

A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism

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Aardonyx celestae gen. et sp. nov. is described from the upper Elliot Formation (Early Jurassic) of South Africa. It can be diagnosed by autapomorphies of the skull, particularly the jaws, cervical column, forearm and pes. It is found to be the sister group of a clade of obligatory quadrupedal sauropodomorphs (*Melanorosaurus* + Sauropoda) and thus lies at the heart of the basal sauropodomorph–sauropod transition. The narrow jaws of *A. celestae* retain a pointed symphysis but appear to have lacked fleshy cheeks. Broad, U-shaped jaws were previously thought to have evolved prior to the loss of gape-restricting cheeks. However, the narrow jaws of *A. celestae* retain a pointed symphysis but appear to have lacked fleshy cheeks, demonstrating unappreciated homoplasy in the evolution of the sauropod bulk-browsing apparatus. The limbs of *A. celestae* indicate that it retained a habitual bipedal gait although incipient characters associated with the pronation of the manus and the adoption of a quadrupedal gait are evident through geometric morphometric analysis (using thin-plate splines) of the ulna and femur. Cursorial ability appears to have been reduced and the weight bearing axis of the pes shifted to a medial, entaxonic position, falsifying the hypothesis that entaxy evolved in sauropods only after an obligate quadrupedal gait had been adopted.

Keywords: sauropod; sauropodomorph; *Aardonyx celestae*; bulk browsing; quadrupedal gait

1. INTRODUCTION

Eusauropod dinosaurs possess a highly specialized set of skeletal adaptations related to their gigantic size, obligate quadrupedalism, graviportal locomotion and strictly herbivorous diets (Upchurch *et al.* 2004 and references therein). Indeed, the evolution of sauropods from earlier basal sauropodomorphs is perhaps the most extreme morphological transformation to have occurred in early dinosaur evolution. The nature of this transition has been obscure but new discoveries over the last dozen years have shed much light upon it. Cladistic analyses of sauropod relationships have identified plesiomorphic members of the Sauropoda and provided an outline of the sequence in which their various specializations were acquired (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al.* 2004). Biomechanical studies have also begun to unravel the functional significance of some of these characters (Bonnan 2003; Carrano 2005). The first Triassic sauropods have also come to light in the last decade, revealing some of the

morphology of the basal-most members of the clade (Buffetaut *et al.* 2000; Yates & Kitching 2003). There has also been a flurry of cladistic analyses on the wider sauropodomorph clade, putting Sauropoda into its wider context (Benton *et al.* 2000; Yates 2003, 2004, 2007; Upchurch *et al.* 2004, 2007a). While it is true that these analyses have produced widely divergent results, there is now general agreement that basal sauropodomorphs (traditionally ‘pro-sauropods’) are paraphyletic to some extent with respect to Sauropoda. Lastly, detailed descriptions of advanced near-sauropod sauropodomorphs have elucidated the morphology of the closest sauropod ancestors (Bonnan & Yates 2007; Kutty *et al.* 2007; Pol & Powell 2007; Upchurch *et al.* 2007b; Yates 2007). Despite all this research, many aspects of the transition remain unknown owing to a combination of uncertainty surrounding the precise phylogenetic relationships of basal sauropodomorphs, gaps in the phylogenetic sequence and the incompleteness of most of the taxa that are known from this transition.

Here, we report on *Aardonyx celestae* gen. et sp. nov., a sauropodomorph that lies in the heart of the basal sauropodomorph–sauropod transition. *Aardonyx* appears to be the closest known sister group to the clade of obligatory quadrupedal sauropodomorphs to retain facultative, if not habitual, bipedalism.

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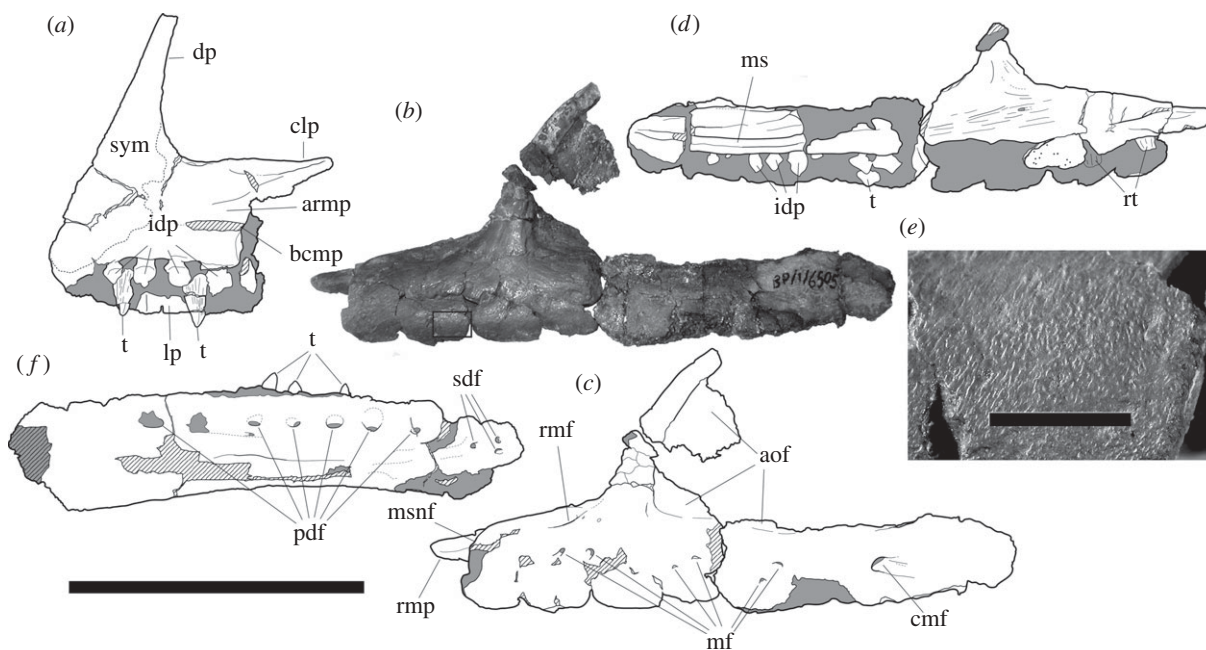


Figure 1. Holotype and other jaw elements of *Aardonyx celestae* gen. et sp. nov. (a) Right premaxilla (BP/1/6584) in medial view. (b–d) Holotype left maxilla (BP/1/6254) and caudal fragment (BP/1/6505) in (b,c) lateral and (d) medial views. Box indicates the area enlarged in (e). (e) Close-up of lateral supra-alveolar surface of the holotype maxilla (BP/1/6254). (f) Right dentary (BP/1/6334) in lateral view. Hatched areas represent broken bone surfaces, grey areas indicate areas of matrix. Abbreviations: aof, antorbital fossa; armp, articulation surface for the rostromedial process of the maxilla; bcmp, base of the caudomedial process of the premaxilla; clp, caudolateral process of the premaxilla; cmf, caudal maxillary foramen; dp, dorsal process of the premaxilla; idp, interdental plate; lp, lateral plate; mf, maxillary foramen; ms, medial sulcus of the maxilla; msnf, maxillary margin of the subnarial foramen; pdf, primary dentary foramina; rmf, rostral maxillary foramen; rmp, rostromedial process of the maxilla; rt, replacement tooth; sdf, secondary dentary foramina; sym, symphyseal surface; t, tooth. Scale bar 100 mm in (a–d,f), scale bar in (e), 5 mm.

2. SYSTEMATIC PALAEOLOGY

Sauropodomorpha Von Huene, 1932

Anchisauria Galton and Upchurch, 2004

Aardonyx celestae gen. et sp. nov.

(a) Holotype

Rostral half of the left maxilla (BP/1/6254) (figure 1b–e). A non-overlapping, weathered, caudal portion of a left maxilla (BP/1/6505) was found about a metre from the holotype, and may well represent the same bone as the holotype.

(b) Type locality and horizon

Marc's Quarry (MQ) bone bed on the farm Spion Kop 932, Senekal District, Free State, South Africa (figure 2a). The bone bed is situated in the Early Jurassic upper Elliot Formation (Bordy *et al.* 2004).

(c) Referred specimens

A large number of disarticulated bones from the type locality, including skull elements, mandibular elements, vertebrae from the cervical, dorsal, sacral and caudal series, cervical ribs, dorsal ribs, gastralia, chevrons, pectoral girdle elements, pelvic girdle elements and bones of both the fore- and hind limbs, manus and pes. All of these bones are from the type quarry and seem to derive from two immature individuals, the smaller with linear dimensions of the postcranial elements that are about 85 per cent of the larger individual.

The referral of the numerous disarticulated elements from MQ to *Aardonyx* is justified by a taphonomic

study of the site (see the electronic supplementary material).

(d) Etymology

Aardonyx from *aard* (Afrikaans for 'Earth') and *onyx* (Greek for 'claw'), gender is masculine; *celestae* for Celeste Yates who prepared many of the bones. Genus name refers to the thick hematite encrustation of many of the bones, particularly the ungual phalanges, in the type quarry.

(e) Diagnosis

A sauropodomorph with the following autapomorphies: five premaxillary teeth (convergent in *Plateosaurus*) (figure 1a); a band of dense, fine pits and small foramina along the lower half of the lateral surface of the maxilla (figure 1e); reduced lateral maxillary neurovascular foramina rostral to the large caudally facing foramen at the caudal end of the maxilla (middle foramina are <6% of the depth of the maxilla caudal to the antorbital fossa) (figure 1c); an elongate rostral ramus of the maxilla combined with a steep dorsal process of the premaxilla to produce an enlarged external naris (area at least subequal to that of the orbit) (figure 2b); a well-developed longitudinal sulcus on the medial side of the caudal maxillary ramus (figure 1d); reduced cervical diapophyses that remain as low tubercles, with a concomitant absence of the diapophyseal laminae, along the full length of the cervical series; large, rugose biceps scar (maximum diameter 13% of the length of the radius) on the craniomedial surface of the shaft of the radius (figure 3h,i);

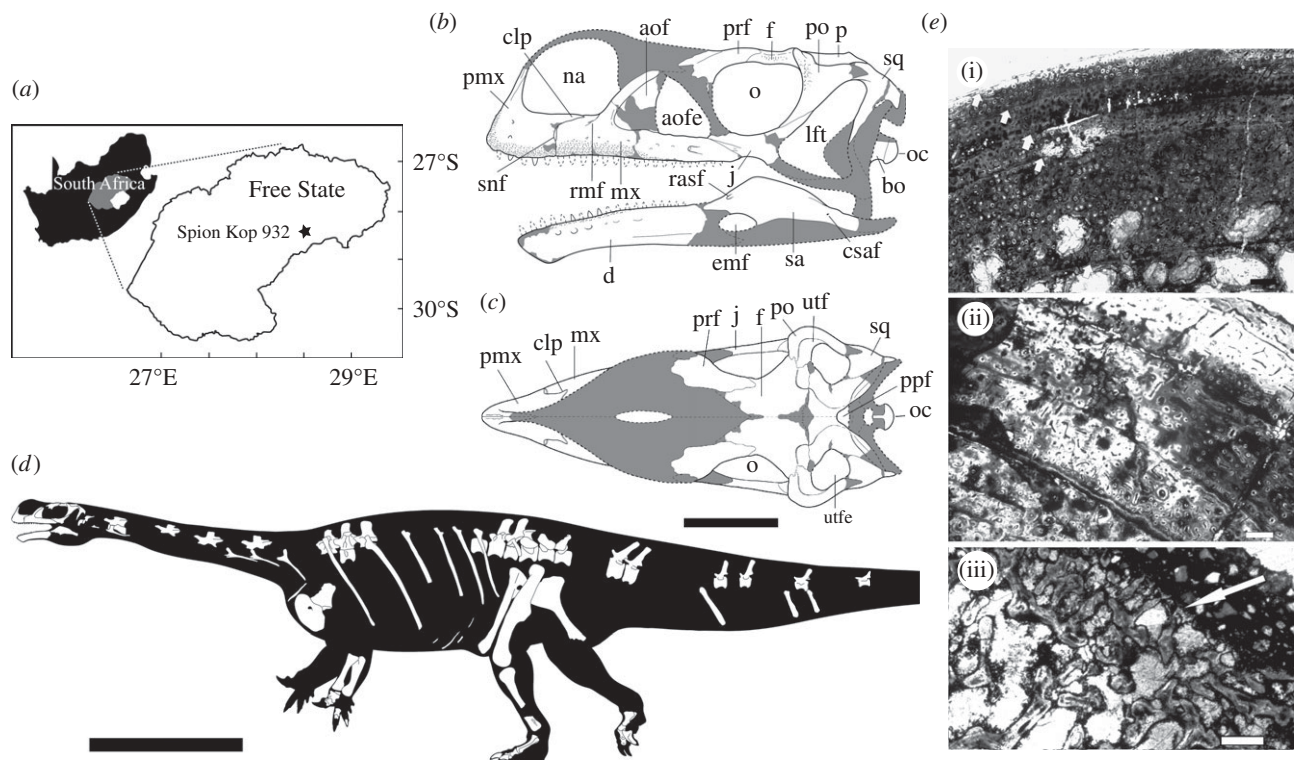


Figure 2. (a) Map of South Africa showing the location of Spion Kop 932. (b,c) Reconstruction of the skull of *Aardonyx celestae* gen. et sp. nov. in (b) lateral and (c) dorsal views. (d) Reconstruction of the skeleton of *Aardonyx celestae* gen. et sp. nov. scaled to the size of the smaller individual. (e) Histological sections of bones from *Aardonyx celestae* gen. et sp. nov. (i) shows a transverse section through a rib. The cortical bone consists of well-vascularized fibro-lamellar bone tissue with distinct lines of arrested growth (arrows) and several secondarily enlarged erosion cavities. (ii) shows a transverse section of a scapula fragment showing the zonal nature of the compacta. (iii) shows a longitudinal section of a scapula fragment with calcified cartilage at the articular edge of the bone (arrowed). Abbreviations: aof, antorbital fossa; aofe, antorbital fenestra; bo, basioccipital; clp, caudolateral process; csaf, caudal surangular foramen; d, dentary; emf, external mandibular fenestra; f, frontal; j, jugal; lft, laterotemporal fenestra; mx, maxilla; na, external naris; o, orbit; oc, occipital condyle; p, parietal; pmx, premaxilla; po, post-orbital; rmf, rostral maxillary foramen; rsaf, rostral surangular foramen; sa, surangular; sq, squamosal; utf, upper temporal fossa; utfe, upper temporal fenestra. Scale bars, 100 mm in (b,c), 1 m in (d) and 500 μm in (e).

exceptionally broad and flat proximal end of metatarsal IV (transverse width is 2.9 times greater than the extensor–flexor depth); distal end of metatarsal IV with a strongly laterally flared caudolateral corner.

In addition to these autapomorphies, *Aardonyx* can be further distinguished from members of the quadrupedal sauropodomorph clade, such as *Melanorosaurus* and *Antetonitrus* by an absence of an inflection in the profile of the snout at the base of the nasal process of the premaxilla; a slender ventral ramus of the squamosal (basal width of the ramus is 33% of its length); a small, poorly developed craniolateral process at the proximal end of the ulna; a sacrum consisting of just three vertebrae; a sinuous lateral margin of the femoral shaft; femoral shaft with a subcircular cross-section; a cranial trochanter that is placed well away from the lateral margin of the femur in cranial view and is not visible when the femur is viewed caudally. It can be distinguished from more primitive near-sauropod sauropodomorphs such as *Jingshanosaurus*, *Anchisaurus* and *Yunnanosaurus* by its broad subtriangular ascending ramus of the maxilla, presence of labial plates on the premaxilla, maxilla and dentary, transversely broad prefrontal, absence of a caudal lateral ridge on the dentary, taller mid-dorsal neural spines, a less strongly developed distal swelling of the pubis, a descending caudolateral process of the distal end of the tibia that fails to extend to the level of the cranial lateral

corner of the distal articular surface, the robust metatarsal I with a proximal end that is about 75 per cent of the total length, and the stout pedal phalanges which are not longer than their proximal transverse width. For a description of the *Aardonyx* remains, see the electronic supplementary material.

(f) Osteohistology and ontogenetic age of the material

Thin sections of a fragment of a rib and scapula from *Aardonyx* were prepared using the methodology described by Chinsamy-Turan (2005) (figure 2e). The cortices of both bones show zonal bone tissue: highly vascularized fibrolamellar bone within zones, alternating with distinct lines of arrested growth. The rib fragment displays five growth rings, whereas the scapula fragment has seven. Neither bone shows any peripheral rest lines to suggest that appositional growth had stopped, therefore indicating skeletally immature individuals. The earliest line of arrested growth in the rib is followed by the widest zone, indicating that it was probably laid down in the rapid growth phase of early ontogeny, suggesting that few, if any, growth lines had been obliterated owing to medullary expansion. That the individual(s) were still growing at the time of death is supported by the presence of calcified cartilage at the articular end of the scapula,



Figure 3. Limb elements of *Aardonyx celestae* gen. et. sp. nov. (a–c) Left femur (BP/1/6510) of small individual in (a) cranial, (b) caudal and (c) medial views. (d–g) Left ulna (BP/1/5379c) of large individual in (d) craniolateral, (e) cranial, (f) proximal and (g) distal views (cranial direction to the top in proximal and distal views). (h–k) Left radius (BP/1/5379d) of large individual in (h) medial, (i) cranial, (j) proximal and (k) distal views (cranial direction is to the right for proximal and distal views). (l,m) Right metatarsal I (BP/1/6602) of the small individual in (l) proximal and (m) cranial views. Abbreviations: bs, biceps scar; clp, craniolateral process of the ulna; cp, cranial process of the ulna; ct, cranial trochanter; ft, fourth trochanter; fh, femoral head; gt, greater trochanter; ls, ligament scar; op, olecranon process; pf, popliteal fossa; rf, radial fossa; tc, tibial condyle; tfc, tibiofibular crest. Hatching represents areas of plaster reconstruction. Scale bars, 100 mm, with the left bar pertaining to (a–c) and the right bar to (d–m).

indicating continued growth in bone length (Horner *et al.* 2001; Chinsamy-Turan 2005). In conclusion, the histological analysis suggests that the individual(s) sampled were actively growing and possibly less than 10 years old at the time of death.

3. PHYLOGENETICS

Aardonyx was added to modified versions of two recent, comprehensive cladistic analyses of basal sauropodomorph relationships (Upchurch *et al.* 2007a; Yates 2007). In both cases (figure 4, and the electronic supplementary material), it was found to lie at the heart of the basal sauropodomorph-sauropod transition as the closest outgroup to the clade containing what we interpret to be the obligatory quadrupedal sauropodomorphs (*Melanorosaurus* + Sauropoda). As such, it is an important morphological intermediate that sheds much light on the nature of this transition. Derived traits supporting this relationship include labial alveolar margins of the premaxilla, maxilla and dentary forming lateral plates (figure 1b); reversal to mid-cervical neural spines that are less than twice as long as high; hyposphenes in the dorsal vertebrae as deep as the neural canal; height of the middle dorsal neural spines greater than the length of the base; reversal to less than 60° of ventrolateral twisting of the first phalanx of manual digit I; proximal tip of the cranial trochanter distal to the femoral head (convergent with many basal sauropodomorphs) (figure 3a); fourth trochanter positioned over the midlength of the femur (figure 3b,c); a robust metatarsal I with a minimum

transverse midshaft diameter that exceeds that of metatarsal II (figure 3m); at least the distal non-terminal pedal phalanges are wider than long; ungual of pedal digit I is longer than the first phalanx of pedal digit I; adult femur length that exceeds 600 mm.

Although the relationships among non-sauropods remain weak in the matrix based on Upchurch *et al.* (2007a), the clade of *Aardonyx* plus the quadrupedal sauropodomorphs is robust in the modified version of Yates' (2007) matrix, once the poorly known, unstable taxa (*Plateosaurus* (= *Gresslyosaurus*) *ingens*, *Camelotia* and *Isanosaurus*) are removed (figure 4).

4. THE EVOLUTION OF SAUROPOD BULK BROWSING

Eusauropods show a complex of derived character states that appear to be adaptations towards a bulk-browsing mode of feeding. Primarily, this complex consists of three characteristics: the development of lateral plates along the alveolar margins of tooth-bearing bones that brace the lingual sides of the teeth against bucco-lingual forces during foliage stripping; broad, U-shaped jaws to allow a wider bite; and loss of fleshy cheeks to increase gape (Upchurch & Barrett 2000; Upchurch *et al.* 2007b).

Aardonyx shows plesiomorphic, narrow, V-shaped jaws combined with the derived absence of a lateral ridge at the caudal end of the dentary (figure 1f). The latter feature is also absent in all known sauropods, except *Chinshakiangosaurus* (Upchurch *et al.* 2007b). It is thought to be related to the loss of fleshy cheeks in order to facilitate

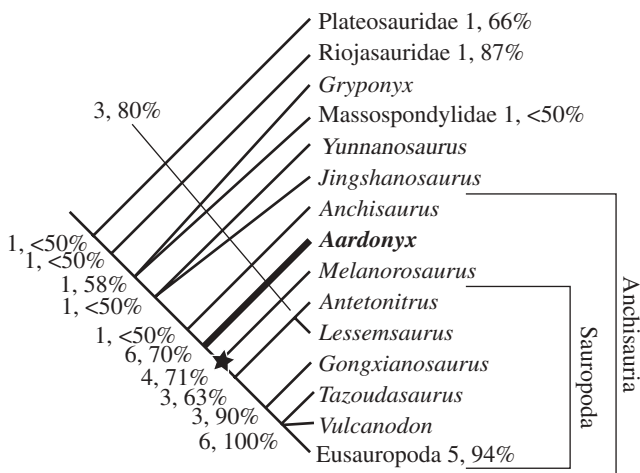


Figure 4. Condensed cladogram based on the strict consensus of 28 most parsimonious trees (tree length = 1119) obtained from a cladistic analysis of a modified version of the Yates (2007) matrix (353 characters; see the electronic supplementary material for details) after the *a priori* removal of the poorly known, and unstable taxa: *Plateosaurus* (= *Gresslyosaurus* *ingens*, *Camelotia*, *Blikanasaurus* and *Isanosaurus* (leaving 44 active taxa in the analysis)). Only the plateosaurian part of the tree is shown here. Named suprageneric taxa are collapsed into single terminals to save space: Plateosauridae contains *Unaysaurus*, *Plateosaurus gracilis* and *Plateosaurus engelhardti*; Riojasauridae contains *Riojasaurus* and *Eucnemesaurus*; Massospondylidae contains *Massospondylus*, *Coloradisaurus* and *Lufengosaurus*; Eusauropoda contains *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, *Barapasaurus*, *Patagosaurus*, *Cetiosaurus* and *Neosauropoda*. Bold numbers given at each node are decay indices, the percentages are bootstrap support values. The star marks the basal node of the quadrupedal clade.

a wider gape for bulk browsing (Upchurch *et al.* 2007b). Further evidence that *Aardonyx* lacked extensive fleshy cheeks can be gleaned from the lateral neurovascular foramina of the maxilla. These openings are smaller than in those of most other basal sauropodomorphs (figure 1c). This indicates that there was a reduction in the blood supply to the buccal tissues which, in turn, suggests the loss, or reduction, of fleshy cheeks. The dense pitting of the labial alveolar margins of the premaxilla, maxilla and dentary is interesting in this respect since pits of similar size and density are also found along the alveolar margins of extant crocodylians. It is possible that, in life, the gum line of *Aardonyx* was lined with tightly adherent cornified tissue like those of extant crocodylians. However, the number of lateral neurovascular foramina on the maxilla and dentary (no more than 11 foramina per bone) suggests otherwise. All modern tetrapods with similar low numbers of lateral neurovascular foramina possess an extra-oral soft-tissue covering of the teeth (Morhardt *et al.* 2009). Thus, it is probable that even if cheeks were not present, the living *Aardonyx* sported thin, lizard-like lips.

The combination of narrowly pointed but cheekless jaws is the opposite of the condition seen in the Chinese basal sauropod *Chinshakiangosaurus*, where the jaws are broad and U-shaped but retain a well-developed caudal lateral dentary ridge (Upchurch *et al.* 2007b). Thus, a wider, cheekless gape may have evolved twice in

Sauropodomorpha: once in *Aardonyx* and once in sauropods more derived than *Chinshakiangosaurus*.

5. THE EVOLUTION OF OBLIGATE QUADRUPEDALISM IN SAUROPODOMORPHS

The clade of *Melanorosaurus* + Sauropoda would appear to be diagnosed by habitual, if not obligate, quadrupedalism. This interpretation is supported by modifications of both the fore- and hindlimbs of members of this clade. These are as follows.

- (i) Increase of the relative length of the forearm relative to the hindlimb (humerus: femur ratio >0.8) in large post-hatching individuals. Lessening the discrepancy between fore- and hindlimb length is clearly advantageous to a quadruped. Sauropodomorphs basal to this clade have a humerus: femur ratio that is less than 0.8, and usually less than 0.7 (Cooper 1981), in large post-hatching individuals. Note that hatchlings and very young basal sauropodomorphs had high humerus: femur ratios but were also obligate quadrupeds (Reisz *et al.* 2005).
- (ii) Development of a large cranial lateral process at the proximal end of the ulna. This process defines a deep cranially facing radial fossa that holds the radius in a medially shifted position, so that the distal end of the radius lays craniomedial to the ulna. This pronates the manus and brings the direction of flexion–extension of the wrist closer to parallel with the direction of travel (Bonnar 2003).
- (iii) Straightening of the femoral shaft. This is particularly apparent along the proximal lateral margin in cranial view (figure 3a,b). In basal sauropodomorphs, this margin is markedly convex, whereas it is straight in *Melanorosaurus* and basal sauropods. The loss of femoral sinuosity is associated with the development of a more columnar stance with reduced limb excursions during locomotion, i.e. a trend towards graviportalism. Only quadrupedal dinosaur clades have evolved graviportalism (e.g. Sauropoda, Stegosauria and Nodosauridae), indicating that the trend towards it in the clade of *Melanorosaurus* + Sauropoda was probably correlated with quadrupedalism.

It should be noted that in basal members of this clade (e.g. *Melanorosaurus* and *Antetonitrus*), the manus still retained some degree of functionality for non-locomotor purposes, including an offset and mobile pollex with some grasping ability (Yates & Kitching 2003; Bonnar & Yates 2007). As a consequence, it has been suggested that these features imply facultative bipedalism (Carrano 2005) but they may simply represent plesiomorphic retentions. In any case, crude grasping ability need not imply bipedalism because their hands could have been employed singly while the animal was stationary.

The quadrupedal clade is also diagnosed by an increase in the number of sacral vertebrae (from three to at least four) and the development of an eccentric femoral shaft (one where the mediolateral dimension of the cross-section exceeds the craniocaudal dimension) to counter increased mediolateral forces. Neither of

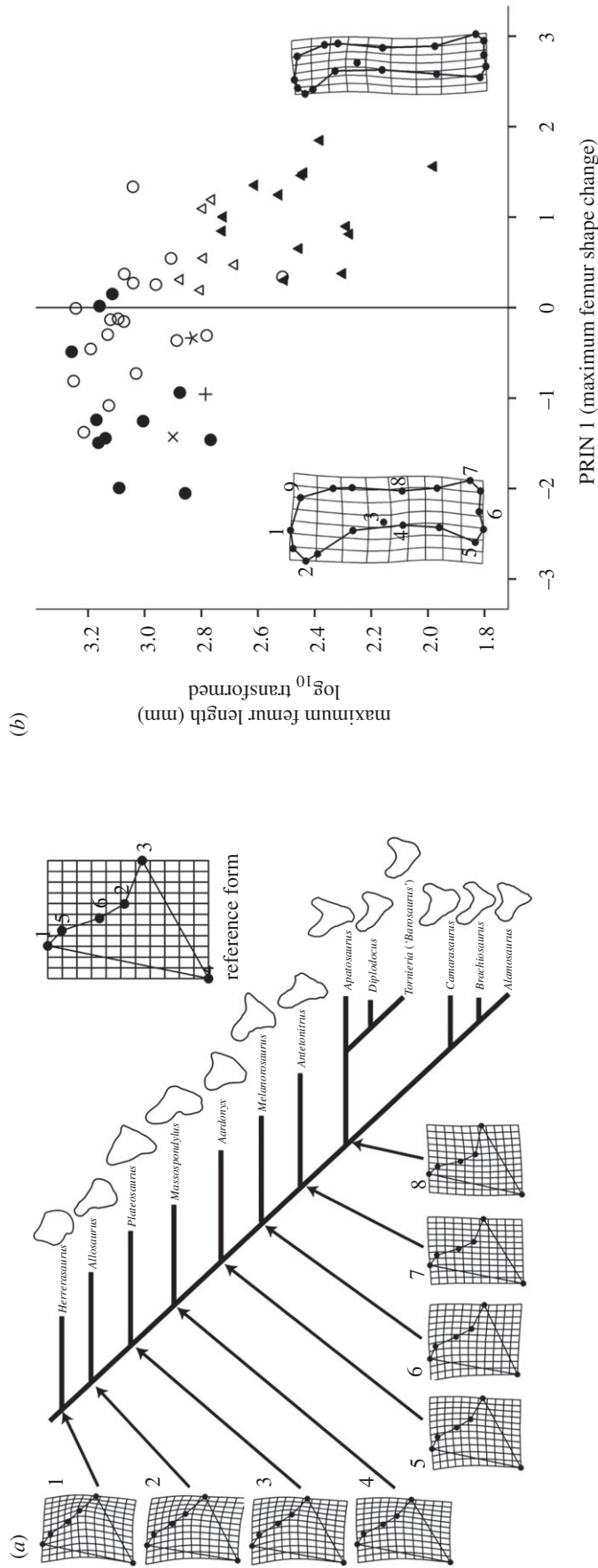


Figure 5. Geometric morphometric analysis of proximal ulna and femur shape in selected saurischian dinosaurs. (a) Proximal ulna shape. The cladogram is based on the topology from figure 4 with additional neosauropod resolution from Upchurch *et al.* (2004). The proximal outline of the ulna of each taxon is shown on the right side of the cladogram. The reference form is the scaled, rotated and aligned average of all specimens in the sample, and the deformation grids show how the proximal ulna differs from the reference form at each node. The deformation grids represent the predicted proximal ulna shape of the hypothetical common ancestor at each node: (1) Saurischia; (2) Eusaurischia; (3) Sauropodomorpha; (4) *Massospondylus* + Anchisauria; (5) *Aardonyx* + quadrupedal clade; (6) the quadrupedal clade; *Melanorosaurus* + Sauropoda; (7) Sauropoda; and (8) Neosauropoda. Note the change in deflection of the cranio-lateral process (landmarks 2,3) at node (5). (b) Sauropodomorph femur shape versus size. Note that the femur of *Aardonyx* is nested within sauropods on the graph, and that it plots within close proximity to both the basal sauropod *Antetonitrus* and sauropod sister taxon *Melanorosaurus*. Triangles are basal sauropodomorphs, circles are sauropods, the × is *Antetonitrus*, the + is *Melanorosaurus* and *Aardonyx* is represented by the asterisk. Filled triangles are *Massospondylus*, open triangles are *Plateosaurus*, filled circles are sauropods, and open circles are diplodocoid sauropods. Numbers on the femur deformation grid correspond to anatomical landmarks described in the electronic supplementary material.

these is necessarily an adaptation to quadrupedalism, although both may be adaptations to support an increasing gut volume and mass, relative to body size, which may have been facilitated by quadrupedalism. Lastly, the quadrupedal clade is diagnosed by an apparent lateral shift in the position of the cranial trochanter relative to the femoral head, such that it is visible in caudal view. The reason for this shift is unclear but it does indicate that the pelvic-femoral musculature was remodelled at this node.

Aardonyx lacks these specializations and was probably bipedal. In particular, the humerus:femur ratio is approximately 72 per cent in the smaller individual (humerus length is estimated from the radius length). The radius and ulna of *Aardonyx* clearly show that it could not actively pronate its manus to any great extent. The shaft of the radius is nearly straight with a slightly medial curvature, and the radial head is ovate, preventing its rotation about the ulna (figure 3*h–k*). Nevertheless, the ulna associated with the radius shares some similarities with those of obligatory quadrupedal sauropodomorphs. The proximal end possesses an incipient craniolateral process which produces a subtle version of the Y-shaped outline that is more fully developed in the quadrupedal clade (Bonnar & Yates 2007) (figure 3*f*). There is a shallow radial fossa, which cradles the radius craniolaterally. In articulation, the position of the radius in relation to the ulna is shifted slightly cranially owing to the presence of the incipient craniolateral process. This is similar to, but less well-developed than, the more derived cranial and medial orientation of the radius in *Melanorosaurus* and sauropods, but is insufficient to translate into a significant excursion of the distal end of the radius (see the electronic supplementary material). The distal ends of the radius and the ulna contain rugose and scarred areas that may be associated with ligaments (Bonnar 2003) (figure 3*e,h*). The presence of these features suggests that these elements were bound distally, precluding any active pronation or supination of the manus.

A geometric morphometric analysis of proximal ulna morphology in saurischian dinosaurs further supports our inferences. Using the thin-plate splines suite of programmes (Rohlf 2005), we digitized the regions of the craniomedial, craniolateral and olecranon processes as well as regions which outline the proximal shape of the radial fossa in selected saurischian ulnae. The program TPSTREE was then used to predict the shape of the hypothetical common ancestral ulna at each node in a simplified cladogram composed of our selected taxa. Landmark coordinates in each specimen were scaled, rotated and aligned and compared against a grand mean form in the sequence predicted by the phylogenetic pattern. This generated a suite of dependent shape variables known as partial warps used to compute deformation grids which predict how and where the ulna changed shape proximally at each hypothetical common ancestor.

Although these data are exploratory and cannot be said to show statistically significant differences (Zelditch et al. 2004; Bonnar 2007), nevertheless, we are intrigued that the ulna of *Aardonyx* is the first in the sequence to show a noticeable craniolateral process (landmark 3) and medially shifted radial fossa (landmarks 2, 5, 6) (figure 5*a*).

Similarly, the femur of *Aardonyx* is intermediate between the basal sauropodomorph condition (typified by *Plateosaurus* and *Massospondylus*) and that of the quadrupedal clade. The shaft retains a convex proximal lateral profile (figure 3*a*), although the sinuosity of the femur is reduced. The transverse section of the femoral shaft is also subcircular and the cranial trochanter lies in the plesiomorphic position, far from the lateral margin.

Other hindlimb features of *Aardonyx* indicate that the evolution of quadrupedalism was preceded by the evolution of a slower gait. A geometric morphometric analysis of femur shape (using TPSRelw: Rohlf (2005)) in caudal view of sauropodomorphs and sauropods shows that the femur shape of *Aardonyx* plots among sauropods, with a relatively straight femoral shaft and, notably, a more distally placed fourth trochanter (figure 5*b*; statistical details in the electronic supplementary material). A subsequent canonical variance analysis of these data assigned *Aardonyx* to sauropod femur shape (see the electronic supplementary material). As the main femoral retractor muscle of non-avian saurians, the *M. caudofemoralis longus*, inserts on the fourth trochanter (Gatesy 1990), a distal shift in this trochanter results in a lower lever ratio, greater mechanical advantage and a decrease in the velocity of femoral retraction as described previously for sauropods (Bonnar 2007).

Lastly, we note that the elements of the foot are relatively short and stout, and that metatarsal I of *Aardonyx* is remarkably robust in comparison with more basal sauropodomorphs. The maximum midshaft width is 46 per cent of its length whereas this ratio is much lower in more basal sauropodomorphs (Yates 2008). Furthermore, the transverse midshaft width of metatarsal I exceeds that of the other metatarsi, another derived sauropod-like characteristic (Wilson & Sereno 1998). These proportions indicate that the weight bearing axis of *Aardonyx* had shifted to a more medial, or entaxonic, position than in more basal sauropodomorphs where the weight bearing axis runs through digit III (mesaxony). The loss of mesaxony in *Aardonyx* is also consistent with the hypothesis that a wider-gauge gait and reduced cursorial ability preceded the evolution of an obligate quadrupedal gait. Previously, the entaxonic pes of eusauropods was thought to have evolved sometime after the divergence of *Vulcanodon* which has a plesiomorphic, mesaxonic pes (Carrano 2005). However, the hyper-robust first metatarsal of *Aardonyx*, together with those of the basal sauropods *Antetonitrus* and *Blikanasaurus* (Yates 2008), suggests that the mesaxonic pes of *Vulcanodon* (Cooper 1984) is an evolutionary reversal. Once again, it appears that our incomplete knowledge of the anatomy of near-sauropods and basal sauropods has masked substantial homoplasy associated with the assembly of the eusauropod bauplan.

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