FORELIMB STANCE AND STEP CYCLE IN *CHASMOSAURUS IRVINENESIS* (DINOSAURIA: NEOCERATOPSIA)

Stefan Thompson and Robert Holmes

ABSTRACT

A half-scale model of the complete forelimb of *Chasmosaurus irvinensis* was fabricated to test current hypotheses of neoceratopsid forelimb stance and step cycle. Using this model in conjunction with trackway data, it was determined that the forelimb stance approximated neither the upright stance of extant graviportal mammals nor the sprawling posture of primitive tetrapods. Rather, at the beginning of the propulsive phase, the distal end of the humerus was directed posteroventrally at approximately 45 degrees to the frontal plane. At this point, the elbow was strongly flexed, with the anteroventrally directed epipodials forming an angle of approximately 90 degrees with the long axis of the humerus. As the propulsive phase proceeded, the humerus gradually moves closer to the horizontal, at the end of the propulsive phase forming an angle of approximately 25 degrees to the frontal plane. At this point, the elbow was extended to its maximum, forming an angle of approximately 115 degrees with the long axis of the humerus, causing the epipodials to assume a vertical orientation. At no point in the propulsive phase did the humerus move in the parasagittal plane. Rather, the elbows were moderately everted, and the long axis of the humerus formed an angle averaging slightly less than 30 degrees to the parasagittal plane. This orientation of the humerus, which resulted in compression of medial side of the metacarpus and manus, may account for bone pathologies observed in some ceratopsid specimens. This stance, in combination with the parasagittal orientation of the rear limbs, has no precise modern analogue.

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INTRODUCTION

The origin of the Ornithodira (Pterosauria+Dinosauria, see Benton 2004) is associated with a fundamental reorganization of the limbs. The sprawling stance characteristic of primitive tetrapods was abandoned as the limbs were rotated

under the body to permit the development of a parasagittal gait. This reorganization was a necessary precondition for the appearance of bipedalism, which evolved in many early archosaurs, including the first dinosaurs. Although many later dinosaurs, such as sauropods, stegosaurs, ankylosaurs, and neoceratopsids reverted to a quadrupedal stance, none returned to the primitive sprawling posture, but rather evolved a stance roughly comparable to that seen in large mammalian quadrupeds.

In the first skeletal reconstruction of a neoceratopsid (Marsh 1891), the limbs of *Triceratops* were depicted in a more or less vertical orientation that resembled the condition in modern graviportal quadrupedal mammals. However, when skeletons were mounted for display, the front limbs were arranged in a sprawling posture, with the long axis of the humerus approximately horizontal, and projecting at a large angle from the parasagittal plane (e.g., Gilmore 1905; Sternberg 1927; Lull 1933; Osborn 1933; Erickson 1966). These reconstructions went unchallenged until the late 1960s, when Robert Bakker launched an extended campaign to revise our notion of dinosaur biology (e.g., Bakker 1968; 1975; 1986; 1987). He argued against the traditional concept of dinosaurs as essentially biologically larger versions of living reptiles, and in favour of the view of dinosaurs as active, endothermic animals. One of the consequences of this paradigm shift was a revision of our view of limb posture in neoceratopsids. The occurrence of sprawling forelimbs in an endothermic, cursorial animal was so incongruous that the possibility was rejected, and various versions of upright posture were proposed (e.g., Alexander 1991; Bakker 1986; Dodson and Farlow 1997; Ford 1997; Garstka and Burnham 1997; Paul and Christiansen 2000). As new neoceratopsid mounts were constructed and old ones refurbished, they were generally assembled with vertical, columnar forelimbs.

These views were not universally held, however. As noted by the early neoceratopsid workers, the structure of the neoceratopsid forelimb did not permit upright posture unless it was forced to do so (Gilmore 1905; Sternberg 1927; Erickson 1966). In an analysis of the biomechanics of an articulated forelimb of *Torosaurus*, Johnson and Ostrom (1995) noted that the glenoid condyle of the humerus is located on the external, rather than proximal, surface of the proximal expansion of the humerus as is the case in most other dinosaurs. They also observed that the glenoid of the scapulocoracoid faces more or less posteriorly rather than ventrally. When the proximal articular condyle of the humerus is placed into the glenoid, the humerus automatically assumed a horizontal attitude. If the humerus is rotated into a vertical position, any attempt to maintain the humeral head in the glenoid forces a rotation of the humerus so that the deltopectoral crest projects anterolaterally, making effective functioning of the pectoralis musculature problematic. Although the rib cage was not included in the model, it was argued that the medial side of the broad proximal humeral expansion (the lesser tubercle) of a parasagittal humerus would have projected into the rib cage. In addition, they pointed out that the articulations for the ulna and radius are "offset," causing the plane of elbow extension and flexion to deviate significantly from the long axis of the humerus, rendering a parasagittal gait in neoceratopsids unfeasible. Johnson and Ostrom (1995) concluded that the humerus of neoceratopsids must have projected horizontally from the trunk at close to right angles to the sagittal plane, with the elbow remaining strongly bent throughout the step cycle. Forward progression occurred as the humerus rotated about its long axis, operating rather like the axis of a wheel, with the epipodials representing one spoke in that wheel, transferring the locomotor force to the foot which functioned as a portion of the rim of the "wheel."

Resolving these diametrically opposed interpretations of neoceratopsid forelimb stance is difficult for a number of reasons. Articulated, complete specimens are rare, and most mounts are composites. The bones are large and fragile, making manipulation problematic. Johnson and Ostrom (1995) had the advantage of an articulated, well-preserved specimen, of which they could make casts. These were used to experiment with various limb positions. However, the scope of their conclusions was limited by the absence of the rib cage, carpus, metacarpus, and manus in this specimen.

In one recent analysis, Paul and Christiansen (2000) argue that the forelimb of neoceratopsids did not conform to either the sprawling or fully erect, essentially graviportal stereotype. Rather, the humerus was strongly retracted posteriorly, and was capable of swinging through a 70 degree arc that took it from approximately horizontal to quasi-vertical in orientation. The traditionally postulated anatomical impediments to parasagittal gait were countered with plausible arguments based on the authors' observations of neoceratopsid osteology. In particular, it was argued that incorrect orientations of ribs and vertebral attachments have

resulted in an inaccurate placement of the scapulocoracoid (and therefore glenoid orientation), and that insufficient use has been made of trackway data. A number of informative figures were produced, but it was not possible at the time to test their hypothesis with a working model.

In 1958, Dr. Wann Langston collected a specimen of *Chasmosaurus* near the town of Irvine, Alberta. The skull was later prepared, and a new species, *Chasmosaurus irvinensis,* was erected to accommodate the specimen (see Holmes et al. 2001 for details). The better part of the postcranial skeleton was preserved, including a largely complete but somewhat distorted rib cage, a complete right front scapulocoracoid, limb, and articulated manus. Anatomical data sets of comparable completeness and quality are rare, but not unknown in ceratopsid neoceratopsians (e.g., Brown 1917; Brown and Schlaikjer 1937; Lull 1933). However, these specimens have been rendered as display pieces, either as a panel mount or otherwise mounted so as to make manipulation of individual elements impossible. The specimen described here has been completely freed from the matrix, permitting access to all aspects of the preserved anatomy. This has provided a unique opportunity to fabricate and assemble an accurate, half-scale model of the girdle and limb to test current hypotheses of neoceratopsian forelimb stance.

MATERIALS AND METHODS

This study is based on the right forelimb of *Chasmosaurus irvinensis* (CMN 41357). Half-scale models of the elements of the girdle and limb were sculpted in modeling clay and plastic foam, using proportional dividers to maintain accuracy. Information from the left scapulocoracoid, as well as from the undistorted scapulocoracoid of CMN 344 (*Styracosaurus albertensis*), was used as a reference during the reconstruction of the scapulocoracoid. Poly 74-30 RTV liquid silicon rubber moulds were taken from these models, and casts were made in thixotropic polyester resin. Thin, flexible wires were imbedded in each replica so that they could be held in place during the simulation of the step cycle. The rib cage, although somewhat distorted, is largely complete. Comparison with the less distorted rib cage of the type of *Styracosaurus albertensis* (CMN 344) indicates that, in both curvature and nature of their articulations to their respective vertebrae, the rib at each segment of the cervical and thoracic column is closely comparable in the two taxa. It was therefore possible, using CMN 344 as a reference, to reconstruct the shapes and orientations of the ninth (last) cervical, second, fifth, seventh, and ninth thoracic ribs with stiff copper wire. Another wire was bent to match the curvature of the presacral column of CMN 344, and the rib replicas were fixed to it. In this way, the approximate size and shape of the rib cage were reconstructed. This assembly was supported on two wooden dowels that were cut to lengths based on the assumption that an individual of *Chasmosaurus* would have stood approximately 1.5 metres at the hip (Dodson 1996). The ends of the dowels were inserted into metal brackets that allowed the entire assembly to stand upright, unsupported. The medial edge of the coracoid was placed close to the midline, and after considerable experimentation to find the best fit between the rib cage and scapula, the scapulocoracoid was wired into place.

Before the rest of the model was assembled, the various subunits (e.g., the ulna-radius and humerus) were articulated, and potential range of motion was investigated. This permitted us to position the elements as we assembled an initial pose.

The metacarpus and manus were assembled and wired together as a unit. In order to estimate the orientation of the digits, as well as the distance of the manus from the midline, published neoceratopsid trackway data (Lockley and Hunt 1995) were used. The trackway, probably made by the much larger (but similar with respect to pectoral girdle and limb anatomy) neoceratopsid *Triceratops,* was scaled down until the assembled manus could be fit inside the boundaries of the manus print. The scaled print was stencilled onto a base. The midline of the trackway, defined as the midpoint between the outer edges of the manus prints, was drawn in, and the rib cage/scapulocoracoid (hereafter referred to as torso) unit was placed so that the sagittal plane was directly over the midline of the track way.

The orientation of the manus was determined by aligning the digits with the individual toe prints preserved in the trackway. With the manus in place, the humerus, ulna, and radius were attached. The torso was moved "anteroposteriorly" along the midline of the track way until all bones attained a "best fit" with the limb in approximately mid-stance. From this reference point, the torso was advanced along the midline as the model was moved through a simulation of a step cycle. At all points, the orientations of all elements were dictated by the following parameters: 1) the digits of the manus were maintained in alignment with the toe marks of the manus print throughout the propulsive phase of the cycle; 2) articulations were

Table 1. Selected parameters of the neoceratopsid step cycle as determined from the model. Orientations of the long axes of the propodium and epipodials of the model (see table illustration next page) with respect to the horizontal (frontal) and parasagittal planes are in degrees. The forelimb positions in the left hand column correspond to those in the text and in Figures 7 and 8. See the text for further explanation. A_1, angle of humeral depression relative to the horizontal, lateral view; A_2, angle of humeral eversion relative to the parasagittal, anterior view; A_3, angle of humeral eversion relative to the parasagittal, dorsal view; B_1, ulnar orientation, angle of long axis to the horizontal, lateral view; B_2, ulnar orientation, angle of the long axis to the horizontal, anterior view; C_1, radial orientation, angel of the long axis to the horizontal, lateral view; C_2, radial orientation, angle of long axis to the horizontal, anterior view; E.E., angle formed by long axes of ulna and humerus; F.M.glen., forward progression of the glenoid since the previous forelimb position (in mm.

| Forelimb Position	A_1	A_2	A_3	B_1	B_2	C_1	C_2	E.E.	F.M. glen.
1	43	32	29	43	3	50	17	89	0
2	37	38	27	50	2	55	8	92	54
3	25	59	32	82	8	90	18	105	120
4	24	55	25	96	8	98	14	114	83
5	23	57	27	97	0	104	9	114	----
6	10	68	23	79	9	89	5	94	----
7	20	61	24	75	3	80	9	91	----
8	33	51	25	55	2	65	16	87	----

maintained at all joints; and 3) the torso did not deviate from the midline (we are not suggesting that this could not have occurred, but simply that, since there is no way to estimate the extent of lateral movement that may have occurred, this potential variable should be held constant for the purposes of this simulation). Each point in the simulated step cycle was photographed in lateral, anterior , and dorsal views. The angular relations of the humerus, ulna, and radius to the parasagittal and horizontal (frontal) planes, as well as the angle formed by the epipodials on the humerus were taken directly from the images (Table 1). For the purpose of these measurements, the long axes of the bones were drawn through the centres of their shafts, in the humerus, extending from the centre of the trochlear notch distally to the lateral edge of the glenoid condyle, and in the ulna, passing through the centre of the semilunar notch and extending distally to bisect the distal expansion (Table 1).

CAVEATS

It is impossible to reconstruct the step cycle of an extinct animal beyond a certain level of accuracy. Even if the bony joints are undistorted, joint cartilages are not preserved, and the underlying joint surfaces can infer only approximate range of movement. This is a particular problem in most dinosaurs, in which the articular surfaces appear to be generally less well ossified than in either living crocodiles or squamates. Other data are com-

Table 1 illustration. *Chasmosaurus irvinensis*, CMN 41357. Long axes of propodium and epipodials used to quantify their orientations relative to the horizontal and parasagittal planes (see Table 1). 1, lateral view; 2, anterior view. a, parallel to the dorsal surface of the humerus, passing through the centre of the trochlear notch and along the outside (anterior) edge of the glenoid condyle; b, parallel to the extensor surface of the radius and bisecting the proximal and distal expansions; c, from the proximal edge of the proximal articular surface, through the center of the semilunar notch, and bisecting the distal expansion.).
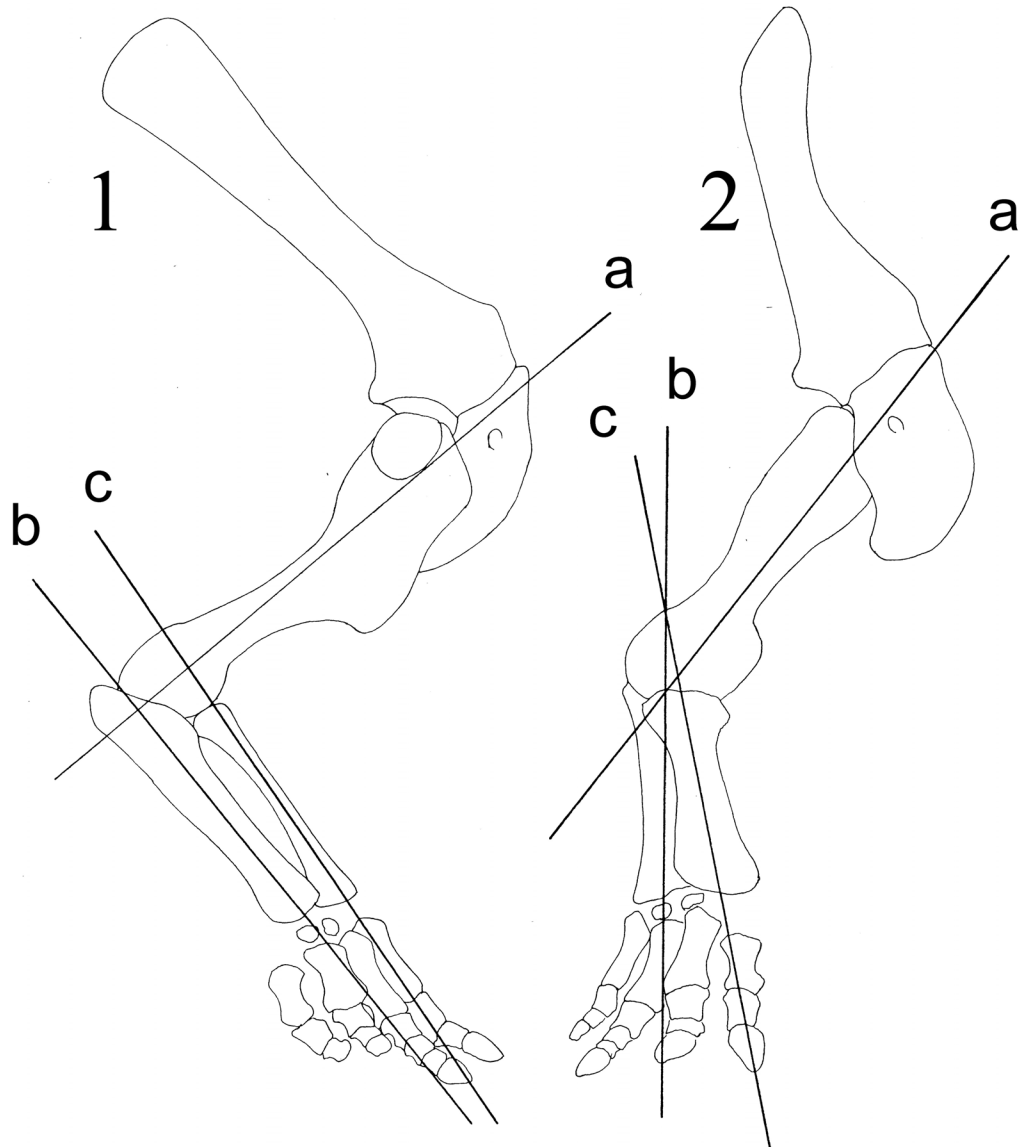
pletely missing. For example, there was almost certainly significant movement of the scapulocoracoid during locomotion (Paul and Christiansen 2000), but since there is no bony articulation with the rib cage, it is impossible to estimate the excursion. Although the presence of ossified tendons, as well as the close association between the pelvic girdle and posterior ribs suggests that, unlike most primitive tetrapods, the vertebral column underwent little or no lateral flexion during locomotion (Ford 1997; Paul and Christiansen 2000), even modest movement, if it did occur, could affect stride length. In any limb with multiple joints, many variants in specific stances are potentially consistent with evidence derived from data such as total joint excursion inferred from osteological features and trackways. In our simulation, we have tried to be conservative in estimating range of movements at joints by keeping well within the physical boundaries of the preserved joint surfaces. Specifically,

we would only move a joint until the edges of the opposing surfaces meet, and further excursion could only be accomplished by separation of the joint surfaces. In cases where it was not possible to even estimate range of movement, such as scapulocoracoid excursion on the rib cage and lateral undulation of the trunk, the joints involved were held immobile.

Although complementary adjustments in angles of some of the joints in the limb can produce multiple postures at each stage of the step cycle (limb segment redundancy – see Hutchinson and Gatesy 2006), we would argue that there are still enough constraints imposed by the manus print and glenoid orientation to restrict the possibilities to a relatively small subset of (for our purposes) very similar possibilities. Thus, even within the limitations of the following admittedly restricted data set, we believe that is possible to draw some useful conclusions regarding limb stance and step cycle in *Chasmosaurus*, and by extension, neoceratopsids in general.

Trackway data are essential if the orientation of the manus is to be estimated. Although numerous trackways attributable to sauropods, ornithopods, and theropods are known (Fastovsky and Smith 2004), neoceratopsid trackways (attributable to *Triceratops*) have been identified unequivocally from only one locality (Lockley and Hunt 1995). Thus, we are obliged to use trackways belonging to another (albeit closely related) neoceratopsid in the current study. However, postcranial anatomy differs little within ceratopsid neoceratopsians (Forster and Sereno 1997), and it is reasonable to assume that forelimb kinematics was closely comparable in all members of this group.

The specific orientations reconstructed for the various elements of the limb of a particular model at each point of a plausible step cycle will no doubt depend on such factors as the preservational quality and extent of ossification that are particular to the specimen upon which it is based. Thus, the angles presented in this study should be taken as representative of this specimen of *Chasmosaurus* only. We ran this simulation several times, and obtained very consistent results. We had considered rounding the measurements taken from the final (and most meticulously executed) simulation presented in this study to avoid giving the impression that these were intended to represent a precise description of the step cycle of *Chasmosaurus*, but decided to leave this to the reader. Rather, these numbers are intended to represent, literally, the results of a simulated step cycle based on a particular specimen of *Chasmosaurus* under the constraints described above. To the extent that the anatomy of the limb elements of other specimens of *Chasmosaurus*, and for that matter, other neoceratopsids, resembles that of our specimen, we predict that their step cycle would approximate ours. We will leave it to others to test that prediction.

DESCRIPTION OF THE RIB CAGE, FORELIMB, AND GIRDLE

The anatomy of the ribs, pectoral girdle, and forelimb of *Chasmosaurus irvinensis* is closely comparable to that described in other ceratopsids (e.g., Hatcher et al. 1907; Brown 1917; Lull 1933, Dodson et al. 2004).

Almost all of the ribs and presacral vertebral column of CMN 41357 are preserved. Although the vertebral column is badly distorted and some of the ribs are crushed, there is a good representative sample of relatively undistorted ribs from all regions of the rib cage. They confirm that the posterior cervical and anterior-most thoracic ribs turn sharply ventrally at their necks, and are otherwise almost completely straight, resulting in a distinctly narrow chest between the pectoral girdles (Paul and Christiansen 2000). A gentle curvature develops by the fourth or fifth thoracic rib, and by about the ninth thoracic rib, the rib cage forms a broad barrel.

Both scapulocoracoids are preserved (Figure 1). Although the coracoids have been folded under slightly, the morphology of the elements is clear. The medial surface of the scapular blade is only slightly concave. The strongly concave coracoid contribution to the glenoid "closes" the articular surface proximally, resulting in a glenoid that faces at right angles to the long axis of the scapulocoracoid.

The humerus, ulna, and radius (Figures 2, 3) are all slightly crushed, but are well preserved and can be articulated without difficulty. As in other neoceratopsids (e.g., Johnson and Ostrom 1995), the proximal humeral condyle is located on the dorsal (external) surface of the proximal humeral expansion and is offset to a position posterior to the axis of the humeral shaft. The distal expansion bears two distal condyles separated by a groove (the trochlea) to receive a ridge on the proximal articular surface of the ulna. The anterior (preaxial) condyle bears a convex capitular facet on its ventral (extensor) surface to receive the radius. The proximal articular surface of the ulna is divided into two concave surfaces by a ridge that fits into the

Figure 1. *Chasmosaurus irvinenesis*, CMN 41357. 1-3, Right scapulocoracoid in lateral, medial, and posterior views. 4-5, left scapulocoracoid in lateral, medial, and posterior views. Scale bar represents 10 cm.

Figure 2. *Chasmosaurus irvinenesis*, CMN 41357. Right humerus in 1, ventral and 2, dorsal views. Scale bar represents 10 cm.

Figure 3. *Chasmosaurus irvinenesis*, CMN 41357. 1, right ulna in anterior view; 2, right radius in anterior view; 3, right radius in posterior view; 4, right ulna in posterior view. Scale bar represents 10 cm.

trochlear notch of the humerus. The posterior of these two surfaces articulates with the anterior half of the posterior distal humeral condyle, and the anterior surface with the posterior half of the anterior humeral condyle. A prominent olecranon projects proximally from the rim of the articular surface. The radius bears an oval, concave terminal facet that articulates with the ventral (capitular) surface of the anterior humeral condyle. When the epipodium is in articulation with the humerus, the proximal head of the radius lies in a bowl-shaped depression on the flexor surface of the ulna. The long axes of the ulna and radius diverge distally. The distal end of the epipodium, formed by the expanded distal ends of the two bones, forms a broad arc.

As in other well-preserved neoceratopsid forelimbs (e.g., *Centrosaurus* AMNH 5351, Brown 1917), all but the third and fourth distal carpals are absent, and probably never ossified. The entire metacarpus and manus (Figure 4) are well preserved in articulation. Five digits are present. As in *Centrosaurus apertus* (Brown 1917), the phalangeal formula is 2-3-4-3-2 (Figure 5). Terminal phalanges of digits 1-3 show clear evidence of keratinous hooves. Terminal phalanges 1 and 2 are distinctly larger, suggesting that the preaxial (medial) side of the manus bore most of the weight or sustained more stress during locomotion. The distal-most phalanx on each of digits 4 and 5 bears

what appears to be a terminal articular facet. However, as in the similarly articulated and well-preserved mani of *Centrosaurus apertus* (Brown 1917), there is no trace of a hoof-bearing terminal phalanx associated with either digit, suggesting that they were not present in life, or possibly never ossified. The distal articular facets of the metacarpals have extensive dorsal exposure, indicating considerable potential for dorsiflexion of the manus, permitting a digitigrade stance. The combined proximal articular surface of the articulated metacarpus forms a broad arch (Figure 4.1). As a result, the digits are distinctly splayed (Figure 4.1).

RECONSTRUCTION OF THE STEP CYCLE

The Neutral Position

When a quadruped takes a step, the front limb is extended, the manus is placed on the substrate, and through contraction of muscles originating from the trunk and inserting on the forelimb, the body is pulled over the manus, while the manus remains stationary. This first half of the step cycle is here referred to as the propulsive phase. Only at the end of the propulsive phase is the manus
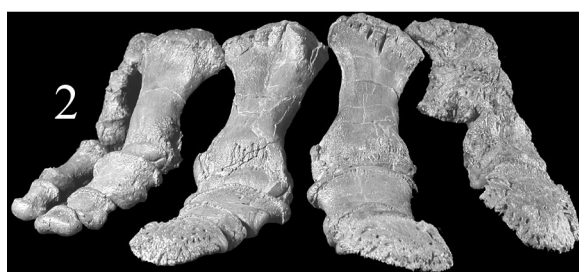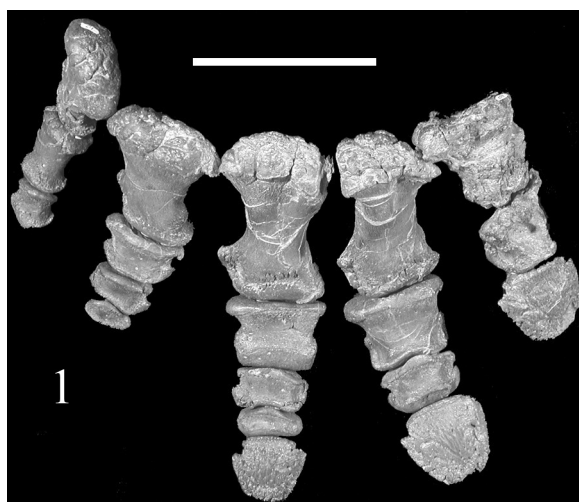
Figure 4. *Chasmosaurus irvinenesis*, CMN 41357. Articulated right metacarpus/manus in 1, dorsal; 2, anterior; and 3, lateral views. Scale bar represents 10 cm.

Figure 5. *Chasmosaurus irvinenesis*, CMN 41357. Disarticulated right metacarpus/manus in dorsal view. Pathological metacarpal I and proximal phalanx of first digit reconstructed in outline. Scale bar represents 5 cm.

raised off the ground. During the second half of the step cycle, referred to here as the protractive phase, the manus is swung forward again. It can be assumed that, at least in a steady walking gait, the protractive phase will comprise approximately half of the complete step cycle, both in terms of time and distance traveled by the animal.

The analysis of the propulsive phase was begun by determining the most comfortable fit between the scapulocoracoid and the rib cage. In this position, the blade is 44 degrees to the horizontal, and the glenoid cavity faces primarily ventrally and posteriorly, and only slightly laterally. The limb was assembled with each element articulated at approximately the midpoint between the
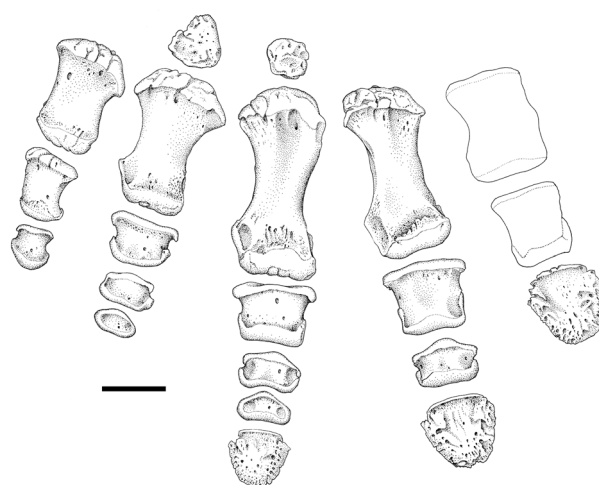
extremes of its joint excursions. This limb stance is hereafter referred to as the "neutral position" (Figures 6, 7.2, 8.2).

The ulna and radius were first articulated with the humerus, and the range of motion of the epipodium on the humerus was estimated. Only modest flexion/extension appears to have been possible, with the epipodium strongly flexed on the humerus. When articulated with the humerus, the transverse axes of the distal expansions of the ulna and radius do not lie in the same plane, but intersect at an angle of nearly 90 degrees. As a result, the combined distal articular surfaces of the ulna and radius describe a broad arc.

When the manus is placed in the manus print, the second digit is directed anteriorly, the first digit anteromedially, and digits three to five are directed progressively more laterally, with the extensor surface of the fifth metacarpal and digit facing more or less directly laterally. The splaying of the digits occurs because the metacarpus is strongly arched, the curvature of which closely matches the arc described by the distal end of the epipodium. A gap of 15 mm was maintained between the epipodium and metacarpus to allow for the cartilaginous carpus. Although the third and fourth distal carpals are preserved, the remainder of the carpus is absent, and presumably never ossified. However, it was possible to align the distal end of the epipodium and proximal end of the metacarpus by matching their arched articular surfaces. When the epipodium is articulated with the metacarpus, and the humerus to the glenoid, the long axis of the
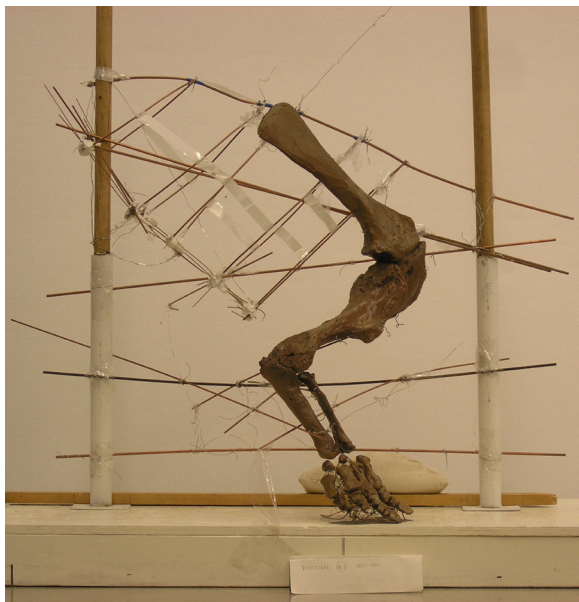
Figure 6. *Chasmosaurus irvinenesis*, CMN 41357. Half-scale model of front right limb mounted on fabricated torso in lateral view.

humerus, viewed laterally, forms an angle of 37 degrees to the horizontal and, viewed anteriorly, is everted 27 degrees from the parasagittal plane. In this position, the medial tubercle of the humerus lies just in front of the ninth cervical rib. To determine the proximity of the medial tubercle to the rib cage, the shape of the rib cage anterior to the ninth cervical rib was conservatively estimated by projecting the straight line connecting the outer surfaces of the second thoracic and ninth cervical ribs anteriorly. This line passes 15 mm medial to the edge of the tubercle. This clearance is likely underestimated, since the more anterior cervical ribs are shorter and straighter than the ninth cervical rib, resulting in an even narrower anterior portion of the chest than indicated by our estimate. In any case, there is no reason to assume interference between the tubercle and rib cage, as has been hypothesized (Johnson and Ostrom 1995; Dodson 1996; Dodson and Farlow 1997) when the humerus is held in this position. The glenoid, taken in isolation, would permit significant medial travel of the distal end of the humerus. However, if the elbow is brought significantly closer to the midline at this point in the step cycle, the medial tubercle of the humerus would interfere with the rib cage. If the elbow were everted further, the humeral head would move laterally out of the glenoid, causing the shoulder joint to disarticulate. In both cases, the manus would move out of the trackway print.

Viewed laterally, the long axis of the ulna is directed anteromedially at 50 degrees to the horizontal and viewed anteriorly, 2 degrees to the parasagittal.

Viewed laterally, the long axis of the radius forms an angle of 55 degrees to the horizontal and, viewed anteriorly, 8 degrees to the parasagittal.

The Propulsive Phase

The beginning of the propulsive phase (Figures 7.1, 8.1), here designated position 1, was established by moving the torso posteriorly from the "neutral position" while maintaining the manus in its print until at least one of the joints in the model could no longer be maintained in articulation (see "Materials and Methods"). The end of the propulsive phase (Figures 7.4, 8.4), here designated position 4, was determined by moving the torso anteriorly over the stationary manus until at least one of the joints had been flexed or extended fully. Two additional positions, the neutral position (position 2 – Figures 7.2, 8.2) and one midway between the neutral position and the end of the propulsive phase (position 3 – Figures 7.3, 8.3), were also simulated. At each position, medial excursion was constrained by the medial tubercle and lateral excursion by glenoid shape. Each position was photographed in lateral (Figure 7) and anterior (Figure 8) views. The angles formed by the projections of the long axes of the humerus, ulna, and radius relative onto the horizontal (frontal) and parasagittal planes (Table 1) were measured directly from the photographs.

Position 1 (Figures 7.1, 8.1) represents the point at which the manus was first placed on the substrate at the beginning of the propulsive phase. The humerus was at its most protracted, with its long axis, viewed laterally, at 43 degrees to the horizontal and everted 29 degrees from the parasagittal (Table 1). Contact between the ventral surface of the humeral head and the ventral rim of the glenoid prevented further protraction. The elbow was flexed so that the ulna formed an angle of 89 degrees with the humerus. The sigmoid notch of the ulna articulated closely with the trochlea of the humerus, restricting rotation of the ulna about its long axis. The ulna and radius "crossed" proximally (Paul and Christiansen 2000), with the proximal head of the radius fitting into a depression on the extensor surface of the ulna immediately distal to the semilunar notch. The ulna formed angles of 43 and 3 degrees, and the radius, 50 and 17 degrees, with the horizontal and parasagittal, respectively.
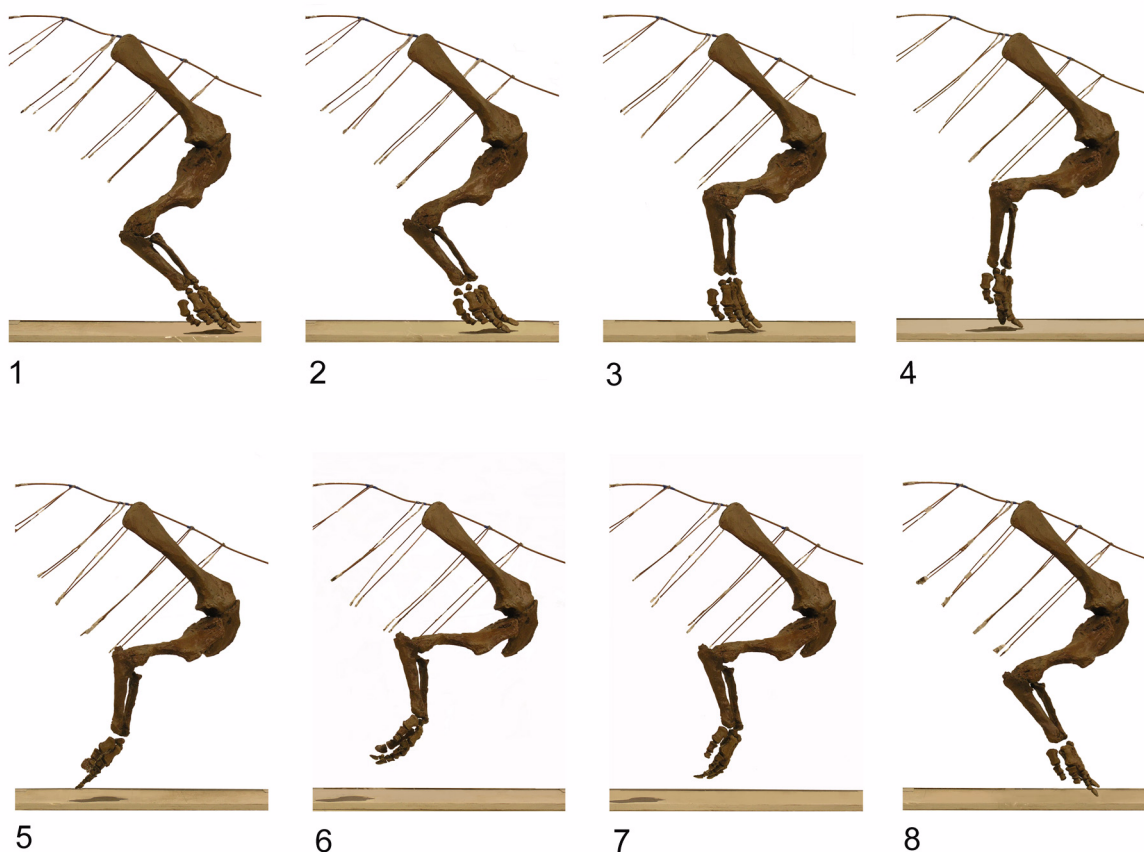
Figure 7. *Chasmosaurus irvinenesis*, CMN 41357. Step cycle in lateral view. For more information, see text and Table 1. 7.9. A simulation of the step cycle of *Chasmosaurus irvinensis* produced by splicing still images together in sequence (online).

As the forelimb moved to position 2 (Figures 7.2, 8.2), the torso of the model advanced 54 mm. The humerus retracted to a slightly more horizontal position, now forming an angle of 37 degrees to the horizontal plane and everted 27 degrees from the sagittal. To maintain the distance between the shoulder joint and the substrate, the elbow joint opened slightly (to 92 degrees) causing the epipodium to attain a more vertical orientation. To remain in articulation with the lateral condyle of the humerus, the ulna, and the manus, the proximal facet of the radius were required to migrate along the humeral condyle. The epipodium rotated closer to vertical. The humerus rotated slightly on its long axis to maintain the distal ulna and radial articulations with the manus.

As the forelimb moved to position 3, the torso advanced an additional 120 mm (Figures 7.3, 8.3). The humerus was more everted than at any other point in the propulsive phase, forming 32 degrees with the parasagittal. This orientation was necessary to maintain the proper relationship between the ulna, radius, and manus, otherwise, the radius moved too far medially, and would have disarticulated from the carpus. In order to maintain the distal end of the ulna in close enough proximity to the metacarpus, the humerus was rotated about its long axis, resulting in a more ventrally directed deltopectoral crest and more laterally facing external surface of its proximal expansion (Figure 7.3). The distal end of the humerus continued to swing dorsally, with the long axis of the humerus now forming an angle of 25 degrees with the horizontal. The elbow continued to open (105 degrees to the humerus), swinging the epipodium into a more vertical orientation. However, this movement was not sufficient to maintain a constant distance between the epipodium and metacarpus. To prevent the shoulder from moving ventrally, the metacarpals and proximal phalanges were rotated into a more vertical position. This is associated with increased dorsiflexion of the manus, but the relative positions of the distal ends of the digits did not change.
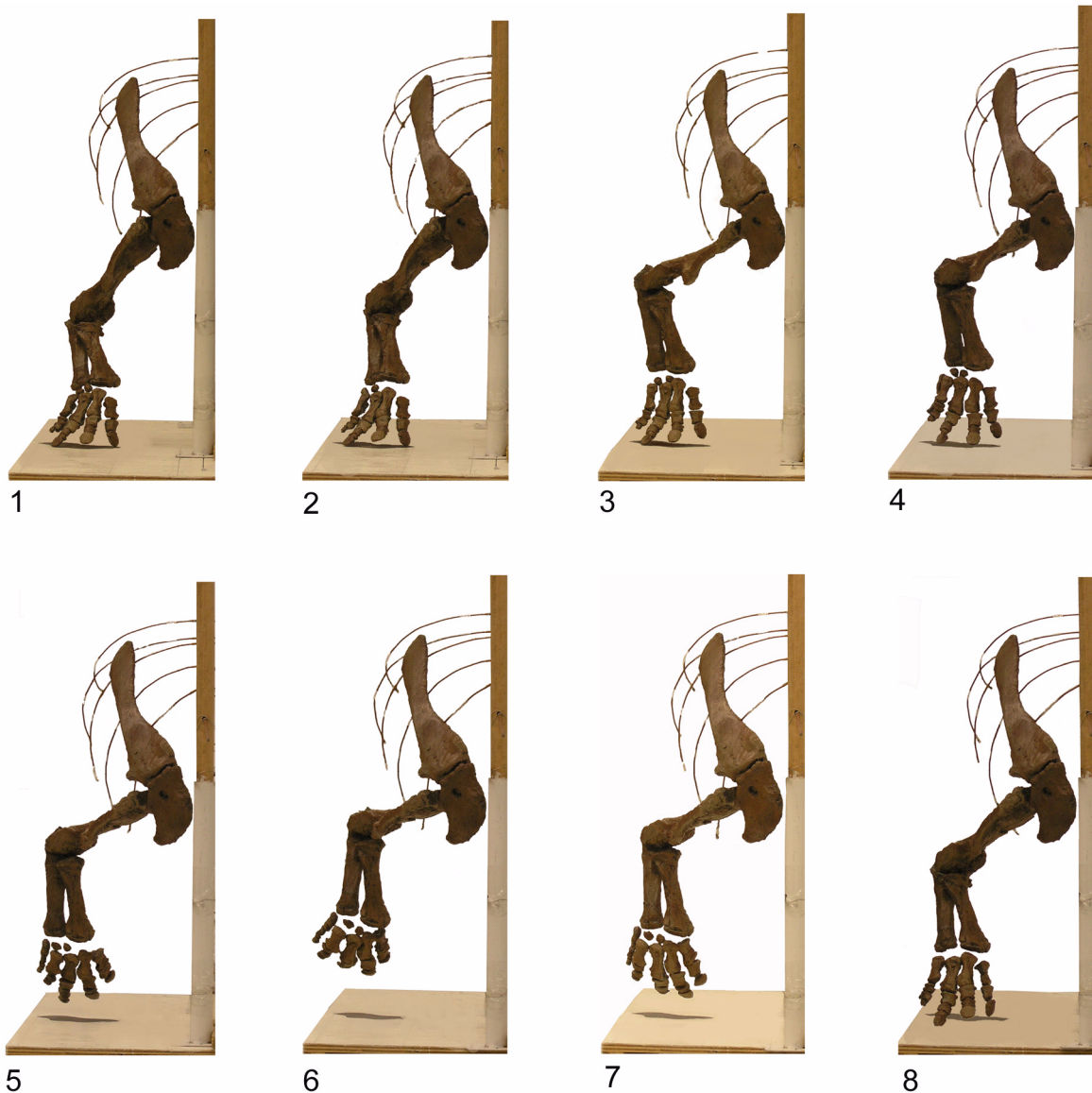
Figure 8. *Chasmosaurus irvinenesis*, CMN 41357. Step cycle in anterior view. For more information, see text and Table 1.

As the forelimb moved from position 3 to position 4 (Figures 7.4, 8.4), the torso advanced an additional 83 mm. Throughout this transition the distal end of the humerus rotated only one additional degree dorsally. Almost all of the forward propulsion during this phase of the cycle was derived from extension of the elbow joint. As the humero-ulnar articulation opened up completely, the distal end of the ulna swung laterally. In order to prevent the manus from being dragged laterally across the substrate, the distal end of the humerus was required to rotate medially. When position 4 was attained, the long axis of the humerus formed an angle of only 25 degrees with the parasagittal plane and 25 degrees from the parasagittal. The ulna became progressively more elevated, raising the lateral side of the manus off the substrate and shifting the weight toward the radial side of the manus. Position 4 represents the orientation of the forelimb just before the foot was lifted off the ground. The manus was at its point of greatest dorsiflexion to maintain proper relations between the epipodium and metacarpus without causing the glenoid to move ventrally. The elbow joint was maximally extended (114 degrees, and the epipodium is directed ventrally and slightly posteriorly.
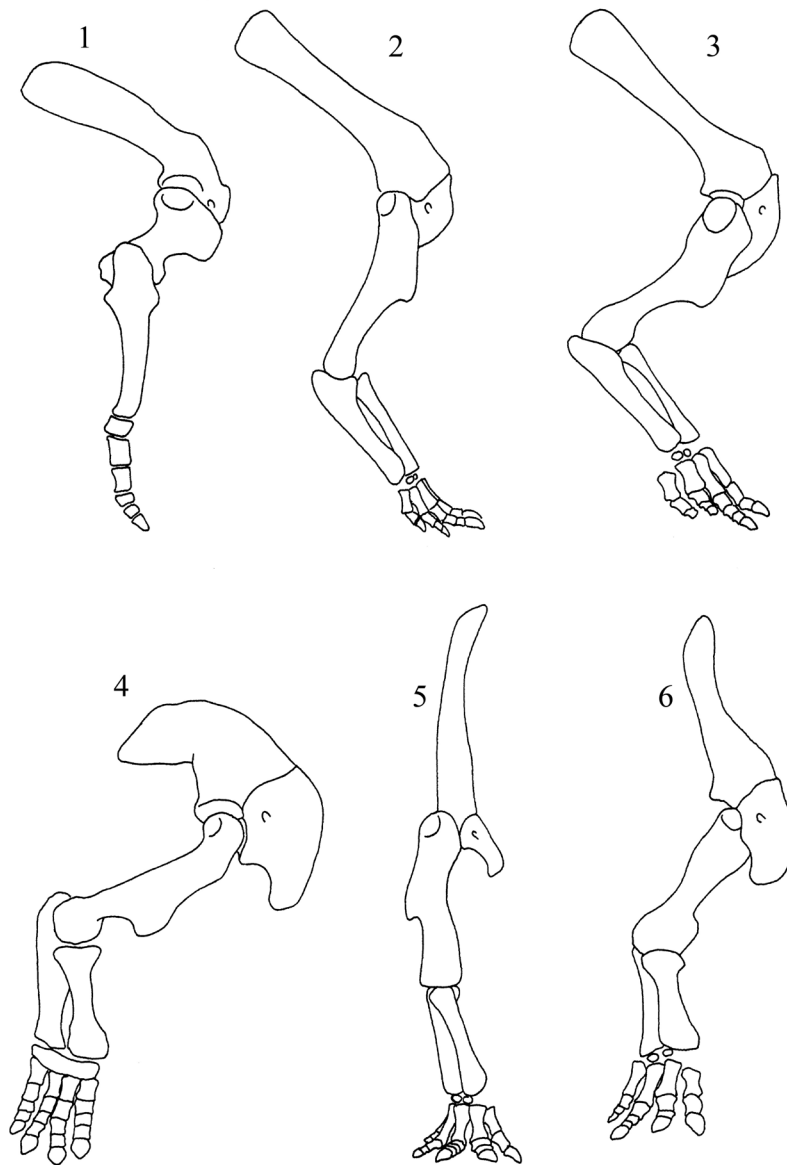
Figure 9. Competing hypotheses of forelimb orientation in ceratopsids. Right front forelimb in anterior (1-3) and lateral (4-6) views. 1 and 4, sprawling stance; 2 and 5, fully upright; 3 and 6, as demonstrated in this paper. 1 and 3 based on information from Johnson and Ostrom 1995; 2 and 5 based on information from Paul 1987.

The lateral digits (four and five) had to be moved well off the substrate in order to maintain articulation between the metacarpus and ulna, shifting the weight to the preaxial side of the manus. As the manus pushed off the substrate, the first digit lost contact first. The second and third digits then appear to have lifted off the substrate simultaneously. In this simulated propulsive phase, the torso advanced a total of 257 mm.

The Protractive Phase

There is no way to determine the orientation of the manus during the protractive phase of the step cycle. However, as in the propulsive phase, the geometry of the joint surfaces sets some limits: the medial tubercle still must not interfere with the rib cage, and since known trackways show no evidence of knuckle drag, there must be an appropriate combination of distal humeral elevation and elbow flexion to allow the digits to remain clear of the substrate throughout the protractive phase. Within these admittedly incomplete parameters, we

have attempted to reconstruct a plausible protractive phase (Figures 7.5-8, 8.5-8). Once the digits have cleared the ground at the end of the propulsive phase, they are free to plantarflex. This, in combination with the posterior flexion of the wrist, is sufficient to keep the digits free of the substrate without requiring significant elevation of the distal end of the humerus during the initial stage of the protractive phase (Figures 7.5, 8.5). However, in order to "set up" the manus for the remainder of the protractive phase, it was necessary to simultaneously elevate the distal end of the humerus to its maximum allowable travel in the glenoid, while simultaneously strongly flexing the elbow joint (Figures 7.7, 8.7). This flexion begins early in the protractive phase (Figure 7.7). If the elbow remains flexed throughout most of the protractive phase, the distal end of the humerus can drop without creating knuckle drag, swinging the manus anteriorly (Figures 7.7-8, 8.7-8). As this occurs, the manus swung through a broad lateral arc (Figure 8.7-8). Since the manus was not constrained by any contact with the substrate, there were no factors preventing such a movement; however, there is no evidence, other than that the model moved most naturally in this manner, that this would have actually occurred in the living animal. In the last portion of the protractive phase, elbow extension combines with continuing humeral depression to place the manus onto the substrate to begin the next step cycle (Figures 7.8, 8.8).

DISCUSSION AND CONCLUSIONS

This simulation demonstrates that, even if a wide margin of error is allowed, the forelimb posture in *Chasmosaurus* cannot be categorized as either upright (Bakker 1987, Figure 9.2, 5 of this paper) or sprawling (Johnson and Ostrom 1995, Figure 9.1, 4 of this paper), but is rather more or less "semi-erect," closer to the stance suggested by Dodson and Farlow (1997) and Paul and Christiansen (2000). Because the posterior cervical and first few thoracic ribs have tightly turned necks and more or less straight shafts, the anterior part of the rib cage is quite narrow. As a result, the scapula diverged posteriorly only slightly from the parasagittal plane, and the glenoid faced primarily posteriorly and only slightly laterally, as suggested by Paul and Christiansen (2000). In order to articulate with the glenoid, the distal end of the humerus had to be rotated posteriorly. However, retraction of the humerus is limited by the medial tubercle. Consequently, the elbows remained somewhat everted, in our simulation varying from 25 to 32 degrees

from the parasagittal plane during the propulsive phase. This is more everted than predicted by Paul and Christiansen (2000), but close to the angle suggested by Dodson and Farlow (1997).

At maximum protraction, the long axis of the humerus was 43 degrees to the horizontal, at maximum retraction, about 24 degrees to the horizontal, with the capacity to elevate the humerus an additional 14 degrees during the protractive phase. Thus, throughout the step cycle, the humerus remained closer to the horizontal than vertical, and its range of motion (33 degrees if the protractive phase is included) was much more restricted than the 70 degrees predicted by Paul and Christiansen (2000, figure 4e). As pointed out by Johnson and Ostrom (1995), the elbow is strongly flexed throughout the entire step cycle, ranging from 87 to 114 degrees to the humerus. A sequence of images of the limb assembled to simulate the step cycle is provided in Figure 7.9.

This simulation makes it clear why many traditional reconstructions of neoceratopsid forelimb stance include a strongly everted humerus. In these analyses, both the distal end of the epipodium and the metacarpus (and therefore manus) has been reconstructed as broad and flat (e.g., Johnson and Ostrom 1995, figure 12.7). Our specimen shows clearly that both were strongly arched, so that even when the humerus was strongly retracted, the distal extensor surface of the radius faced almost directly anteriorly. As noted by Paul and Christiansen (2000), footprint data (Lockley and Hunt 1995) indicates that the manus is directed anterolaterally (or to be more precise, the digits splay so that the first digit actually is directed somewhat medially, the second more or less directly anterior, and digits three through five are directed progressively more laterally) during the propulsive phase. If the humerus of our model is forced into the classic sprawling position, the manus is rotated so that all but the most lateral digits are directed medially at an improbable angle, and certainly into a position inconsistent with the trackway data.

This locomotor pattern is highly derived relative to that of basal tetrapods, but shows some interesting parallels with the primitive sprawling stance. The humerus is maintained relatively close to the horizontal throughout the step cycle. The elbow is relatively inflexible and remains strongly flexed throughout the step cycle. Although *Chasmosaurus* can hardly be described as a "sprawler," the elbows are everted to a greater degree than in quadrupedal mammals. As a result, as the propul-

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sive phase progresses, the weight gradually shifts to the radial side of the carpus as the ulnar side is lifted off the ground near the end of the phase. This is functionally analogous to the "metatarsal rotation" (Brinkman 1980) observed in the rear limb of extant lizards. This posture, which has no precise analogue in other tetrapods, and the resulting forces generated in the metacarpus and manus during propulsion, may explain the common occurrence of bone pathologies in the front foot of ceratopsids. The metacarpal and first phalanx of the medial (first) digit of the specimen described here are highly pathological (Figure 5). Significantly, in a specimen of *Chasmosaurus belli* (ROM 843), both left and right medial metacarpals and associated phalanges are similarly pathological. Such bilateral deformities are highly unlikely to be the result of acute trauma, but are consistent with chronic injury resulting from repetitive stress associated with compression of the medial side of the manus during walking (Rega and Holmes 2006), particularly in large, older individuals. Since it appears that primitive marginocephalians such as psittacosaurs, from which neoceratopsids presumably evolved, were bipedal (You and Dodson 2004), it is improbable that these features represent remnants of the primitive sprawling posture. Instead, it is likely that they evolved, de novo, within the group. Although it is now clear that *Chasmosaurus*, and probably all neoceratopsids, did not have sprawling front limbs, this simulation shows clearly that their elbows were distinctly everted, causing the front feet to track wider than the hind (Lockley and Hunt 1995). Extension of the elbow during the propulsive phase probably generated some transverse movement of the trunk, resulting in a slightly waddling gait. Whether these were adaptations to stabilize the huge heads of these dinosaurs, or simply reflect a secondary consequence of the evolution of the ability to assume a "secondary, wider forelimb gauge" (Paul and Christiansen 2000) is a matter for speculation.

Although both lateral bending of the trunk and transverse movement created by extension of the everted elbows during the final stages of the propulsive phase would almost certainly have occurred, it is difficult to assess in a quantitative manner its effects on the step cycle of *Chasmosaurus*. The presence of ossified tendons would have stiffened the vertebral column, limiting lateral flexure and its effect on the length of the stride. Transverse movement of the trunk, produced by elbow extension, would have been modest given the restricted range of motion at this joint. As a result,

we would predict that these excursions would be limited and would not affect fundamentally the model presented here.

Inferred Stride Length – Does It Agree with Trackway Data?

Although the position and orientation of the manus with respect to the sagittal plane in this simulation was based directly on the trackway data, the resulting estimate of stride was not. Rather, this was determined by the limitations placed on the range of motion by the morphology of the joints as preserved in the specimen. The stride of the trackway (Lockley and Hunt 1995) scaled to our half-scale model of *C. irvinensis* is approximately 600 mm. During the propulsive phase, the glenoid of our model moved forward a total of 257 mm (positions 1- 4). It is reasonable to assume that the propulsive phase would make up approximately half the distance between consecutive manus impressions, with the other half made by the opposite front limb while the manus swung forward to begin the next propulsive phase. This would give a stride of 514 mm in our model, only slightly less than the stride independently estimated from the scaled trackways derived from Lockley and Hunt (1995). The remainder of the stride could easily have been made up by modest excursion of the scapulocoracoid on the rib cage, a movement that almost certainly occurred during the step cycle (Paul and Christiensen 2000) and/or slight lateral undulation of the trunk. This provides independent corroboration for the step cycle hypothesized here.

SUMMARY

Very few well-preserved, articulated, and complete pectoral girdle and forelimbs of ceratopsids are known. The specimen described here provides a rare opportunity to document these aspects of ceratopsid anatomy. In addition, because all elements were completely freed from the matrix during preparation, it was possible to fabricate an accurate replica of all elements that could then be conveniently manipulated without risk to the fragile bones. This permitted us to assemble a working model of the forelimb skeleton to test current hypotheses of ceratopsid limb stance that had been generated using incomplete or composite material, or based on qualitative assessments of museum skeletal mounts. Manipulation of this model suggests that neither the classic sprawling stance (Figure 9.1, 4), nor the completely upright stance (Figure 9.2, 5) was possible. Rather, the humerus maintained a relatively low angle to the

frontal plane throughout most of the step cycle. The elbow was moderately everted. Such a fore-limb stance is not incompatible with a moderately well-developed cursorial gait, but hardly implies that they approached extant quadrapedal or gravi-portal mammals in their range of locomotor abili-ties. Compression on the medial side of the metacarpus and manus that occurred during the propulsive phase as a result of this unique humeral orientation may explain the occurrence of bone abnormalities in this region in some ceratopsids.

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REFERENCES

Alexander, R.M. 1991. How dinosaurs ran. *Scientific American*, 264(4):62-68.

Bakker, R.T. 1968. The superiority of dinosaurs. *Discov-ery*, 3:11-22.

Bakker, R.T. 1975. Dinosaur renaissance. *Scientific American*, 232:58-78.

Bakker, R.T. 1986. The Dinosaur Heresies. William Mor-row, New York.

Bakker, R.T. 1987. The return of the dancing dinosaurs, p. 38-69. In Czerkas, S.J. and Olson, E.C. (eds.), *Dinosaurs Past and Present*, Vol. 1. University of Washington Press, Seattle.

Benton, M.J. 2004. Origin and relationships of Dinosau-ria, p. 7-24. In Weishampel, D.B., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria*. University of California Press, Berkley.

Brinkman, D. 1980. Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia; Iguanidae) and other lizards. *Canadian Journal of Zoology*, 58:277-289.

Brown, B. 1917. A complete skeleton of the horned dino-saur *Monoclonius* and description of a second skele-ton showing skin impressions. *Bulletin of the American Museum of Natural History*, 37:281-306.

Brown, B., and Schlaikjer, E.M. 1937. The skeleton of *Styracosaurus* with the description of a new species. *American Museum Novitates* 955:1-12.

Dodson, P. 1996. The Horned Dinosaurs. Princeton Uni-versity Press, Princeton.

Dodson, P., and Farlow, J.O. 1997. The forelimb carriage of ceratopsid dinosaurs, p. 393-398. In Wolberg, D.L., Stump, E., and Rosenberg, G.D. (eds.), *Dinofest International: proceedings of a symposium held at Arizona State University*. Academy of Natural Sciences, Philadelphia.

Dodson, P., Forster, C., and Sampson, S. 2004. Ceratop-sidae, p. 494-513. In Weishampel, D., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria* (second edition), University of California Press, Los Angeles.

Erickson, B.R. 1966. Mounted skeleton of *Triceratops prorsus* in the Science Museum. *Scientific Publica-tions of the Science Museum*, 1:1-16.

Fastovsky, D.E., and Smith, J.B. 2004. Dinosaur Paleo-ecology, p. 614-626. In Weishampel, D., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria* (second edition), University of California Press, Los Angeles.

Ford, T. 1997. Ceratopsian stance, *Dinosaur World*, 1(3):12-17.

Forster, C.A., and Sereno, P. 1997. The Marginocepha-lia: a Common Ancestry, p. 317-329. In Farlow, J.O. and Brett-Surman, M.K. (eds.), *The Complete Dino-saur*, Indiana University Press, Blooming.

Hatcher, J.B., Marsh, O.C., and Lull, R.S. 1907. The Cer-atopsia. *U.S. Geological Survey Monograph,* 49:1-300.

Hutchinson, J., and Gatesy, S. 2006. Beyond the bones. *Nature* 440: 292-294.

Garstka, W.R., and Burnham, D.A. 1997. Posture and stance of *Triceratops*: Evidence of digitigrade manus and cantilever vertebral column, p. 385-390. In Wol-berg, D.L., Stump, E., and Rosenberg, G.D. (eds.), *Dinofest International: proceedings of a symposium held at Arizona State University*. Academy of Natural Sciences, Philadelphia.

Gilmore, C.W. 1905. The mounted skeleton of *Tricer-atops prorsus*. *Proceedings United States National Museum*, 29:433-435.

Holmes, R.B., Forster, C.A., Ryan, M., and Shepherd, K. 2001. A new species of *Chasmosaurus* from the Dinosaur Park Formation of southern Alberta. *Cana-dian Journal of Earth Sciences*, 38:1423-1438.

Johnson, R.E., and Ostrom, J.H. 1995. The forelimb of *Torosaurus* and an analysis of the posture and gait of ceratopsian dinosaurs, p. 205-218. In Thomason, J.J. (ed.), *Functional Morphology in Vertebrate Palaeontology*. Cambridge University Press, New York.

Lockley, M.G., and Hunt A.P. 1995. Ceratopsid tracks and associated ichnofauna from the Laramie Forma-tion (Upper Cretaceous: Maastrichtian) of Colorado. *Journal of Vertebrate Paleontology*, 15(3):592-614.

Lull, R.S. 1933. A revision of the Ceratopsia, or horned dinosaurs. *Memoirs of the Peabody Museum of Nat-ural History*, 3:1-175.

Marsh, O.C. 1891. Restoration of *Triceratops* and *Bron-tosaurus*. *American Journal of Science*, *series 3*, 41:339-342.

Osborn, H.G. 1933. Mounted skeleton of *Triceratops elatus*. *American Museum Novitates*, 654:1-14.

Paul, G.S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. p. 4-49. In Czerkas, S.J. and Olson, E.C. (eds.), *Dinosaurs Past and Present*, Vol. 2. University of Washington Press, Seattle.

Paul, G.S., and Christiansen, P. 2000. Forelimb posture in neoceratopsian dinosaurs: Implications for gait and locomotion. *Paleobiology*, 26(3):450-465.

Rega, E., and Holmes, R. 2006. Manual pathology indicative of locomotor behavior in two chasmosaurine ceratopsid dinosaurs. *Journal of Vertebrate Paleontology* 26, supplement to number 3:114A.

Sternberg, C.M. 1927. Horned dinosaur group in the National Museum of Canada. *The Canadian Field-Naturalist*, 41(4):67-73.

You, H., and Dodson, P. 2004. Basal Ceratopsia, p. 478-493. In Weishampel, D., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria* (second edition), University of California Press, Los Angeles.