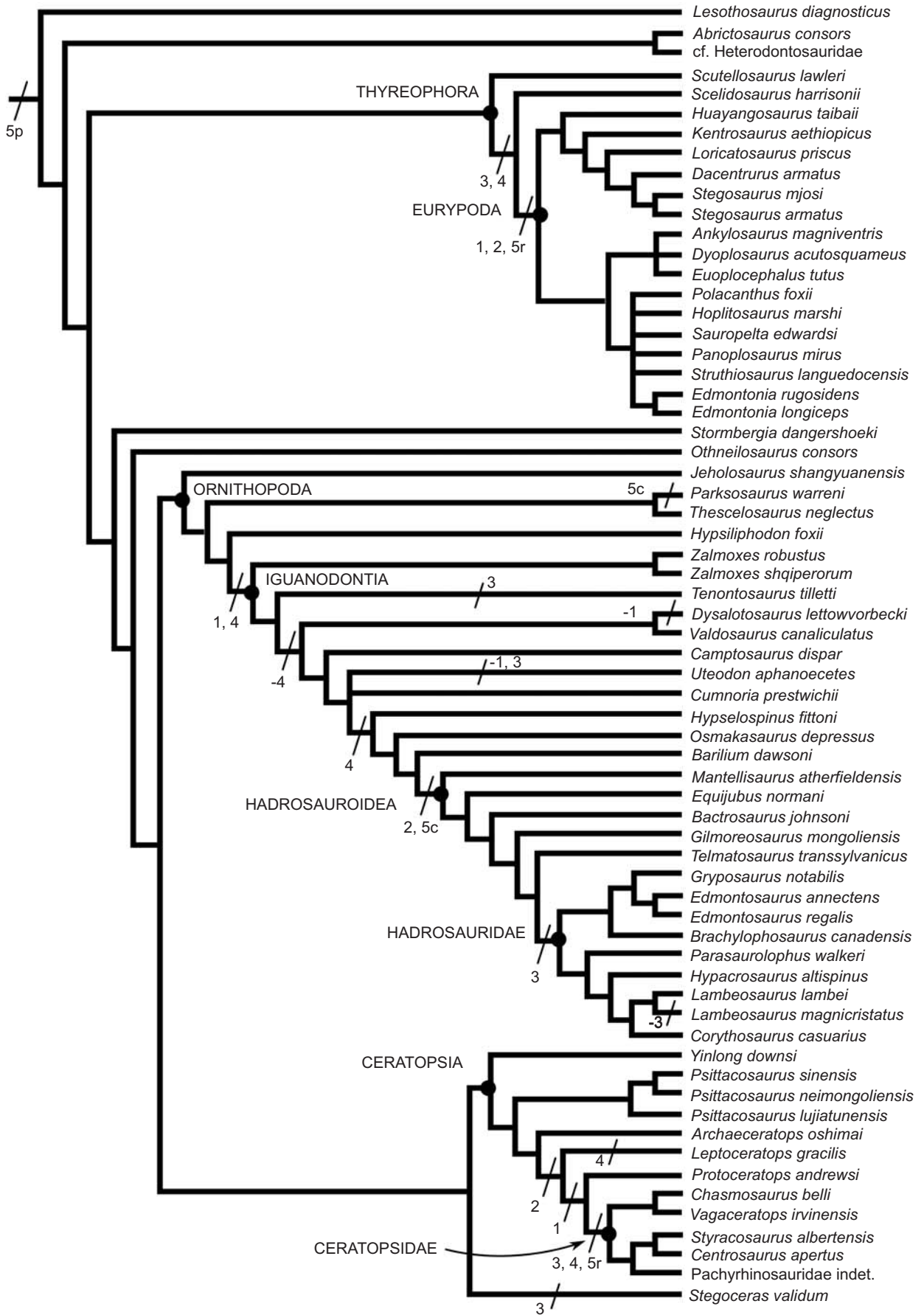
Hoof-like manual unguals.—The presence of hoof-like unguals on the manus is thought to indicate quadrupedality (e.g., Galton 1970; Norman 1986). This feature was scored as a discrete character (Fig. 3). Hoof-like manual unguals are absent in unambiguously bipedal taxa, but are present in all eurypodan thyreophorans, ceratopsids, the basal neoceratopsians *Leptoceratops* and *Protoceratops*, and in all ornithopods more derived than *Mantellisaurus*. Hoof-like manual unguals are present in unambiguous quadrupeds, but absent in unambiguous bipeds. This character therefore represents a potentially robust correlate for ornithischian quadrupedality based on optimization alone.

In our sample there is a 16% overlap in the total femoral length range between taxa that possess hoof-shaped manual unguals and those that do not (Fig. 4B). There therefore appears to be some correlation between large size and hoof-like manual unguals.

Forelimb/hind limb length ratio.—Several authors have proposed that bipeds have shorter forelimbs than quadrupeds (e.g., Galton 1970). This was assessed by reconstructing ancestral states and optimizing the ratio between humerus+radius length/tibia+femur length (Table 2; SOM 1: fig. S3). This suggestion implies that bipeds should exhibit low ratios, while those of quadrupeds should be higher. The ancestral reconstructed value for the basal ornithischian node is 0.476. Unfortunately, there are no "hypsilophodontids" in our sample that possess complete fore- and hind limbs, so the bipedal values are based only on character states for *Lesothosaurus* (0.45) and *Abrictosaurus* (0.48). Eurypodan thyreophorans possessed higher reconstructed values than either those for the basal ornithischian node or for bipeds (a basal eurypodan nodal value of 0.617 and other eurypodan nodes and taxa with values in the range 0.592–0.71), as did ceratopsids (0.668 for the ceratopsid basal node; 0.643 for centrosaurines; 0.699 for chasmosaurines). The nodal value for Marginocephalia (0.447) is slightly lower than the basal ornithischian condition, but lies within the range occupied by unambiguous bipeds, whereas the pachycephalosaur *Stegoceras* possesses a very low value (0.31). Forelimb elongation relative to hind limb length appears to have occurred in a stepwise fashion along the ceratopsian "stem" lineage, with the high values observed in ceratopsids being the culmination of this trend. Sampling among ornithopods is inadequate to derive a full picture of the distribution of forelimb/hind limb ratios, but ratios in all taxa and reconstructed values at nodes (0.5–0.67) are greater than those for the unambiguously bipedal taxa. However, given the absence of unambiguously appropriate data from bipedal basal ornithopods, it is not clear whether this difference is genuine or simply reflects missing data.

Forelimb elongation relative to hind limb length is present in all quadrupedal ornithischians and is absent in our

Fig. 3. Discrete character optimization shown on the composite ornithischian cladogram. 1–5 indicate presence of derived character states; -1 to -5 indicate →
secondary loss of derived character states. The basal ornithischian condition is absence for characters 1–4 and 5p for character 5. Abbreviations: 1, anterolateral process on ulna present; 2, hoof-like manual ungual phalanges present; 3, femur longer than tibia present; 4, femur straight in lateral view present; 5p, fourth trochanter pendant; 5c, fourth trochanter reduced to a crest; 5r, fourth trochanter reduced to a rugose ridge or absent.
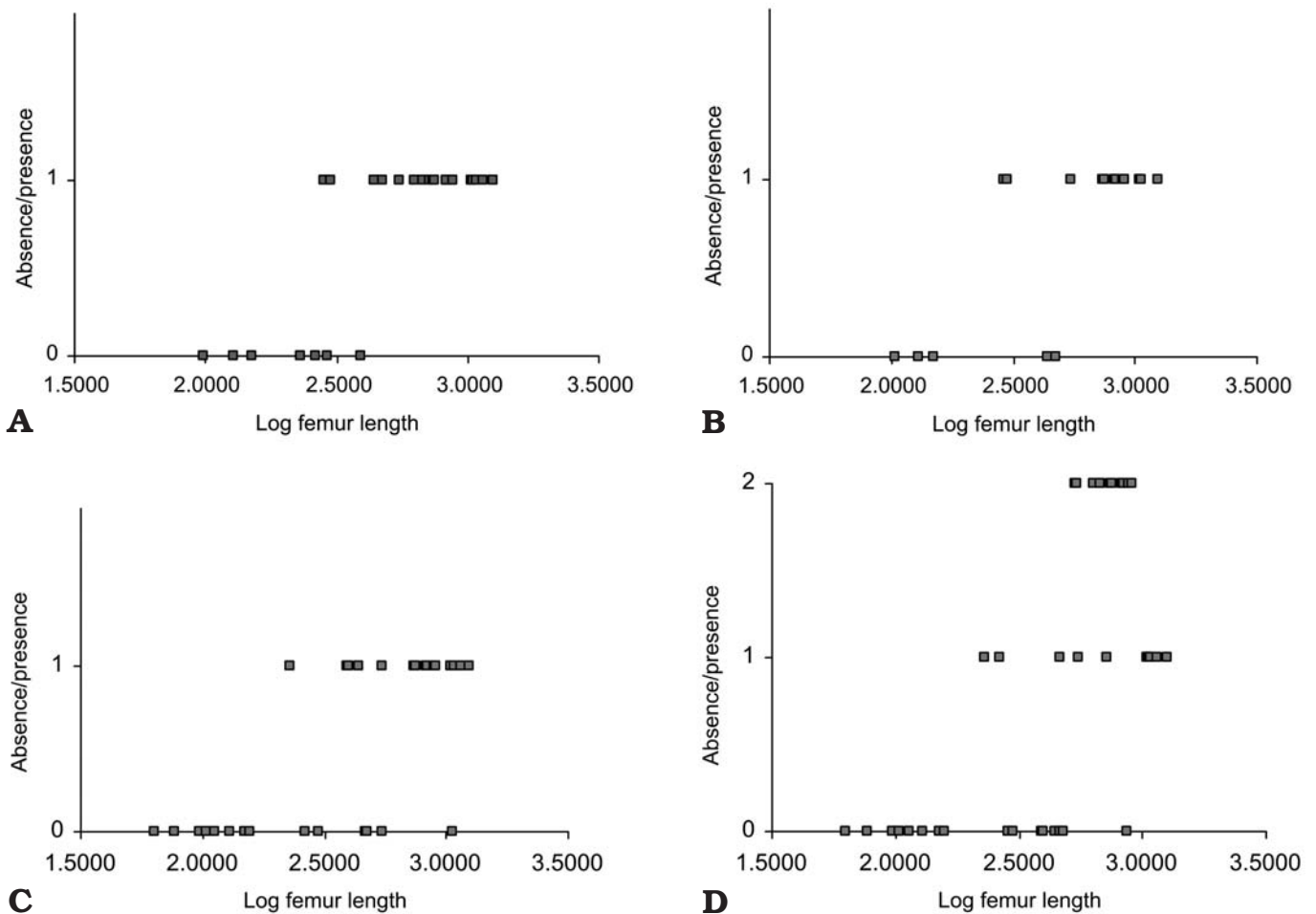
Fig. 4. Correlations between body size (using femoral length as a proxy) and discrete characters. **A**. Anterolateral process on proximal ulna. **B**. Manual unguals. **C**. Femur longer than tibia. **D**. Fourth trochanter morphology. For A–C, 0, feature absent; 1, feature present; for D, 0, fourth trochanter pendant; 1, fourth trochanter reduced to crest; 2, fourth trochanter reduced to rugose ridge or absent.

small sample of unambiguous bipeds. However, forelimb elongation appears to have occurred in all genasaurians, and sample sizes are rather small to robustly assess whether this character is an osteological correlate of ornithischian quadrupedality. It is also difficult to assess whether the forelimb/hind limb ratio is correlated with large size, because we lack an independent metric of body size in our sample, and generally use either femur length or humerus length as a proxy.

Femur length > tibia length.—Bipeds generally have longer tibiae than femora, while quadrupeds show the opposite (Colbert 1964; Galton 1970). This feature was optimized as a discrete character (Fig. 3). All unambiguous bipeds optimize as having a tibia that is longer than the femur, while the unambiguous quadrupeds (ceratopsids, stegosaurs, and ankylosaurs) all have a femur that is longer than the tibia. The basal thyreophoran *Scelidosaurus* and the pachycephalosaur *Stegoceras* also possess a femur that is longer than the tibia. Among ornithopods, the basal iguanodontids *Tenontosaurus* and *Uteodon* both possess femora longer than tibiae, as do

all hadrosaurs except *Lambeosaurus magnicristatus*, whose femur and tibia are of equal length: the latter optimizes as an autapomorphic reversal within Hadrosauridae.

The presence of a femur that is longer than the tibia is absent in all unambiguous bipeds and present in all unambiguous quadrupeds, and therefore appears to be a potentially robust osteological correlate for ornithischian quadrupedality based on optimization alone.

In our sample there is a 70% overlap in the total femoral length range between taxa that possess a femur longer than the tibia and those that do not (Fig. 4C). There is therefore little correlation between body size and relative femur: tibia length, based on our sample.

Fourth trochanter reduction.—A large fourth trochanter has been suggested as a feature of bipeds (Galton 1970; Yates and Kitching 2003). Ornithischians possess a variety of fourth trochanter morphologies, so this feature was assessed as a correlate for quadrupedality by coding it as a discrete character with three states, allowing the variation

in fourth trochanter morphology to be optimized (Table 1, Fig. 3). All unambiguous bipeds except *Parksosaurus* possess a pendant fourth trochanter. The loss of this structure in *Parksosaurus* optimizes as an autapomorphic reversal. In ceratopsids and eurypodan thyreophorans, the fourth trochanter is either reduced to a rugose ridge or absent. *Parksosaurus, Stegoceras* and all ornithopods more derived than *Mantellisaurus* have a fourth trochanter that is not pendant, but is a prominent crest.

Reduction of the fourth trochanter does not occur in any unambiguous biped, but is present in all unambiguous quadrupeds, and is therefore a potentially robust correlate for ornithischian quadrupedality based on optimization alone.

In our sample there is a 54% overlap in the total femoral length range between taxa that possess a pendant fourth trochanter and those that do not (Fig. 4E). There is therefore little correlation between body size and reduction of the fourth trochanter, based on our sample.

Femur bowed in lateral view.—Chinnery (2004) and Yates et al. (2010) suggested that the femur was bowed in lateral view in bipeds, but straight in lateral view in quadrupeds. This feature was optimized as a discrete character (Fig. 3). The femur is bowed in lateral view in all unambiguous bipeds, and straight in lateral view in unambiguous quadrupeds (ceratopsids and eurypodan thyreophorans). The femur is also straight in lateral view in the basal thyreophoran *Scelidosaurus* and the neoceratopsian *Leptoceratops*. Among ornithopods, a femur with a shaft that is straight in lateral view is present in *Zalmoxes, Tenontosaurus* and all ornithopods more derived than *Hypselospinus*. Consequently, it appears that possession of a femur with a shaft that is straight in lateral view is a potentially robust osteological correlate for ornithischian quadrupedality based on optimization alone.

In our sample there is a 16% overlap in the total femoral length range between taxa that possess a femur that is bowed in lateral view and those that do not. There therefore appears to be some correlation between body size and the possession of a femur that is bowed in lateral view.

Pes/hind limb length ratio.—Bipedal taxa have been noted to have longer feet relative to hind limb length than quadrupeds (Colbert 1964; Galton 1970; Yates and Kitching 2003). This character was assessed by reconstructing ancestral states and optimizing the metatarsal 3 length/ femur+tibia length ratio as a continuous character in order to maximize sample size (Table 2; SOM 1: fig. S5). This form of the character implies that bipedal taxa should have higher ratios than quadrupeds. The basal nodal value for Ornithischia is 0.264. Unambiguously bipedal taxa have values that vary from 0.22 (*Parksosaurus*) to 0.28 (*Lesothosaurus*), with the non-iguanodontian ornithopods displaying lower ratios than the basal ornithischians. The reconstructed ratio is reduced to a nodal value of 0.13 in eurypodan thyreophorans, with a particularly low ratio of 0.08 in *Stegosaurus mjosi*. Reconstructed values and actual values are also reduced in ceratopsids, which

possess a reconstructed basal nodal value of 0.137, although sample sizes are very low in all quadrupedal clades (one stegosaur, two ankylosaurs and two ceratopsids). In the basal thyreophoran *Scelidosaurus*, the metatarsal 3/hind limb ratio is reduced to 0.19, while the ratios in non-ceratopsid marginocephalians and the reconstructed nodal values in these parts of the marginocephalian tree (0.213–0.23) are within the range of unambiguously bipedal taxa. A reduction in the metatarsal 3/hind limb ratio occurs along the ornithopod lineage, culminating in reconstructed nodal values of 0.184 in saurolophines and 0.187 in lambeosaurines, although the non-hadrosaurid iguanodontian sample size is small (three taxa).

The pes/hind limb ratio is reduced in all unambiguous quadrupeds relative to the condition in unambiguous bipeds, and is therefore considered a potentially robust correlate of ornithischian quadrupedality based on optimization alone. However, a relatively good correlation between pes/hind limb ratio and humerus length (as a measure of body size) is found: coefficient of determination (r^2) = 0.664; p<0.001 (Fig. 5A). These results suggest a relatively good correlation between pes/hind limb ratio and body size in ornithischians.

Iliac width/iliac blade length ratio.—Here, we suggest that the ilium is transversely broader in quadrupedal taxa than in bipedal taxa (new character). This was assessed by reconstructing ancestral states and optimizing the maximum iliac width/iliac blade length ratio (Table 2; SOM 1: fig. S4). Iliac blade length is measured from the point where the preactabular process joins the pubic peduncle. This ratio should be lower in bipeds that in quadrupeds. The reconstructed basal ornithischian nodal value for iliac width/iliac blade length is 0.095. Values possessed by unambiguously bipedal taxa range from 0.03 (*Jeholosaurus*; c.f. Heterodontosauridae) to 0.06 (*Lesothosaurus, Othnielosaurus*). In eurypodan thyreophorans, the ratio is greatly increased to a reconstructed nodal value of 0.863 for stegosaurs and 0.654 for ankylosaurs. In ceratopsids the ratio also increases, with a reconstructed nodal value of 0.246 for Ceratopsidae. The basal thyreophoran *Scelidosaurus* has a ratio intermediate between those of unambiguous bipeds and eurypodan thyreophorans (0.41), whereas basal neoceratopsians possess ratios (0.04–0.072) similar to unambiguously bipedal taxa. The pachycephalosaur *Stegoceras* has a ratio of 0.13. Non-hadrosaurid iguanodontians generally have ratios within the range occupied by the unambiguous bipedal taxa, although *Uteodon* has a value of 0.22. Hadrosaurids + *Gilmoreosaurus* have increased ratios, with a reconstructed nodal value for hadrosaurids of 0.186 and individual ratios for these taxa ranging from 0.20–0.24.

All unambiguous quadrupeds possess a transversely broad ilium relative to the iliac blade length, while all unambiguous bipeds lack this feature. This character therefore appears to be a potentially robust correlate of ornithischian quadrupedality based on optimization alone. A regression of iliac width/iliac blade length versus femoral length suggests
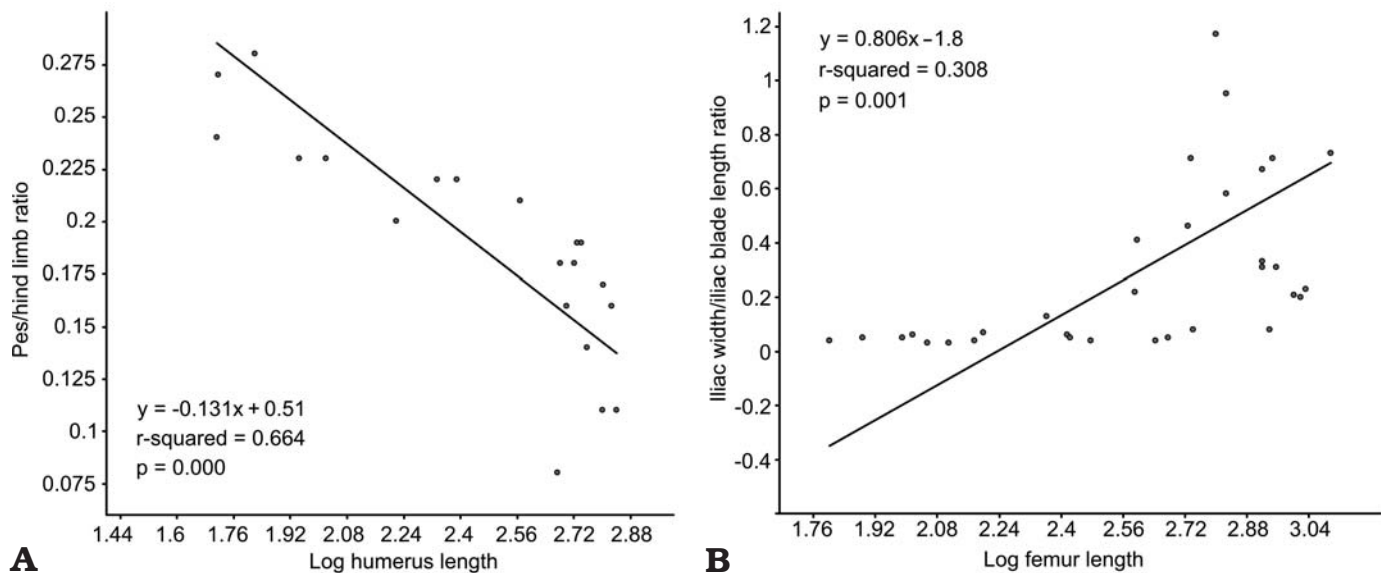
Fig. 5. Reduced major axis regressions showing correlations between body size (using humerus and femur length as proxies) and continuous characters. **A**. Pes/hind limb ratio. **B**. Iliac width/iliac blade length ratio. R-squared, Pearson's correlation coefficient; p, probability that x and y are uncorrelated.

that there is some correlation with body size ($p = 0.001$), but the r^2 value is rather low (0.308) and the trend appears to be mainly driven by the thyreophorans, all of which lie above the regression line, suggesting autapomorphically high values in these taxa (Fig. 5B).

Discussion

Osteological correlates for ornithischian quadrupedality. —The possession of a femur longer than the tibia and a reduced fourth trochanter appear to be robust osteological correlates for ornithischian quadrupedality and are not strongly correlated with body size in our sample (Figs. 3, 4C, D). Biomechanical factors that might have driven these changes are not immediately obvious, however. Elongation of the femur relative to the tibia would have moved the attachment sites of the pelvic locomotor muscles that attach distally on the femur (e.g., m. caudofemoralis longus, m. caudofemoralis brevis, m. adductor femoris; Romer 1923; Hutchinson 2001; Maidment and Barrett 2011) relatively further ventrally. The limb can be considered as an inverted pendulum oscillating around the foot (Hildebrand 1985; Carrano 1999), so increased locomotor performance can be achieved by restricting muscle mass to an area proximal to the hip joint (Hildebrand 1985). Indeed, elongate epipodials relative to metapodial length are considered a "cursorial" modification (Coombs 1978b). Cursorial morphologies are associated with increased locomotor performance (although not necessarily speed; Garland and Janis 1993; Carrano 1999). On the basis of these observations, ornithischian quadrupeds must have had reduced locomotor performance in comparison to bipeds.

The fourth trochanter is the insertion of the caudofemoralis musculature, which originates on the caudal vertebrae

and ventral postacetabular iliac blade (Romer 1923; Gatesy 1990; Maidment and Barrett 2011). The pendant fourth trochanter is thought to arise from ossification of the proximal part of a secondary "Sutton's tendon", which extends from the caudofemoralis musculature to the lower limb (Dollo 1888). A Sutton's tendon is present in extant crocodilians (Romer 1923), which do not possess a pendant fourth trochanter, so reduction in the fourth trochanter does not necessarily indicate loss of the tendon or reduction in the area of muscle attachment. The reduction of the fourth trochanter to a rugose ridge in ceratopsids and eurypodan thyreophorans may arise from a slight reorientation of forces applied by the caudofemoralis musculature, perhaps associated with a change in stance relating to quadrupedality, although this is speculative and warrants further investigation.

An anterolateral process on the proximal ulna and hoof-like manual unguals both optimize as potentially robust correlates for ornithischian quadrupedality (Figs. 3, 4A, B), but there is little size overlap between those taxa that possess them and those that do not. Some correlation with body size is to be expected, because the size range of the unambiguous bipeds in our sample does not overlap with the size range of the unambiguous quadrupeds.

Despite potential correlations with body size, there are good biomechanical reasons to consider that the presence of an anterolateral process on the ulna and hoof-like manual unguals are correlates of quadrupedality rather than large size alone. In basal ornithischians, as in basal bipedal sauropodomorphs (Bonnan 2003), the radius lies anterior to the ulna and as a result, the manus is supinated with the palms facing medially. This allows manual manipulation, grasping of foodstuffs, for example, between the palms. The development of the anterolateral process of the ulna results in movement of the radius medially, so that in ceratopsids, an-

kylosaurs and stegosaurs, the ulna lies lateral to the radius as in sauropods (Bonnan 2003). This results in pronation of the manus, with the palms facing ventrally. A fully pronated manus is required if the manus is to be used for locomotion and weight-bearing, and similar development of the anterolateral process of the ulna through bipedal basal sauropodomorphs to quadrupedal sauropods has been noted (Bonnan 2003). In unambiguous quadrupeds and hadrosaurs, facets and scarring on the ventral ulna and radius indicate that these elements would have been tightly bound, and it is unlikely that the radius could rotate around the distal ulna. As such, active supination of the manus would have been impossible, and the opposing hands could not have been brought together to hold food items.

Hoof-like unguals on the manus are broad and rounded anteriorly in dorsal and ventral view. Basal bipedal ornithischians have claw-like manual unguals, and the evolution of broad, hoof-like unguals similar to those of the hind limbs strongly suggests that the manus was being used, at least some of the time, for weight-bearing (also suggested by Norman 1980, 1986).

The transversely expanded ilium (Table 2), a femur that is straight in lateral view (Fig. 3) and a low pes length/hind limb ratio (Table 2) all optimize as correlates for ornithischian quadrupedality, but all also show some correlation with body size (Fig. 5). The transversely broad ilium shows weak correlations with body size, but there are clear morphological differences between unambiguous bipeds and unambiguous quadrupeds that cannot be explained by body size alone. The broadest surface of the ilium in eurypodan thyreophorans and ceratopsids faces ventrally, whereas in basal bipedal ornithischians and iguanodontids it faces laterally. Thyreophorans clearly have much broader ilia than other taxa of similar femoral length, and they plot well above the regression line, suggesting that at least in thyreophorans, lateral broadening of the ilium is not controlled by size alone.

Lateral expansion of the ilium fundamentally affects the lines of action of the muscles that attach to this surface, such as the m. iliotibiales, m. iliofemorales, m. iliofibularis, and m. femorotibialis externus (Romer 1927; Hutchinson 2001; Carrano and Hutchison 2002; Maidment and Barrett 2011), moving them laterally. This may have resulted in increased abduction moment arms (Maidment et al. in press) although it is possible that some of these muscles were also reduced (Maidment and Barrett 2012). Increased abduction moment arms would be required in taxa with wide bodies that placed their feet lateral to the centre of mass in a wide-gauged stance in order to counteract increased adduction moment arms generated about the hip joint by the ground reaction force, which acts upwards from the foot to the centre of mass. The ground reaction force has a greater transverse vector in wide-bodied quadrupedal taxa that placed their feet lateral to their centre of mass than in those with narrow bodies that placed their feet under their centre of mass on the midline during locomotion (Wilson and Carrano 1999). A wide-gauged stance can only be employed by an obligate

quadruped, because a biped must place the stance-phase foot under the centre of mass (on the midline) to maintain balance during locomotion. In contrast, quadrupeds are able to use the forelimbs to contribute to balance, and the centre of mass must only be within a triangle defined by the forelimbs and stance phase hind limb (Henderson 2006), allowing the stance-phase foot to be placed lateral to the centre of mass.

Trackway data for thyreophorans and ceratopsids is limited, but those trackways that have been associated with thyreophorans (McCrea et al. 2001; Lockley et al. 2008) and ceratopsids (Lockley and Hunt 1995) support the suggestion of a relatively wide-gauge stance. If the lateral expansion of the ilium is related to the possession of a wide body and a wide-gauged stance, it is a robust correlate for quadrupedality, but taxa that do not possess a broad ilium cannot be ruled out as quadrupeds because they may adopt a form of quadrupedal locomotion where the feet are placed on the midline. Track evidence suggests at least some Late Cretaceous ornithopods adopted this form of midline quadrupedal locomotion (Lockley and Wright 2001).

The possession of a femur with a shaft that is straight in lateral view correlates with both size and quadrupedality in our sample. Limb bones are strongest when axially loaded and straight bones that are axially loaded are capable of carrying large loads with little strain. In contrast, curvature of a long bone will result in higher strain at a smaller load (Lanyon and Rubin 1985). A femur with a shaft that is straight in lateral view may therefore be related to higher body mass, and correlations with quadrupedality exist because the taxa in our quadrupedal sample are heavier than those in our unambiguously bipedal sample. As we cannot exclude the influence of body size, this character is probably not as robust a correlate of quadrupedality as suggested by our optimizations.

There is a relatively strong negative correlation between humerus length and pes/hind limb ratio, suggesting that in larger ornithischians the pes is shorter. Unambiguous quadrupeds all lie below the regression line, suggesting that their pes is even shorter than would be expected for a given humeral length, but a high r^2 value and significance level ($r^2 = 0.664$; $p<0.000$) strongly suggest that pes/hind limb length and body size are correlated in ornithischians (see above). This character is probably not as robust a correlate of quadrupedality as suggested by ancestral state reconstruction and optimization alone.

The possession of an elongate forelimb relative to hind limb length shows some correlations with quadrupedality, but the sample size is rather small (Table 2). Furthermore, correlations with body size cannot be robustly assessed because our measures of body size are based on the length of the humerus or femur, leading to some redundancy in measures. It might be expected that quadrupeds have longer forelimbs relative to hind limb length than bipeds because the forelimbs are required to touch the ground during locomotion, but all ornithischians have much shorter forelimbs

than hindlimbs, probably as a consequence of their bipedal ancestry (similar discrepancies also occur in the majority of quadrupedal sauropodomorphs). A larger sample size and better measures of body size or mass are needed to adequately assess the robustness of this character as a correlate for either body size or quadrupedality.

To summarize, the following characters are considered to be osteological correlates for ornithischian quadrupedality because of their correlation with quadrupedality based on optimization, and either their lack of correlation with body size or because there are biomechanical reasons to link them with quadrupedality rather than large body size: (1) an anterolateral process on the proximal ulna; (2) hoof-like manual unguals; (3) a femur that is longer than the tibia; (4) a reduced fourth trochanter; (5) a transversely broadened ilium.

We now use these characters to assess probable stances in those ornithischian taxa that were assigned to the "unknown" category in our optimizations (Table 3).

Stance in basal thyreophorans.—*Scutellosaurus* can only be scored for characters 1, 3, and 4 above, and it scores as a biped in all cases. Colbert (1981) suggested that *Scutellosaurus* was facultatively quadrupedal because of its body proportions in comparison to *Lesothosaurus*. However, we find no osteological correlates indicative of quadrupedality in *Scutellosaurus*, so we consider it an obligate biped.

Scelidosaurus is usually considered to have been quadrupedal (e.g., Paul 1997) although we did not determine its stance a priori. *Scelidosaurus* could only be scored for characters 3–5 above. It scored as a quadruped for characters 3 and 5, but it retains a pendant fourth trochanter. The combination of quadrupedal and bipedal characters is perhaps to be expected in a taxon that occupies a phylogenetic position between the bipedal *Scutellosaurus* and the eurypodan quadrupeds, and suggests that it may have been predominantly quadrupedal while retaining some aspects of its bipedal ancestry relative to the condition present in the more derived eurypodan quadrupeds.

A juvenile specimen of *Scelidosaurus* for which some hind limb material is preserved is also known (NHMUK R6704). This specimen was excluded from the original analyses because it has a femoral length that is less than 50% of the adult's (NHMUK R1111; see Methods). Like the adult, the juvenile has a straight femur in lateral view and a pendant fourth trochanter, but its iliac width/iliac blade length ratio is 0.23, just over half that of the adult (0.41) and similar to the reconstructed nodal value obtained for Genasauria. This perhaps suggests that basal thyreophorans were quadrupeds as adults, but may have developed their quadrupedal characteristics through ontogeny, and may even have been facultatively bipedal as juveniles. Remains of *Scelidosaurus* in public institutions are, unfortunately, rather rare, and more specimens from a variety of ontogenetic stages are required to test this hypothesis.

Stance in *Stegoceras*.—The only pachycephalosaur included in this study, *Stegoceras* (UAVLP 2) possesses a combi-

Table 3. Summary of quadrupedal character states among taxa, for which adequate data is known. Abbreviations: +, character state present; –, character state absent; ?, character state unknown.

	Antero-lateral process on ulna	Hoof-like manual unguals	Ilium trans-versely broadened	Femur longer than tibia	Fourth tro-chanter reduced
Lesothosaurus	–	–	–	–	–
Parksosaurus	–	–	–	–	+
Hypsilophodon	–	–	–	–	–
Stegosauria	+	+	+	+	+
Ankylosauria	+	+	+	+	+
Ceratopsidae	+	+	+	+	+
Scutellosaurus	–	?	?	–	–
Scelidosaurus	?	?	+	+	–
Zalmoxes	+	?	+	?	–
Tenontosaurus	+	–	–	+	–
Dysalotosaurus	–	–	–	–	–
Camptosaurus	+	–	–	–	–
Uteodon	–	?	+	+	–
Mantellisaurus	+	+	–	–	+
Gilmoreosaurus	+	+	+	?	+
Hadrosauridae	+	+	+	+	+
Stegoceras	–	–	–	+	–
Yinlong	–	–	–	–	–
Leptoceratops	–	+	–	–	–
Protoceratops	+	+	–	–	–

nation of bipedal and quadrupedal characteristics. It lacks an anterolateral process on the ulna, has claw-shaped manual unguals, and has a pendant fourth trochanter, but it has a femur slightly longer than the tibia. Its ilium is slightly transversely broadened, but not to the degree seen in unambiguous quadrupeds, or in hadrosaurs and some iguanodontids such as *Uteodon*. Inspection of the ilium of *Stegoceras* shows that transverse broadening arises from a medially-directed flange, rather than a lateral folding or thickening, as in all other ornithischians in which this feature occurs. The forelimb of *Stegoceras* is gracile and is not functionally adapted for weight-bearing, and we therefore consider *Stegoceras* a biped. However, the unusual pelvic morphology and hind limb proportions warrant further functional investigation that is beyond the scope of the current study.

Stance in basal ceratopsians.—*Yinlong*, all species of *Psittacosaurus* and *Archaeoceratops* display bipedal character states for all the osteological correlates they can be coded for, and are therefore all considered as bipeds. Most previous workers have also considered these taxa to be bipedal (e.g., Sereno 1990; Xu et al. 2006).

Leptoceratops displays bipedal character states for characters 1, 3, and 4 above, but does possess hoof-like manual unguals. *Leptoceratops* could not be scored for iliac width (character 5 above) because the ilium is not present in the

specimen examined in this study (CMN 8889). However, Sternberg (1951) noted that the dorsal margin of the ilium was not everted in the two other CMN specimens (CMN 8887 and CMN 8888; these specimens were not accessible for measurement and study). Sternberg's description of the ilium suggests that it was more similar to a biped in morphology. Most authors who have examined *Leptoceratops* have come to the conclusion that it was a quadruped (e.g., Russell 1970; Senter 2007), but the osteological correlates identified herein suggest that it was primarily bipedal. However, the presence of hoof-shaped manual unguals suggests it spent at least some of the time either standing or moving quadrupedally.

Protoceratops could be scored for all characters 1–5 above, and it possesses a mosaic of character states. It has an anterolateral process on the ulna and hoof-like manual unguals, both characteristic of quadrupedality, but its tibia is longer than its femur, it has a pendant fourth trochanter and a narrow ilium, which are all bipedal features. This suggests that *Protoceratops* was likely facultatively quadrupedal, using quadrupedal stance and/or locomotion more than *Leptoceratops*. Previous workers have also generally considered *Protoceratops* to have been a facultative (Senter 2007) or obligate (Tereschenko 1996) quadruped.

Character changes related to quadrupedality along the ceratopsid "stem" lineage indicate that characters were acquired in a stepwise fashion, and that forelimb characters associated with quadrupedality were acquired before hind limb changes.

Stance in non-hadrosaurian iguanodontians.—As far as can be determined, the dryosaurid iguanodontians *Dysalotosaurus* and *Valdosaurus* and the ankylopollexian iguanodonts *Hypselospinus* and *Barilium* possess bipedal character states and are therefore considered as potential obligate bipeds. However, it should be noted that *Valdosaurus* and *Hypselospinus* can only be coded for two of the five osteological correlates for quadrupedality, while *Barilium* can only be coded for one, so more complete specimens of these species are required.

All other non-hadrosauroid iguanodontians possess a mosaic of bipedal and quadrupedal character states. The rhabdodontid *Zalmoxes* has an anterolateral process on the ulna, but a pendant fourth trochanter. It could not be coded for other character states. Two partial ilia of *Zalmoxes* (NHMUK R3813; NHMUK R3810) could not be coded because they are incomplete, but both are transversely broad, leading Weishampel et al. (2003: 90) to suggest that in *Zalmoxes* "… hindlimb carriage and hip kinematics differed greatly from all other known ornithopods". If a transversely broad ilium is related to a wide-gauged stance (see discussion of the biomechanical causes for this character, above), *Zalmoxes* must have been an obligate quadruped, because animals with a wide-gauged stance must use their forelimbs to balance. However, *Zalmoxes* retains a pendant fourth trochanter, which is present in bipeds.

Tenontosaurus, *Camptosaurus*, *Uteodon*, and *Mantellisaurus* could be coded for the majority of osteological correlates, and each possesses a different combination of bipedal and quadrupedal character states. *Tenontosaurus, Camptosaurus*, and *Mantellisaurus* all possess an anterolateral process on the ulna, absent in *Uteodon*, while *Uteodon* and *Tenontosaurus* both have a femur longer than the tibia. The tibia is longer than the femur in *Camptosaurus* and *Mantellisaurus*. *Uteodon* possesses a transversely broadened ilium, absent in *Tenontosaurus, Camptosaurus*, and *Mantellisaurus*. *Mantellisaurus* possesses a non-pendant fourth trochanter, while it is pendant in the other taxa. *Camptosaurus* therefore possesses one osteological correlate of quadrupedality, while *Uteodon* and *Tenontosaurus* possess two and *Mantellisaurus* three. *Camptosaurus* was likely primarily bipedal, but had a partially pronated manus, suggesting it spent some of time either standing or locomoting quadrupedally. *Tenontosaurus* and *Uteodon* may have been facultatively quadrupedal, although the possession of a transversely broad ilium in *Uteodon* suggests that it may have been an obligate quadruped if this character is related to wide-gauge stance. Carpenter and Wilson (2008) also argued for quadrupedality in *Uteodon* based on forelimb morphology. Norman (1986) suggested that *Mantellisaurus* was a facultative quadruped. We find that *Mantellisaurus* possesses the most osteological correlates for quadrupedality, and it may have used quadrupedal stance and/or locomotion more than the other taxa.

All hadrosauroids more derived than *Equijubus* (which can only be coded for one of the osteological correlates) including hadrosaurids, possess all osteological correlates for quadrupedalism. The fourth trochanter, although not reduced to the degree seen in ceratopsids and eurypodan thyreophorans, is reduced as it is no longer pendant. The ilium is broadened transversely, although not to the same degree as in thyreophorans and ceratopsids. Character distributions in these hadrosauroids strongly suggest that they were predominantly quadrupedal, and perhaps only rarely stood or moved bipedally. The transition to predominant quadrupedalism occurred prior to the origin of Hadrosauridae, as these features were already present in "stem" hadrosauroids such as *Gilmoreosaurus* and *Bactrosaurus*.

Different combinations of quadrupedal correlates are present in the various iguanodontian taxa, rendering the identification of locomotory evolutionary trends difficult. Unlike in ceratopsids, the acquisitions of forelimb quadrupedal characters in iguanodontians do not necessarily precede those of the hind limb. The mosaic of different characters displayed by iguanodontids suggests that facultative quadrupedality may have arisen in each taxon for different reasons: for example, *Mantellisaurus* may have used a quadrupedal stance while moving quickly, while *Tenontosaurus* may have used quadrupedality during feeding. The acquisition of features related to quadrupedal locomotion in non-hadrosaurid iguanodontids was clearly labile.

Conclusions

Osteological features correlative of quadrupedality in ornithischian dinosaurs have been identified. Characters relating to quadrupedality were acquired in different orders in the ceratopsian and ornithopod "stem" lineages. Among ceratopsians, changes to the forelimb occurred before changes to the hind limb, and these accumulated in a stepwise fashion. In contrast, quadrupedal characteristics in ornithopods accrued in a mosaic fashion, with various ornithopods acquiring these characters in different sequences. Ornithopods more derived than *Equijubus* appear to have been predominantly quadrupedal, and may have been obligate quadrupeds. Quadrupedalism, whether facultative or obligate, therefore evolved on numerous occasions within Ornithischia, particularly within Ornithopoda. Differences in the order of character acquisition suggest that the evolutionary driving forces for the evolution of quadrupedality were varied, that taxa were not constrained by their bipedal ancestry to acquire these characters in a particular order, and that the resulting locomotor styles in different quadrupedal lineages were likely quite different.

Acknowledgements

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