

Forelimb posture in neoceratopsian dinosaurs: implications for gait and locomotion

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Abstract.—Ceratopsid dinosaurs traditionally have been restored with sprawling forelimbs and were considered unable to run at high speeds. An alternative view restores the ceratopsids as rhinoceros-like with parasagittal forelimb kinematics and the ability to run faster than extant elephants. Several anatomical difficulties concerning the mounting of ceratopsid skeletons with nearly parasagittal forelimbs stem not from the forelimb itself, but from errors in rib and vertebral articulation. Matching a skeletal restoration to a probable ceratopsid trackway shows that the hands were placed directly beneath the glenoids, and that manual impressions were directed laterally, not medially as in sprawling reptiles. Pedal impressions in trackways are medial to the manual impressions, owing to the slightly averted elbow and to the asymmetrical distal femoral condyles, which directed the crus slightly medially. The limbs of ceratopsians of all sizes display substantial joint flexure, strongly indicating that the elephantine forelimb posture that has sometimes been suggested as the alternative to a sprawling posture is erroneous. The articular surfaces of uncruised ceratopsian scapulocoracoids and forelimb joints confirm that the forelimb operated in a near-parasagittal plane with the elbows only slightly averted. The maximal running speed of even the largest ceratopsids is inferred to have significantly exceeded that of elephants and was probably broadly similar to that of rhinos.

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Introduction

Large ceratopsids (Dinosauria: Ornithischia) have often been considered the dinosaurian equivalent to the Rhinocerotidae because of convergent resemblances in overall morphology (e.g., Alexander 1985, 1989, 1991; Bakker 1986, 1987). Dodson and Farlow (1997), however, cautioned that these resemblances in some cases appear to have been overemphasized, as dinosaurs are phylogenetically distinct from mammals. Nonetheless, solutions to the problems of terrestrial support of mass and locomotion with a large body mass may well be constrained, implying similar solutions to similar problems, as appears to be the case in the sauropod-proboscidian analogy (e.g., Christiansen 1997). A representative sample of several ceratopsian genera is presented in Figure 1 and compared with large perissodactyls (Paul 1997: Appendix figs. 2,6).

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The forelimb posture and locomotion of ceratopsians, particularly the ceratopsids, has been controversial. As noted below, most previous attempts to solve this problem have often either neglected several anatomical aspects or failed to fully incorporate the important evidence provided by trackways. Forelimb posture in ceratopsians has been restored as wide-gauge and sprawling by Gilmore (1905), Sternberg (1927), Tait and Brown (1928), Osborn (1933), Russell (1935), Erickson (1966), Farlow and Dodson (1975), Russell (1977), Czerkas and Czerkas (1990), and most recently Johnson and Ostrom (1995) and Dodson (1996). A narrower forelimb gauge and a more parasagittal limb posture were favored by Marsh (1891a,b), Hatcher et al. (1907), Bakker (1971, 1986, 1987), Ostrom and Wellnhofer (1986: Fig. 8), Paul (1987, 1991, 1997), Adams (1991), Tereshchenko (1994), Lockley and Hunt (1995), Ford (1997), Garstka and Burnham (1997), and in part Dodson and Farlow (1997), the latter view in accord with available trackway evidence. Forelimb posture is more

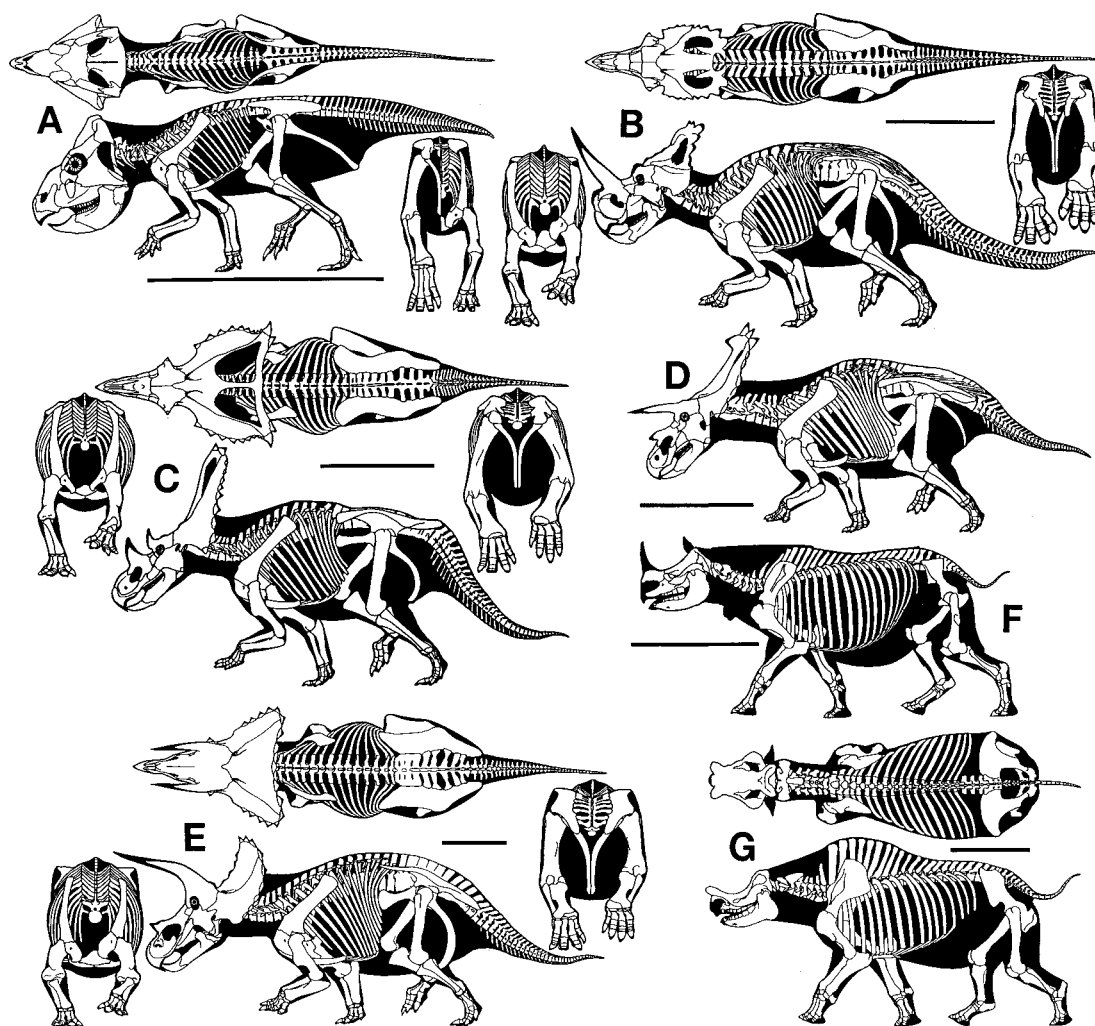


FIGURE 1. Skeletal restorations in side- and multiview of ceratopsians compared with large perissodactyls. A, *Lptoceratops* NMC 8889 (93 kg). B, *Centrosaurus* AMNH 5351 (1460 kg). C, *Chasmosaurus* NMC 2280 (1520 kg). D, *Anchiceratops* NMC 8538 (1180 kg). E, *Triceratops* or *Torosaurus*, based primarily on USNM 4842 (6420 kg). F, *Rhinoceros* USNM 12450 (1000 kg). G, *Brontops* YPM 12048 (3300 kg). Scale bar, 1 m.

difficult to restore than that of the hindlimb, as the latter presents the advantage of a pelvis firmly attached to the vertebral column.

The debate over forelimb posture in ceratopsians often appears unnecessarily polarized, forcing a choice between a fully erect, almost elephantine posture, with all three long-bones kept essentially vertical, or a sprawling posture, with the humerus held horizontally (e.g., Czerkas and Czerkas 1990: p. 212; Johnson and Ostrom 1995: Fig. 12.1; Dodson 1996: Fig. 9.7). This is an oversimplification and is actually misleading, because the available evidence suggests that neither posture was like-

ly. In fact, the common use of the word "erect" can cause confusion (e.g., Dodson 1996; Dodson and Farlow 1997), as this could be taken to suggest a nearly columnar stance. By this definition most large mammals are not erect either (Fig. 1). The issue of forelimb posture in ceratopsians is primarily a question of whether the humerus operated in a largely parasagittal fashion or employed significant medio-lateral rotation during locomotion.

The question of restoring limb posture has two basic and related aspects. One is fore and aft limb posture in lateral view, which ranges from highly flexed, the plesiomorphic tetra-

pod condition (e.g., Romer 1956; Young 1981), to fully erect. The other is transverse limb posture, which ranges from sprawling (the plesiomorphic tetrapod condition), through semierect, largely parasagittal, to nearly columnar. It is important to bear in mind that even fully erect limbs usually do not operate in an entirely parasagittal manner, as humeral and femoral aversion and inversion is often present (Muybridge 1957; Gambaryan 1974; Paul 1991). Most ceratopsids were large animals, although no larger than extant rhinos, but *Triceratops*, *Torosaurus* (Fig. 1), and *Pentaceratops* were elephant-sized (Paul 1997).

Restoring limb posture in dinosaurs presents problems, however, largely because their distal articulating facets often show a considerably poorer degree of ossification than those of mammalian longbones. This often precludes articulating the bones and observing their tightly controlled limits of protraction-retraction and abduction-adduction. Attempting to restore dinosaur limb posture is somewhat analogous to restoring limb posture in immature birds and mammals, in which cartilaginous joints are still present. Whether protoceratopsids sometimes employed bipedality during fast locomotion (Bakker 1968; Coombs 1978) or remained quadrupedal (Thulborn 1982; Tereshchenko 1994) has been controversial, but it is unlikely that ceratopsids used bipedality.

In this paper we aim to show that the most likely posture of the ceratopsian forelimb was largely parasagittal, albeit far from columnar, and that several of the difficulties encountered in mounting skeletons with a parasagittal forelimb posture, e.g., the medial tuberosity proximally on the humerus discussed by Dodson and Farlow (1997), in fact appear to be the result of errors in articulating the axial skeleton. Thus, morphology of the axial skeleton will also be discussed. We will also use the trackway evidence as a reference for assessing limb posture and gait.

Institutional abbreviations are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; MPM, Milwaukee Public Museum; NMC, National Museum of Canada; PMU, Pa-

laeontological Institute of Uppsala University; TMM, Texas Memorial Museum; UNM, University of New Mexico; USNM, National Museum of Natural History; UTEP, Centennial Museum, University of Texas; WFQ, Warfield Fossils; YPM, Yale Peabody Museum.

Limb Posture and Trackways

Trackways can provide good evidence for limb posture in the transverse plane for extinct animals, providing that the track maker can be identified with a reasonable degree of certainty. It is therefore important to recognize the role trackways can play in restoring limb posture in dinosaurs. Any restoration of normal walking posture and limb action must be in full accord with available trackways in terms of manual and pedal placement, orientation, and stride length.

Ceratopsian tracks have been reported previously (e.g., Lockley 1986, 1991; Currie 1993; Ford 1997), but probably one of the best ceratopsid trackways, *Ceratopsipes goldenensis*, has been recognized only recently (Lockley and Hunt 1995). The track maker was almost certainly a gigantic ceratopsid, perhaps even *Triceratops*, as it was not only by far the most common ceratopsian at the time (Lockley and Hunt 1995; Dodson and Farlow 1997) but it is also one of the few ceratopsids so far discovered that was large enough to have been able to make the trackway.

The trackway is about 1.25 meters across (Lockley and Hunt 1995). However, this figure represents the width across the lateral edges of the manual impressions, whereas their medial edges are less than one meter apart, approximately the width between the glenoids of a *Triceratops* with similar-sized hands. The trackway shows that the hands were almost directly beneath the glenoids, and thus strongly argues against a sprawling forelimb posture (Fig. 2A) (Ford 1997). The trackway indicates that forelimb gauge was, however, slightly wider than shown in previous restorations (compare Figs. 1E, 2 with Paul 1987: Fig. 23). Rough calculations indicate that the width across the lateral edges of the manual impressions of a *Triceratops*-sized animal would have been in excess of two meters if the animal walked with a posture similar to the



FIGURE 2. A, Multiview limb-skeletal restoration of *Triceratops* or *Torosaurus* based primarily on USNM 4842 (see Fig. 1E), shown walking out a probable ceratopsid trackway (from Lockley and Hunt 1995). Anteriormost manus print about to be impressed is outlined (modified after Paul 1991: Fig. 2). Skeleton and trackway shown to scale; scale bar, 1 m. Because breadth of manus (about 400 mm) and pes (about 500 mm) and estimated glenoacetabular length (1.5–1.7 m) are similar in both skeleton and trackway, the skeleton appears to approximately match or only slightly exceed the size of the trackmaker. B, C, Trackways of walking *Dicerops* (B) and *Connochaetes* (C) (modified after Bird 1987). All trackways drawn to same manus stride length. Manus prints indicated by short medial lines.

one suggested by Gilmore (1905), Sternberg (1927), Osborn (1933), Russell (1935), Halstead and Halstead (1981), Czerkas and Czerkas (1990), Johnson and Ostrom (1995), and Dodson (1996), among others.

Dodson (1996) suggested that the fact that the manual impressions were slightly lateral to the pedal impressions was inconsistent with a parasagittal forelimb posture, because the pelvic region is wider than the shoulder region in ceratopsids. However, as noted below and shown in Figure 1, the pelvic region of ceratopsids is not markedly wider than the shoulder region. Additionally, the morphology of the distal femoral articulating facet indicates that the crus was turned slightly medially during normal walking. We agree with Ford (1997) that the sprawling posture would

probably also imply that the hands would tend to “smear” the toe imprints, but this is not present in the trackway series. No one has yet attempted to mount a ceratopsid skeleton in a walking pose that paces out one of these trackways. In this paper, only results that successfully place the feet of ceratopsids into their trackway positions will be accepted as likely.

Axial and Girdle Morphology

Presacral Column.—We agree with Osborn (1933) that the presacral vertebrae of ceratopsians articulated in a gentle S-curve, with the dorsally convex part of this curve along the dorsals (Fig. 1A–E) (Hatcher et al. 1907: Plate XL; Brown and Schlaikjer 1940: Fig. 24; Sternberg 1951: Plate LIVB; Garstka and Burnham

1997). This curvature is also present in the best naturally articulated specimens, e.g., *Centrosaurus* AMNH 5351 (Brown 1917; Lull 1933) and is correctly reproduced in most restorations and mounted skeletons. In life this curvature was fixed not only by the angulation of the central articulating facets, but also by a series of well-developed ossified tendons, as can be seen in *Triceratops* USNM 4928 (Hatcher et al. 1907) *Centrosaurus* AMNH 5351 (Brown 1917), and *Triceratops* WFQ 9309 (Garstka and Burnham 1997), among others. A dorsally concave dorsal vertebral column is therefore the result of postmortem distortion due to desiccation of epaxial muscles and ligaments, rather than the natural condition during life (contra Garstka and Burnham 1997: Fig. 5).

Two important, and often overlooked pieces of evidence in the presacral column of ceratopsians that contradict a sprawling forelimb posture are the above-mentioned ossified tendons and the tight fit of the prepubic process with the posterior ribs, described below. These would have significantly stiffened the trunk. Sprawling reptiles extensively use lateral undulations of the vertebral column during locomotion (e.g., Romer 1956; Young 1981; Carrier 1987; Sennikov 1989; Reilly and Delancey 1997). These undulations are an extension and slight modification of the lateral undulations employed by fish (Romer 1956; Edwards 1976; Young 1981).

Large mammals walk and run with significantly less crouched limbs than small mammals, in order to maintain bone stresses within reasonable limits (e.g., Biewener 1990), even though their longbones scale almost isometrically (Christiansen 1999). Accordingly, small mammals run in a slightly different fashion than larger mammals (Alexander 1991). Like reptiles, most small mammals use significant lateral bending moments of the trunk during slow locomotion (e.g., Gambaryan 1974; Pridmore 1992). During faster forms of locomotion, small mammals shift to sagittal trunk bending instead, and in this respect they differ markedly from reptiles (Carrier 1987). At least in certain reptiles it appears that the amplitude of lateral undulation decreases with increasing speed (Auffenberg 1981). Some authors, however, have found just the opposite

(Edwards 1976). Certain large mammals also use lateral trunk movements during slow locomotion, e.g., plantigrade ursids, but relatively stiff-trunked ungulates have no such shift in locomotory mechanics. There is little reason to suppose that this was the case in ceratopsids either, particularly as they also appear to have had relatively stiff trunk regions.

Rib Cage.—The posterior ribs of ceratopsids were subvertical in lateral view. In anterior view they were curved, thus forming a broad, roundish abdominal cavity, similar to the large subcircular abdominal cavity present in many extant ungulates (see, for instance, posterior views of *Bos* and *Equus* in Muybridge 1957). The belly appears to have been relatively broadest in *Chasmosaurus* (Fig. 1C), which in part could be the reason for modification of the distal femoral condyles, described below. Rib cages from well-preserved ceratopsid specimens indicate that the mid- and posterior ribs became increasingly curved in lateral view, closely approaching each other distally, e.g., *Centrosaurus* AMNH 5351 or *Anchiceratops* NMC 8535 (Brown 1917; Lull 1933).

Osborn (1933) suggested that one of the posterior ribs articulated with the anterolateral edge of the prepubic process. The articulated contact is preserved in *Anchiceratops* NMC 8535 (Lull 1933), and the articular rugosity is present on a partly disarticulated posterior rib of *Centrosaurus* AMNH 5351, in which the rib heads are partially disarticulated from the diapophyses. The great majority of skeletal restorations and mounts, however, lack this unusual posterior rib cage articulation, probably erroneously. The bracing provided by this tight-fitting complex appears to have further stiffened and strengthened the trunk.

In most ceratopsian restorations the anterior ribs are positioned subvertically in lateral view (Gilmore 1905; Sternberg 1927; Osborn 1933; Brown and Schlaikjer 1940; Erickson 1966; Russell 1970; Bakker 1987; Johnson and Ostrom 1995), as they are in large mammals (Fig. 1F,G) (Ellenberger et al. 1956). The best articulated ceratopsian specimens indicate that this is incorrect, e.g. *Centrosaurus* AMNH 5351 or *Anchiceratops* NMC 8535 (Brown 1917; Lull 1933). As in all other extant and extinct



FIGURE 3. Multiple views of right scapular glenoid of *Triceratops* or *Torosaurus* USNM 8013 in lateral (A), posterior (B), posteroventral (C), and ventral (D) views. The scapula is oriented to show the glenoid in natural articulation, as per Figure 1.

archosaurs, the anterior ribs appear to have been swept strongly posteroventrally (Paul 1987, 1997; Carpenter et al. 1994; Ford 1997; correctly mounted in *Centrosaurus* YPM 2015, Plate IIA in Lull 1933).

This rib cage morphology had two effects. First, as the capitulum and tuberculum are set at a quite acute angle with respect to the long axis of the rib, a posterior inclination also twists the ribs medially, thus narrowing the anterior chest region (Fig. 1B,C,E) (Paul 1987, 1997; Carpenter et al. 1994; Ford 1997). This allowed the coracoids to articulate with the lateral grooves of the transversely narrow, poorly ossified, and therefore rarely preserved episternum of quadrupedal dinosaurs (Norman 1980; Paul 1987; Carpenter et al. 1994). A deep narrow chest preceding a transversely wide abdominal region differs markedly from the morphology of sprawling reptiles, in which the chest is shallow. Ceratopsid rib cage morphology bears much closer resemblance to that of large herbivorous mam-

mals (Ellenberger et al. 1956; Paul 1987; Carpenter et al. 1994). The shoulder region, however, remained almost as transversely wide as the hip region (Fig. 1A–E), a condition similar to that of extant large ungulates and elephants (Ellenberger et al. 1956).

Pectoral Girdle.—The second consequence of the posterior sweep of the anterior ribs is the more posterior placement of the pectoral girdle (Paul 1987, 1997; Ford 1997) than is usually displayed in most skeletal mounts (Gilmore 1905; Sternberg 1927; Lull 1933: Plate IIA; Osborn 1933; Brown and Schlaikjer 1940; Erickson 1966; Russell 1970; Ostrom and Wellnhofer 1986; Bakker 1987; Johnson and Ostrom 1995). In articulated, dorsoventrally compressed ceratopsid fossils (Brown 1917: Figs. 3, 4, Plate XVII; Lull 1933: Plate IVA) the posterolateral corner of the paired sternals articulates with the distal ends of the anterior dorsal ribs. This is the normal tetrapod condition, and restorations that depict ceratopsian sternals widely separated and far anteroventrally

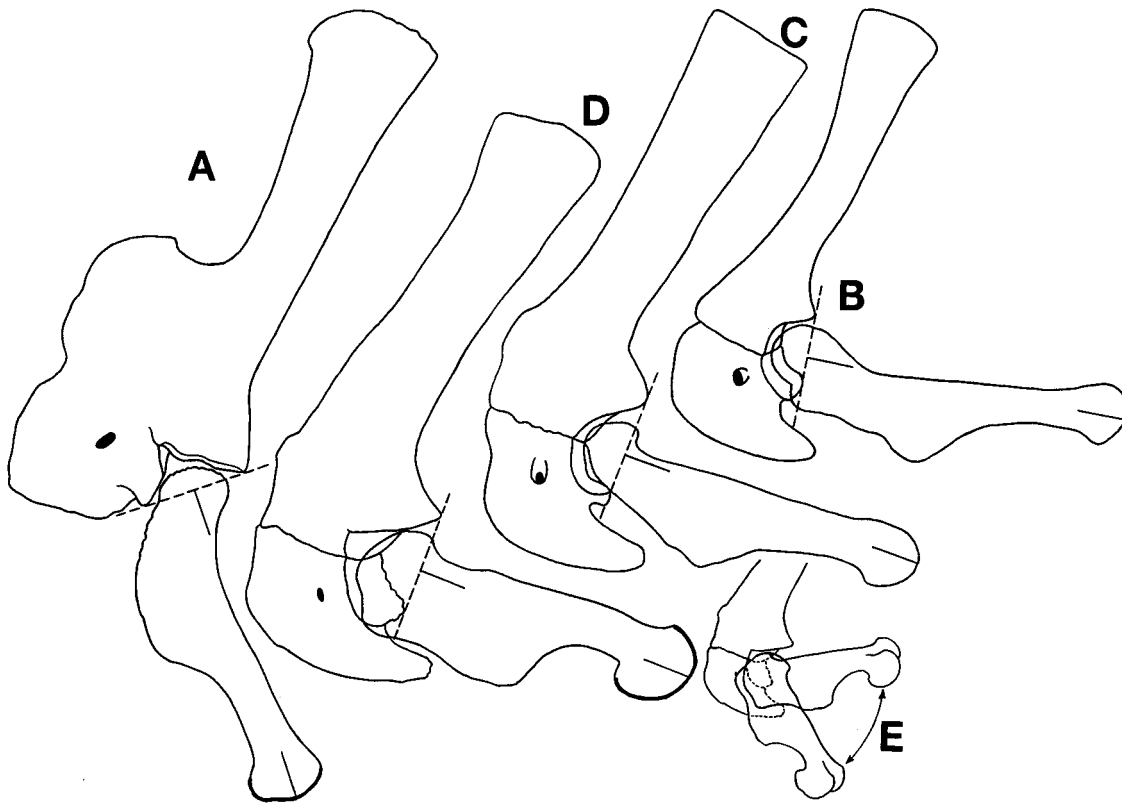


FIGURE 4. Comparison of relative forelimb flexion, with left limb elements in planar lateral view, drawn to same humerus length. A, Columnar-limbed *Apatosaurus* (A). B–D, Animals with joint flexure in the limbs: *Leptoceratops* (B), *Chasmosaurus* (C), and *Triceratops* (D). E, Estimated maximum protraction and retraction of humerus in *Triceratops*.

to the ribs (Lull 1933: Plate IIA; Osborn 1933; Erickson 1966) are probably erroneous, as also concluded by Adams (1991) and Ford (1997).

In laterally compressed, articulated specimens the sternals are usually displaced anteroventrally, perhaps because of bloating of the carcass (e.g., Lull 1933: Plates IXA, X). Anteroventral displacement of the sternals would also tend to pull the episternum and scapulocoracoid anteriorly, thus giving the false impression of a substantial part of the shoulder girdle being anterior to the chest ribs (e.g., *Centrosaurus* AMNH 5351; Brown 1917: Plate XI). Apart from being unrealistic, such a position would leave the girdle with insufficient support from the *M. serratus ventralis*.

Rather, the scapula was astride and connected to the chest ribs as in extant tetrapods except turtles (Romer 1956; Pritchard 1979; Young 1981; Ford 1997). It is important to bear in mind, however, that although the pectoral

girdle was set far posteriorly in ceratopsians, the posterior sweep of the anterior chest ribs meant that the glenoid was still situated anterior to the ribs (Fig. 1A–E). This is similar to the condition in many extant birds and reptiles, but it differs from the condition in mammals, in which the glenoid is lateral to the ribs (Fig. 1F,G).

The glenoids of sprawling reptiles face predominantly laterally to allow the humerus to perform significant dorsoventral and antero-posterior movements, and it is usually somewhat saddle-shaped (e.g., Romer 1956; Young 1981; Bakker 1986, 1987). The glenoids of ceratopsians did not look like this (Fig. 3). The glenoids of parasagittal mammals are cotyloid in shape and the articulating facet faces posteroventrally. Well-preserved, largely uncrushed ceratopsian scapulocoracoids, e.g., *Pentaceratops* PMU.R268 (Wiman 1930), *Centrosaurus* YPM 2015 (Lull 1933), or *Styracosaurus*

AMNH 5372 (Brown and Schlaikjer 1937), have cotyloid glenoids that mainly face posteroventrally and that have only a moderate ventrolateral flaring, especially on the coracoid part. Good examples are *Triceratops* USNM 4800 (Hatcher et al. 1907), *Chasmosaurus* TMM 42303-1 (Lehman 1989), *Pentaceratops* UNM FKK-081 (Lehman 1993). Crushing sometimes exaggerates this lateral flaring, as in *Torosaurus* MPM VP6841 (Johnson and Ostrom 1995).

The dorsal part of the glenoid appears mainly to have faced slightly medially in most cases. With a correctly oriented, sharply inclined scapula and coracoids that almost meet at the midline, the dorsal part of the glenoid would face even slightly more medially, as also concluded by Ford (1997). This appears to have been the case in well-preserved ceratopsids as well as protoceratopsids. This posterioventral orientation of the glenoid probably would have prevented the humerus from significant lateral mobility.

The cotyloid glenoid fossa also strongly argues against a sprawling forelimb, as the thrust from carrying the body mass would have been directed mediodorsally upon contraction of the presumably massive *M. pectoralis*. However, the glenoid does not have a wide flaring to brace the humeral caput medially, and thus there appears to have been little osteological support for a lateral thrust, as noted for the acetabulum-femur articulation in *Plateosaurus* by Christian et al. (1996). Even columnar-limbed sauropods often have some lateral flaring of the glenoid, especially in the coracoid part, although it is usually less than in ceratopsians. The rugosity of the sauropod glenoid often makes this character hard to verify, however, and some specimens appear to lack this feature. In ceratopsids the glenoid was directed as much as 50° more posteriorly along the parasagittal plane than in columnar-limbed sauropods and stegosaurs (Fig. 4A–D).

Glenoid morphology indicates that the humeral posture was ungulate-like (Figs. 5B,C and 6) with flexion primarily in the anteroposterior plane, rather than transverse as in reptiles. In ceratopsids the glenoids were probably directed approximately 10° more ventrally than was the case in small protocer-

atopsids (Fig. 4B–D). The slight lateral flaring of the ventral part of the glenoid probably allowed the humerus to slope an estimated 20–25° ventrolaterally (Figs. 1A–E, 3A, 4E, 6D).

The orientation of the scapula ranges from horizontal to almost vertical in articulated ceratopsian specimens (Lull 1933: Plate IXA). The former is depicted in some restorations (Sternberg 1927; Erickson 1966; Johnson and Ostrom 1995), but horizontal scapulae appear to be largely limited to specialized tetrapods with very elongated coracoids, such as certain advanced non-avian theropods, birds, and pterosaurs (Paul 1987, 1988). In most tetrapods the scapula is posteriorly inclined, and this is the most likely orientation in ceratopsian dinosaurs as well (Fig. 1A–G) (Russell 1970; Ostrom and Wellnhofer 1986; Tereshchenko 1994; Ford 1997; Garstka and Burnham 1997).

Scapular Mobility.—One aspect of ceratopsian limb function that has generated substantial controversy is scapular mobility. Well-developed scapular mobility is favored by Bakker (1986, 1987), Paul (1987), Tereshchenko (1994), and in part Gilmore (1919), while Bennett and Dalzell (1973), Coombs (1978), Thulborn, (1982), Adams (1991), and Dodson (1996) suggested that it was either very limited or did not occur. Scapular mobility is present in a variety of amniote groups; it occurs in several lizards (Jenkins and Goslow 1983) and is well developed in chameleons (Peterson 1984; Bakker 1986, 1987), crocodilians, and many mammals (Fig. 5B–D) (Gambaryan 1974; Jenkins and Weijs 1979). Although the functional anatomy differs markedly among the various groups, it is clear, however, that scapular mobility is common among amniotes.

A substantial degree of mobility is retained among large mammals, although it is reduced in columnar-limbed elephants (Fig. 5D) (Gambaryan 1974). To attain scapular mobility the coracoids can be lost, as in most mammals, or alternatively, the coracoids can be allowed to slide fore and aft in a groove on the lateral edge of the sternum, as in *Varanus* (Jenkins and Goslow 1983). Paired clavicles are present in *Protoceratops* and *Leptoceratops* but have not been found in ceratopsids yet (Dod-

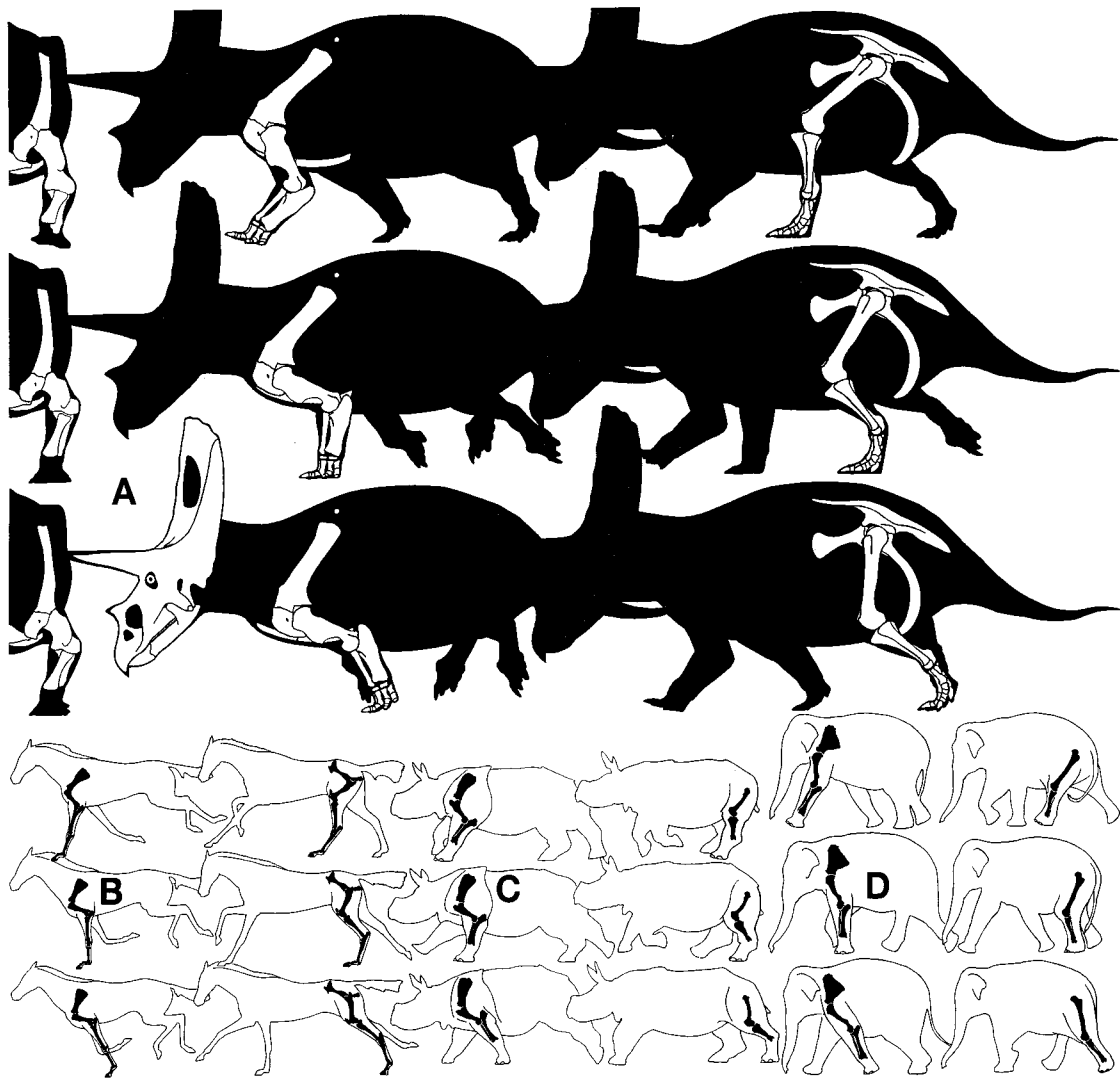


FIGURE 5. Motion studies showing limb flexion and action. A, Restored galloping *Triceratops* or *Torosaurus* based primarily on USNM 4842, includes anterior view of forelimb and possible point of scapular rotation indicated by a white dot. B, Fast galloping *Equus*. C, Slow galloping juvenile *Rhinoceros*. D, Ambling *Elaphus*. B and D after Muybridge 1957, and C after film. Not to scale.

son and Currie 1990). Ceratopsians lacked interclavicles and fused clavicles, and thus no anatomical structure impaired scapular mobility.

No realistic figure illustrating exactly what would have prevented ceratopsian scapulocoracoid mobility has yet been published. Illustrations depicting a mobile coracoid pressed against the ventral part of the neck or a scapula projecting far anteriorly to the ribs, as per Bennett and Dalzell (1973), involve an initial incorrect, horizontal scapulocoracoid posture.

There appear to be no anatomical difficulties in rotating a posteriorly inclined scapulocoracoid (Fig. 5A). Coombs (1978) and Dodson (1996) suggested that ceratopsian scapulocoracoids were too large to be mobile, but it remains elusive why size and mobility should be correlated. In contrast, a long scapular blade could potentially provide great mechanical leverage and thus enhance propulsive power from the forelimb.

Dodson (1996) further argued that the strong scapulocoracoid curvature prevented

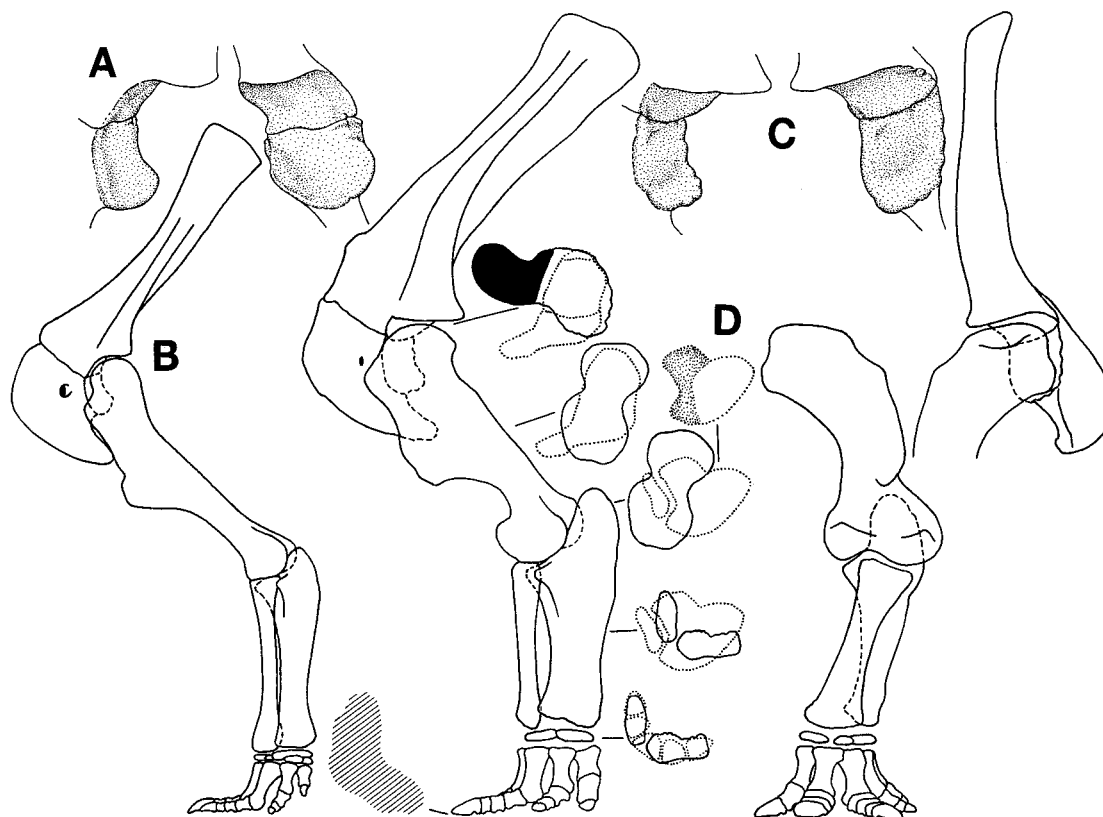


FIGURE 6. Forelimb articulation and posture studies. Shoulder glenoids in naturally articulated lateral and posterior views of *Leptoceratops* (A) AMNH 5205 (in part after Brown 1914) and *Triceratops* or *Torosaurus* (C) USNM 8013 and other specimens (modified after Paul 1987). Left forelimb in neutral standing pose of *Leptoceratops* (B) AMNH 5205, in naturally articulated lateral view, and *Triceratops* or *Torosaurus* (C) USNM 4842, USNM 8013, AMNH 970, and other specimens, in lateral, anterior, and posterior views. In D, stippling on proximal ulna delineates articular facets from olecranon process; manus print orientation indicated. Illustrations not to scale.

mobility. As described above, the anterior chest region in ceratopsians was deep and only gently curved, and correspondingly, ceratopsian scapulocoracoids are not strongly curved (see also Ford (1997). We suggest that ceratopsian scapulocoracoids were free to rotate (Fig. 5A), although the great scapular mobility displayed by many larger mammals (Gambaryan 1974) appears less likely. Because the coracoid-sternal articulation is lacking, the exact amount of scapular mobility possible cannot be estimated, nor the exact point of rotation.

Appendicular Morphology

Forelimbs.—Many aspects of forelimb morphology in conjunction with the trackways also strongly argue against a sprawling forelimb posture. In many ceratopsian mounts

with sprawling forelimbs (e.g., Sternberg 1927; Osborn 1933; Brown and Schlaikjer 1940; Erickson 1966; Johnson and Ostrom 1995; or the *Triceratops* mount at FMNH) the ribs are too vertical and broad, as noted above, and the coracoids set too far apart. As a result, the glenoids are rotated laterally and the humerus is prevented from operating in an approximately parasagittal manner (see also Ford 1997), although it probably did diverge slightly laterally from the parallel plane with respect to the long axis of the body (see above). Additionally, the humeral caput often does not articulate properly with the glenoid in mounts with sprawling or semierect forelimbs (Osborn 1933: Fig. 2; Erickson 1966: Plate 1B; Johnson and Ostrom 1995: Figs. 12.2, 12.7, and 12.8).

Dodson (1996) and Dodson and Farlow

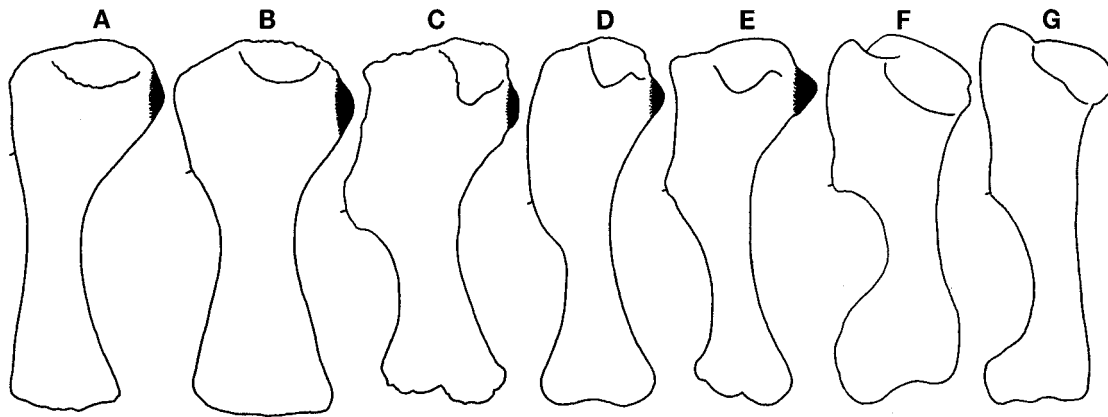


FIGURE 7. Left humeri in posterior view, drawn to same length. A, *Camarasaurus* YPM 1901. B, *Apatosaurus* CM 3018. C, *Torosaurus* MPM VP6841. D, *Chasmosaurus* UTEP P.37.7.006. E, *Leptoceratops* AMNH 5205. F, *Rhinoceros*. G, *Equus*. Proximomedial lesser tubercle is black; short lines indicate deltopectoral crests.

(1997) argued that the prominent lesser tubercle of ceratopsids (Fig. 7C–E), which is usually greatly reduced in mammals (Fig. 7F,G) would interfere with the ribs if the humerus moved in a near-parasagittal plane. However, this process is often fairly well developed in columnar-limbed sauropods, which often have a narrow gauge (Fig. 7A,B) (Paul 1987). With the scapulocoracoid properly articulated there is also a free space medial to the proximal part of the humerus (Adams 1991; Ford 1997). Additionally, there is little conflict between a prominent lesser tubercle and a parasagittal gait in dinosaurs, as the glenoid was anterior to the ribs, as noted above.

As the humerus retracted and the caput articulated increasingly with the more laterally oriented coracoidal part of the glenoid, the humerus may have swung slightly more posterolaterally, helping to clear the capacious gut. The more lateral orientation of the anterior glenoid surface suggests that it may have been possible to adopt a secondary, wider forelimb gauge, when the humerus was held almost horizontally. This could have been useful under special circumstances, such as grazing, drinking, or static interspecific agonistic behavior.

Another feature of forelimb morphology that some have argued supports a wide-gauge forelimb posture is the extremely well developed deltopectoral crest in ceratopsids, particularly in the large chasmosaurines. Russell

(1935), Johnson and Ostrom (1995), and Dodson (1996) suggested that the associated musculature was similar to that of sprawling reptiles, but perissodactyls also have well-developed deltopectoral crests (Fig. 7F,G) (Gambaryan 1974). Dodson (personal communication 1999) suggested that deltopectoral crest morphology in ceratopsians differs markedly from that of large mammals, indicating different axes of humeral rotation. Rhinos, however, like ceratopsians, have large deltopectoral crests, virtually at right angles to the long axis of the bone, and they are mainly rugose on the proximolateral sides. Overall they show great resemblance to the deltopectoral crests of ceratopsids.

The slight differences from extant rhinos in projection of the crest relative to the long axes of the humeri and the humeral heads could suggest that ceratopsid humeri were turned slightly more outward than are the humeri of large mammals (e.g., Hatcher et al. 1907: Plate XLIXB). Deltopectoral crest morphology does not indicate major differences in the axes of rotation of the humerus between ceratopsians and large mammals. Prominent deltopectoral crests among quadrupedal dinosaurs are also found in the Ankylosauria and Stegosauria, and in the columnar-limbed Sauropoda.

There has been virtually unanimous agreement that ceratopsian forelimbs were flexed (Gilmore 1905; Sternberg 1927; Tait and Brown 1928; Osborn 1933; Brown and Schlaik-

jer 1940; Erickson 1966; Bakker 1971, 1986, 1987; Russell 1977; Paul 1987; Tereshchenko 1994; Johnson and Ostrom 1995; Ford 1997). This orientation is easily recognized because the humeral caput extends much onto the caudal side of the humerus and the distal condyles face anteriorly, thus undoubtedly causing substantial elbow flexure. It is the plane of flexion that is in dispute. The distal condyles, however, do not face ventrally as in sprawling reptiles (see also Ford 1997). Both the morphology of the glenoid and the lateromedially rectangular humeral caput strongly suggest that this flexion was primarily in the antero-posterior, not the transverse, plane. In fact, the morphology of the humeral caput makes it doubtful that ceratopsians would have been able to protract the humerus past vertical. In this respect they resemble large ungulates and rhinos and differ from elephants (Fig. 5A–D).

In various reconstructions with sprawling forelimbs (Gilmore 1905; Sternberg 1927; Osborn 1933; Erickson 1966; Johnson and Ostrom 1995) the radius and ulna are straight. It is more likely, however, that the radius and ulna crossed over (Fig. 6D), albeit probably not markedly (see Carpenter 1982; Paul 1987; Carpenter et al. 1994; Ford 1997). A straight radius also makes parasagittal mounting of the forelimbs difficult, as the distal articulating facet then appears disarticulated from the proximal carpal; however, this problem largely disappears once the radius crosses the ulna for support of the lateral humeral condyle. Thus articulated, the proximal radial articulating surface also fits properly into the radial fossa anteroproximally on the ulna (see Ford 1997).

Ceratopsian trackways are incompatible with wide-gauge forelimbs on an additional point besides the width of the manual prints compared with the width between the glenoids, as described above. The manus imprints face anterolaterally (Figs. 2A, 6D), a feature common in quadrupedal dinosaur trackways (e.g., Carpenter 1982; Paul 1987; Currie 1993; Thulborn 1993; dos Santos et al. 1994; Lockley and Barnes 1994; Lockley et al. 1994). Carpenter (1982), Paul (1987), and Ford (1997) all noted, that if the manus is rotated laterally the elbow could not also be directed strongly

laterally, as this would rotate the manus medially, especially during protraction (see, e.g., Gilmore 1905: Plate 1; Lull 1933: Plates IIIA, XIVB, XVII; and illustrations in Dodson 1996: p. 275, and in Czerkas and Czerkas 1990: p. 212]).

As a result of the most likely orientation of the glenoid and the orientation of the footprint impressions in trackways, the elbow is bowed slightly laterally (contra the perfectly parasagittal forelimbs restored by Tereshchenko [1994]), the radius and ulna slope ventromedially about 15–20°, and the distal end of the radius is beveled to form a proper articulation with the carpus (Fig. 6D). In most large extant mammals the elbows are also bowed slightly laterally and the manus imprints almost touch the midline, especially in the long-limbed elephants. Manus gauge is usually the same as, or slightly less than, pedal gauge, hence clearly narrower than was the case in ceratopsids (Fig. 2B) (Bird 1987; Lockley and Hunt 1995). Extant wildebeest, however, also place the manus impressions lateral to the pedal impressions (Fig. 2C).

The fact that most dinosaurs are hindlimb dominant and most mammals forelimb dominant (e.g., Alexander 1985, 1989; Christiansen 1997; Christiansen and Paul in press) may also affect this comparison, although it is difficult to assess to what extent. Exact forelimb posture and placement of the manus may have varied among ceratopsians, although the similarity in joint orientation suggests that variation was minor.

Hindlimbs.—It is almost universally agreed that the hindlimbs of ceratopsians worked in a near-parasagittal manner (Gilmore 1905, 1919; Sternberg 1927; Osborn 1933; Russell 1935; Brown and Schlaikjer 1940; Erickson 1966; Bakker 1971, 1986, 1987; Paul 1987, 1991; Johnson and Ostrom 1995; Lockley and Hunt 1995; Dodson 1996; Dodson and Farlow 1997; Ford 1997). This in accord with the medially directed femoral caput, the open acetabulum, the morphology of the knee, and the hemicylindrical mesotarsal ankle. Trackways, which show the hindfeet touching the midline (Figs. 1B,C,E and 2A; Dodson and Farlow 1997: Fig. 4), support this view.

As described above, the ceratopsian dorsal

vertebral column was rather rigid, and a narrow pedal gauge could not have been due to extensive spinal flexion as suggested by Carpenter et al. (1994). Because the pelvic region was broad, the hindlimbs would have had to slope a few degrees ventromedially to achieve this narrow pedal gauge. To clear the capacious stomach during walking, the knees would have had to be bowed somewhat laterally. In most ceratopsids the femur was kept nearly vertical and the tibia and fibula sloped an estimated 15° ventromedially. This was possible because of the asymmetrical distal femoral condyles, with the lateral condyle extending slightly distally beyond the medial condyle (e.g., Marsh 1891a: Plate VIII; Hatcher et al. 1907: Plate XIV; Brown 1917: Plate XVII; Langston 1975: Fig. 10; Lehman 1989: Fig. 20).

Dodson and Currie (1990) suggested that this femoral morphology implied a non-parasagittal femoral action, but this is probably incorrect. Rather, it would most likely have served to direct the crus medially, thus allowing the knees to be fairly wide apart while maintaining a narrow pedal gauge. Femoral action would probably not have been affected. Lehman (1989) noted that the strong lateral curve of the femoral diaphysis in *Chasmosaurus* indicated that the hindlimbs were bowed out more than in other ceratopsids, probably owing to the great broadness of their abdomen (Fig. 1C). It is possible, although by no means certain, that pedal gauge in *Chasmosaurus* was wider than in other ceratopsians. A similar morphology is present in *Pentaceratops* (Wiman 1930: Plate VI).

Discussion

It is evident that a wide-gauge, sprawling forelimb posture with a horizontal humerus runs counter not only to available trackway evidence, but also to forelimb anatomy. This reconstruction must be rejected. If a large ceratopsid with sprawling forelimbs and a horizontal humerus were made to walk out trackways of *Ceratopsipes* (Lockley and Hunt 1995) or *Tetrapodosaurus*, the epipodium would have to be directed sharply medially (Ford 1997: Fig. 8C), the hands would be twisted medially, which is contrary to trackway evidence, and the whole anterior part of the body would be

tilted markedly toward the ground in a body posture that appears highly unusual for a large terrestrial quadruped. Such a reconstruction would also imply that ceratopsian locomotion was by default slow and cumbersome, but it cannot be labeled elephantine, because of numerous differences in appendicular functional anatomy between ceratopsids and proboscideans. As Bakker (1986) noted, the discrepancy in inferred limb kinematics between forelimbs and hindlimbs of such an animal would be very pronounced, and that in itself appears dubious.

Analyses of limb proportions and bone strengths of ceratopsians (Alexander 1985, 1989, 1991; Christiansen and Paul in press) tend to reveal similarities with large mammals for both forelimbs and hindlimbs. There has been little dispute that ceratopsid hindlimbs were kinematically similar to the limbs of extant large mammals. One could reasonably suppose that the allometry of ceratopsian forelimbs, if their kinematics differed so markedly from their hindlimbs, would differ more from extant large mammals than the allometric trends of their hindlimbs. This, however, is not the case (Christiansen and Paul in press). Analyses of bone strengths (Alexander 1985, 1989, 1991; Christiansen and Paul in press) suggest that ceratopsids may have been capable of running in a fashion comparable to that of extant rhinos, and considerably faster than elephants.

Johnson and Ostrom (1995: p. 216) are incorrect in their assertion that Paul's (1991) conclusions on ceratopsid limb posture and locomotory capability are based not on "compelling anatomical evidence, but rather on assertions that such energetic locomotion was consistent with the suggestion that all dinosaurs were endothermic with a high metabolic rate." Paul has not linked metabolism with a running gait because extant endothermic and ectothermic tetrapods include both species capable and those incapable of galloping (see Webb and Gans 1982 for galloping in reptiles). Among extant terrestrial tetrapods, however, traditional anatomical adaptations for sustained fast locomotion are found in the skeleton of endotherms only. In this respect ceratopsids again show some resemblance to large

mammals, not large reptiles (Christiansen and Paul in press). To restore locomotion in extinct forms Paul has instead used several of the anatomical characters outlined more specifically in this paper. It would appear that Ostrom and Johnson (1995) have based their conclusions on a questionable anatomical reconstruction, inconsistent with trackway evidence.

Although we believe that it is likely, it is not certain that ceratopsids were able to attain a full gallop (Christiansen and Paul in press). The rather inflexible dorsal series may have imposed limits on the asymmetry of the gaits possible, although this appears not to be the case among relatively stiff-trunked extant ungulates. However, scapular mobility among extant ungulates is usually well developed, and although we suggest that it was present in ceratopsians also, it would probably have been less intense. Russell (1977) suggested that ceratopsids lacked special structures for support of the large head during a gallop; however, withers were present in at least *Chasmosaurus* (Fig. 1), and the cervicodorsal series of ceratopsids appears more massively built than in comparably sized elephants or perissodactyls (Fig. 1). The validity of Russell's suggestion thus appears dubious.

It might seem that giant terrestrial animals would need pillarlike limbs to support their own mass, as in elephants, stegosaurs, and sauropods (Paul 1987; Christiansen 1997). Large ceratopsids, however, were not the only possible examples of extinct terrestrial giants whose appendicular anatomy suggests a locomotory potential exceeding that of extant elephants. Granger and Gregory (1936) noted that joint flexion was present in the largest known land mammals, the indricotheres rhinoceroses. The limbs of indricotheres are morphologically significantly different from those of elephants and are more similar to those of extant running ungulates, even at body masses of up to 15–20 metric tons (Fortelius and Kappelman 1993; Paul 1997). The humerus is short and the elbow appears to have been flexed and held posterior to the glenoid, rather than the long, subvertical humeri of proboscideans. The knees and ankles of indricotheres were also flexed. The metapodials were elon-

gated compared with those of elephants, the number of digits was reduced, and the hemicylindrical astragalus allowed the ankle to rotate. Possibly indricotheres retained the ability to attain at least a trot.

Recently extinct rhinos, such as *Elasmotherium* or *Megacerops*, strongly resembled extant rhinos. *Elasmotherium* and *Megacerops* also had longbones indicating permanent joint flexure, and they reached 2–5 metric tons in body mass (Paul 1997). Uintatheres, arsinoitheres, and brontotheres were archaic mammalian giants, approximately the same size as extant rhinos, with roughly similar appendicular anatomy. Osborn (1929) restored titanotheres, which reached an estimated 3–5 metric tons, with flexed limbs, and giant theropods and hadrosaurs appear to have had flexed knees also (Paul 1987, 1988). It is true, as Dodson and Farlow (1997) stated, that ceratopsians are not mammals, but the functional anatomy of their limbs clearly resembled that of large mammals much more than that of large reptiles. In this respect the ceratopsians are no different from the other dinosaur groups.

Conclusion

The traditional mounting of ceratopsid skeletons with either very wide gauge forelimbs, as in sprawling reptiles, or near-columnar, elephantine forelimbs is strongly at odds with both trackway evidence and anatomy. Rather, both trackways and anatomy appear to support a forelimb posture similar to that of large, extant mammals, albeit probably with slightly more averted elbows. Several problems with mounting the forelimbs in flexed, near-parasagittal fashion stem from errors in mounting the axial skeleton. Some of the anatomical characters usually cited as evidence of a sprawling forelimb posture, such as a prominent lesser tubercle or the morphology of the deltopectoral crest, are erroneous. We conclude that the best extant analogues for forelimb posture in ceratopsid dinosaurs are rhinos. The two groups share a number of convergent anatomical resemblances probably forced upon them by the influence of gravity and by the need to support a large body mass while retaining the ability to perform true running with a suspended phase.

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