

THE EVOLUTION OF MANUS SHAPE IN SAUROPOD DINOSAURS: IMPLICATIONS FOR FUNCTIONAL MORPHOLOGY, FORELIMB ORIENTATION, AND PHYLOGENY

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ABSTRACT—Sauropods have a unique digitigrade and semi-tubular manus whose shape has been used as a synapomorphy that unites most sauropod taxa. The vertical orientation and semi-tubular arrangement of the metacarpals suggest the sauropod manus improved the mechanical ability of the forelimb to support great weight. However, the evolutionary mechanism responsible for modifying the relatively flat metacarpus of basal saurischians into a semi-tubular arrangement has remained uninvestigated. Furthermore, trackway evidence shows that manus pronation was more developed in sauropods than other saurischians. However, because the radius and ulna do not cross completely in sauropods, reconciling manus print orientation with forelimb osteology has been difficult. Restudy of North American neosauropod appendicular osteology and anatomy suggests that the unique manus shape of sauropods is linked temporally with reversion to a quadrupedal posture and the necessity of manus pronation. Articulation and manipulation of neosauropod forelimbs and casts, as well as a scale model of *Apatosaurus louisae*, suggest that, as the sauropod forelimb resumed a weight-bearing role, the primitively anterolateral position of the radius shifted to assume a more internal (anteromedial) orientation in relation to the ulna proximally and distally. The internal shift of the radius may have subsequently pronated the manus while simultaneously altering the shape of the digital arch, transforming a flat dinosaurian manus into a digitigrade, semi-tubular structure. Morphological evidence presented here suggests a semi-tubular manus was an exaptation that ultimately functioned as a weight-distributing structure, and that this unique morphology may have been present in basal sauropods.

INTRODUCTION

The gigantic size, extensive fossil record, and global distribution of sauropod dinosaurs have made them the focus of a wide range of paleontological studies (Dodson, 1990; McIntosh et al., 1997). Due to the paucity of complete skull material, the evolutionary history and phylogenetic relationships of sauropods have been evaluated and established predominantly on postcranial characters (Bonaparte, 1986; McIntosh, 1990; Upchurch, 1995, 1998; Wilson and Sereno, 1998). Although Sauropoda itself is diagnosed primarily on appendicular characters related to locomotion (e.g., Upchurch, 1998; Wilson and Sereno, 1998), the functional morphology of these characters remains poorly understood because of the size, mass, and roughened articular surfaces of sauropod limb and foot bones. However, the selection, evaluation, and interpretation of these appendicular characters require inferences about bone and landmark shapes that were influenced by function in the living animal. Therefore, the examination of appendicular functional morphology in sauropods complements current phylogenetic approaches by evaluating and illuminating the origins and roles of characters selected and implemented in the construction of various phylogenetic hypotheses. Within this context, the unusual shape of the sauropod manus has significant implications for sauropod evolution and locomotion.

Most sauropods have a unique, semi-tubular and digitigrade manus in which five robust metacarpals form a vertical, U-shaped colonnade (Upchurch, 1995, 1998; Eusauropoda; Wilson and Sereno, 1998; Neosauropoda). The triangular and wedge-shaped proximal articular surfaces of the metacarpals form an arc of nearly 270° in proximal view (McIntosh, 1990; Upchurch, 1994; Wilson and Sereno, 1998) (Fig. 1), and when articulated, the shafts of the metacarpals are tightly appressed against one another such that their distal ends do not splay apart. That this configuration was held during locomotion is confirmed by the U-shaped manus prints of most known sauropod trackways (e.g., Farlow et al., 1989; Lockley, 1991; Farlow, 1992; Santos et al., 1994). This peculiar metacarpus shape

is used currently as a synapomorphy that unites most sauropod taxa (Upchurch, 1995, 1998; Eusauropoda; Wilson and Sereno, 1998; Neosauropoda).

The shape of the sauropod manus differs significantly from other saurischians. In contrast to the digitigrade manus of sauropods, basal dinosaurs, theropods, and prosauropods possess a flattened metacarpus in which digits IV and V are reduced or absent (Sereno, 1993; Benton, 1997; Galton, 1990a), and in which the articulated metacarpus forms an arc of approximately 90° proximally (Wilson and Sereno, 1998:48) (Fig. 1). In combination with the columnar limb posture of sauropods, it is tempting to view the vertical and tubular arrangement of the sauropod metacarpus simply as a graviportal adaptation that allowed their manus to reduce and redistribute tensile and shearing forces during locomotion. As Christiansen (1997) has suggested, the manus appears perfect for distributing great mass and extending the columnar nature of the forelimb. However, unlike sauropods, the manus of other graviportal dinosaurian or mammalian quadrupeds is usually short and broad. In articulation, the metacarpals of thyreophoran and neoceratopsian dinosaurs, as well as those of elephants, form a broad proximal arc and splay apart from one another distally (*Stegosaurus*: Galton, 1990b; Ankylosauria: Coombs and Maryanska, 1990; Neoceratopsia: Dodson and Currie, 1990; Proboscidea: Sikes, 1971; Shoshani, 1996) (Fig. 2). Therefore, whereas the sauropod manus may have ultimately functioned as an important weight-supporting component of the forelimb, the development of its unique shape was probably not tied directly to large size or graviportal constraints. Thus, despite its unique shape and phylogenetic significance, the evolution and development of the sauropod manus remain uninvestigated.

Manus Pronation: Conflict Between Trackways and Osteology?

In many mammals, the manus can be rotated so that the palmar surface faces anteriorly in supination or posteriorly in pronation; this action is facilitated by a rounded radial head that

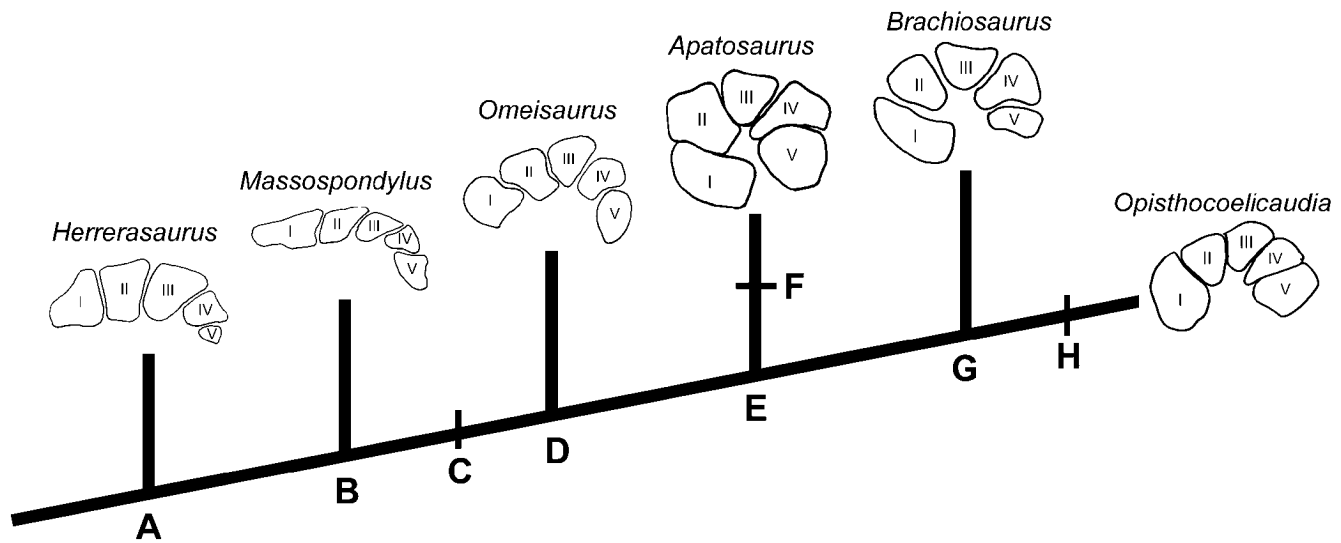


FIGURE 1. Phylogenetic diagram of proximal manus shape in *Herrerasaurus*, *Massospondylus*, and selected sauropods. Simplified cladogram based on data from Upchurch (1998) and Wilson and Sereno (1998). Proximal shape of *Omeisaurus* manus differs from previously published reconstructions and is described in the discussion. *Herrerasaurus* after Sereno (1993); *Massospondylus* after Cooper (1981); *Omeisaurus* modified from He et al. (1988); *Apatosaurus* after Gilmore (1936); *Brachiosaurus* after Janensch (1922); *Opisthocoelicaudia* modified from Borsuk-Bialynicka (1977). Nodes/Stems: A, Saurischia; B, Sauropodomorpha; C, Sauropoda; D, Eusauropoda; E, Neosauropoda; F, Diplodocoidea; G, Macronaria/"Brachiosauria"; H, Titanosauria. Roman numerals indicate metacarpal of same number. Not to scale.

pivots in a facet on the proximal and lateral aspect of the ulna (Hildebrand, 1995). This movement allows the distal end of the radius to rotate about the ulnar shaft, changing the orientation of the manus actively. In contrast, the head of the radius in elephants is angular and locked in a triangular fossa on the anterior and lateral face of the ulna, thereby immobilizing the forearm and preventing supination of the manus during locomotion. The distal half of the radial shaft is very sigmoidal and wraps or crosses over the ulna completely to lie internally (medially) in the forearm (Sikes, 1971:68), resulting in permanent pronation that allows the manus to function like the pes by flexing and extending anteroposteriorly (Fig. 3A). Active pronation of the manus is precluded or was very poorly developed in most saurischians because the oblong morphology of the radial head in these dinosaurs prevents the radius from rotating about the ulna. Complete pronation was not likely in theropods or prosauropods because the radius lies lateral and anterior to the ulna at the elbow, and the radial shaft lies anterior, not medial, to the ulna distally (Fig. 3B, C, D). This incomplete crossover directs the palmar surface of each manus inward in a permanent "prayer-like" or semi-pronated orientation (e.g., in *Herrerasaurus*: Sereno, 1993:figs. 7, 16 *Allosaurus*, *Plateosaurus*: pers. obs.).

Most sauropod trackways show clearly that manus pronation was well developed in sauropods (Farlow et al., 1989; Ishigaki, 1989; Lockley, 1991; Farlow, 1992; Santos et al., 1994; Lockley and Hunt, 1995), but not as well developed as it is in proboscideans (Wilson and Sereno, 1998:26). Most known sauropod manus prints are oriented anterolaterally in relation to the direction of travel (Wilson and Sereno, 1998:26), and variation is present in the degree of manus "supination" from the track midline. Measurement of the supination angle in Middle Jurassic (Ishigaki, 1989; Santos et al., 1994), Late Jurassic (Lockley and Hunt, 1995), and Early Cretaceous (Farlow et al., 1989) published trackways reveals a range of lateral manus rotation from as little as 5–10° to as much as 55° (Fig. 4). Although the manus is not as completely pronated as observed in proboscideans, it does face more anteriorly than laterally (Wilson and Sereno, 1998:26) and this orientation suggests it likely extended

and flexed in an anteroposterior plane as in proboscideans. For the remainder of the paper, "pronation" refers generally to the anterolateral orientation observed in known sauropod trackways, and extremes and variation will be discussed in more depth throughout the paper.

Surprisingly, although manus pronation is observed in sauropod trackways, the radius of sauropods does not wrap over or completely cross the distal end of the ulna as might be predicted. Instead, both bones more or less parallel one another throughout the entire length of the forearm (Fig. 5A, B, C). The radius of Eusauropods and Neosauropods is nearly straight and the proximal end is triangular (Hatcher, 1902; Gilmore, 1936; McIntosh, 1990). Although Wilson and Sereno (1998:26, fig. 20) describe the radius of *Camarasaurus* as strongly curved, personal examination of their illustrated specimen (*C. grandis* [YPM 1901]) suggests that the radial shaft is deformed diagenetically in this particular individual because no other examined *Camarasaurus* radii exhibited strong shaft curvature. The triangular head of the radius articulates inside a deep, triangular radial fossa on the anterior face of the ulna, and the distal ends of the radius and ulna are flat, forming part-counterpart articulations. A gently convex process on the lateral and distal face of the radius articulates with a shallow, fist-sized fossa on the medial and distal end of the ulna (Hatcher, 1902; Gilmore, 1936; pers. obs.). Furthermore, rugose ridges on the lateral, distal fourth of the radial shaft interfinger with similar ridges on the medial, distal ulna. These ridges may represent ligamentous or tendonous attachment sites (Hatcher, 1902; Gilmore, 1936; pers. obs.) that may have further restricted radial or ulnar movements. Such an antebrachial morphology probably prevented active pronation or supination of the manus.

Assuming the radius in sauropods was anterior and lateral to the ulna proximally as it is in other saurischians, it would at most partially cross the ulna to lie anterior in the forearm distally (Fig. 5D). In all amniotes, there is a strong association between the radius and digit I, and the ulna and digit V (Shubin, 1995). Given these simple constraints, if the distal end of the radius in sauropods was anterior and lateral to the ulna proximally and anterior to the ulna distally, the manus would be

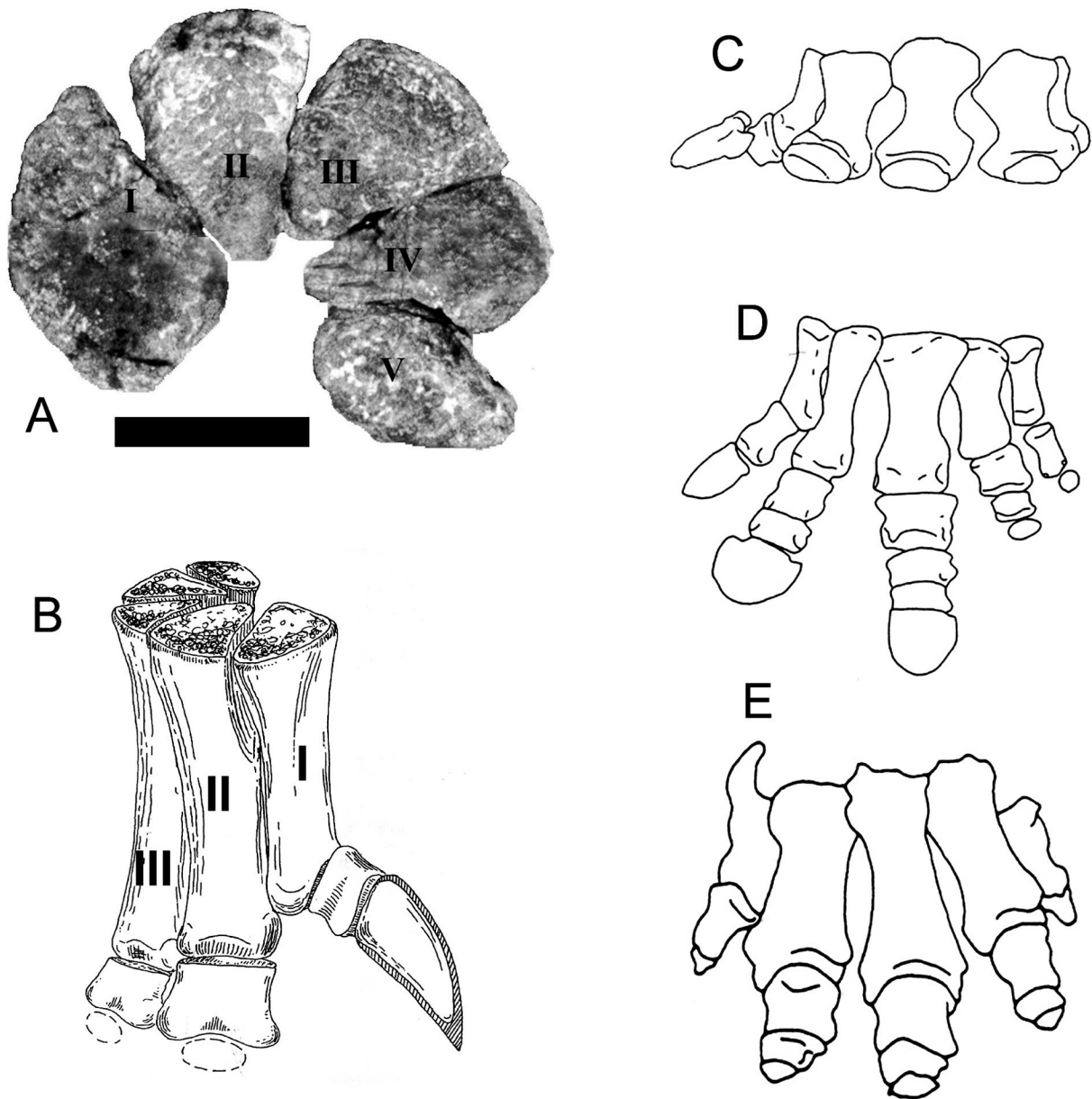


FIGURE 2. Comparing sauropod manus shape to other graviportal tetrapods. **A**, *Camarasaurus* sp. KUVF 129713 articulated right manus in proximal view; **B**, stylized reconstruction of *Camarasaurus* right manus in anterolateral view; **C**, anterior left manus of *Stegosaurus* sp.; **D**, anterior left manus of *Styracosaurus* sp.; **E**, anterior left manus of *Loxodonta africana*. **C**, **D**, and **E** from Coombs (1978); **B**–**E** not to scale. Scale bar equals 10 cm. Roman numerals indicate metacarpal of same number.

oriented lateral to the direction of forward travel (Fig. 5). In other words, metacarpal I (aligning with the radius) would lie anterior, metacarpal V (aligning with the ulna) would lie posterior, and the anterior (cranial) faces of digits II–IV would face laterally. Such an orientation would “supinate” the manus almost 90° laterally in relation to the direction of travel. This orientation, which will be termed semi-supination, contradicts known sauropod manus prints and has never been reported. This apparent difference between forelimb osteology and trackway orientation remains unresolved, and previous interpretations of the relationships of the humerus, radius, and ulna to one another differ considerably.

Osborn and Granger (1901) were the first to address antebrachial orientation in sauropods during their description of “*Morosaurus*” (= *Camarasaurus*). Although Osborn and

Granger (1901:fig. 3) illustrated the radius crossing the ulna in their restoration of the *Camarasaurus* forelimb, the radius is angled steeply medially such that it is disarticulated both proximally and distally from the ulna. Riggs (1901:pl. 40) illustrated another *Camarasaurus* forelimb (FMNH P6668) with the radius and ulna parallel to one another. Unlike Osborn and Granger (1901), Riggs (1901) placed the radius anterior to the ulna. However, he concurred with Osborn and Granger (1901), and described the radius as being anterior proximally but bending medially to cross over the ulna distally. Restudy of this *Camarasaurus* specimen (*C. grandis* FMNH P6668) showed no such crossover.

Hatcher (1902) described and extensively figured a relatively complete forelimb of *Apatosaurus* (*Brontosaurus excelsus* [CM 563]) in which the forearm and manus were partially articulat-

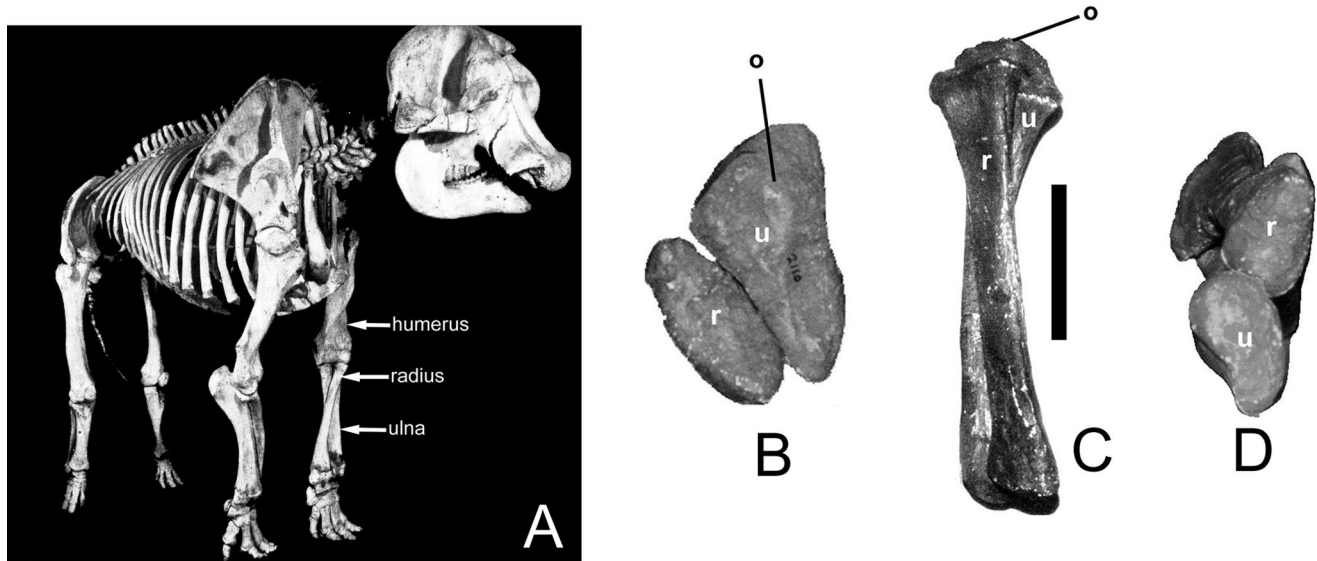


FIGURE 3. Elephant and prosauropod forearms. **A**, *Loxodonta africana* (African elephant) in oblique anterior view showing complete crossing of the radius over the ulna distally in the left forelimb (from Sikes, 1971); *Plateosaurus* sp. (AMNH 2104) in **B**, proximal, **C**, anterior, and **D**, distal view. Scale bar equals 10 cm. **Abbreviations:** h, humerus; o, olecranon process; r, radius; u, ulna.

ed. Photographs of the anterior and posterior sides of the unprepared forelimb suggested to Hatcher (1902) that the radius did not cross the ulna, but instead appeared to lie anterior and medial (internal) to the ulna. Because the forearm and manus were disarticulated, the exact positions of the bones could not be determined. However, as Hatcher (1902:pls. 19, 20) described after preparation and articulation of the humerus with the radius and ulna:

Proximally the radius articulates only with the anterior and internal portion of the distal articular surface of the humerus. The proximal end of the ulna entirely encloses that of the radius posteriorly and externally so that its articular surface is opposed to that of the distal end of the humerus posteriorly throughout its entire breadth, while at the same time presenting a broad and deep articular surface on the anterior projection which encloses the radius externally for contact with that of the anterior and external surface of the humerus. The contact of the radius with the humerus is thus limited to the antero-internal surface of the humerus instead of the antero-external as determined by Osborn and Granger [1901], so that these bones are not so completely crossed as these authors had supposed . . .

Gilmore (1936:fig. 13, pp. 218–219) later concurred with Hatcher's forearm orientation for *Apatosaurus* in his monograph on *Apatosaurus louisae*:

The radius and ulna of the left forelimb were found articulated and these furnish corroborative evidence of the correctness of Hatcher's determinations as to the proper articulation of these bones. That is, the proximal end of the radius is entirely enclosed by the ulna posteriorly. . . and thus the two elements did not cross, as first thought by some paleontologists but remain more or less parallel in the articulated limb. . . Viewed from above. . . the ulna is triangular in outline with a deep concavity in front for the reception of the angularly rounded head of the radius. . . On the inner or radial side of the ulna, near the distal end, is a fossa for the reception of the rounder, posterior, external angle of the radius.

The reconstruction by Sidney Prentice at the close of the Gilmore (1936) *Apatosaurus* monograph leaves little doubt that Gilmore oriented the forearm such that the radius lay anterior

and internal to the ulna, and articulated with the humerus in similar fashion to that proposed by Hatcher (1902). Such an orientation would allow for the manus pronation observed in trackways because the radius would lie anterior and medial to the ulna distally, but would constitute a unique morphological forearm exaptation that is unknown in other tetrapods.

In the past 30 years, three other articles on sauropods have addressed forearm orientation. Borsuk-Bialynicka (1977:fig. 19) reconstructed the titanosaurid sauropod *Opisthocoelicaudia skarzynskii* with the radius anterior to the ulna and the manus rotated laterally (=semi-supinated). Borsuk-Bialynicka (1977:46) recognized that the orientation of the manus contradicted known manus prints, and stated the following:

The basic configuration of the forearm bones is designated by the structure of the joint surfaces of the elbow articulation. . . the radius lying in front, the ulna behind. Such a position is very mammal-like but there is no indication of the crossing-over of the bones. The relation of the metacarpals to each other is very well determined too. In the articulated position they interlock at their proximal ends forming a semi-circle, their shafts being situated almost vertically. This would result in a lateral direction of the anterior (dorsal) surface of the manus if the sagittal plane of the limb as a whole were parallel to that of the main body. A rather broad cross-section of the thorax must have caused a somewhat oblique position of the limb as a whole, the elbow joint being directed slightly outwards and the anterior surface of the manus forwards and outwards.

Wilson and Sereno (1998:26), in contrast to Hatcher (1902) and Gilmore (1936), state the following:

. . . the proximal end of the radius is lodged within a deep radial fossa on the anterolateral side of the ulna. The curvature in the radial shaft accommodates its partial crossover of the ulnar shaft, and the flattened distal end of the radius articulates against the flat anterior margin of the ulna. The resultant median axis of the manus is directed mostly anteriorly and laterally as shown by many trackways. . .

Wilson and Carrano (1999:258) also reiterate the Wilson and Sereno (1998) proposal:

Unlike the condition in many mammals, however, the flat articular surfaces of the distal humerus and proximal radius

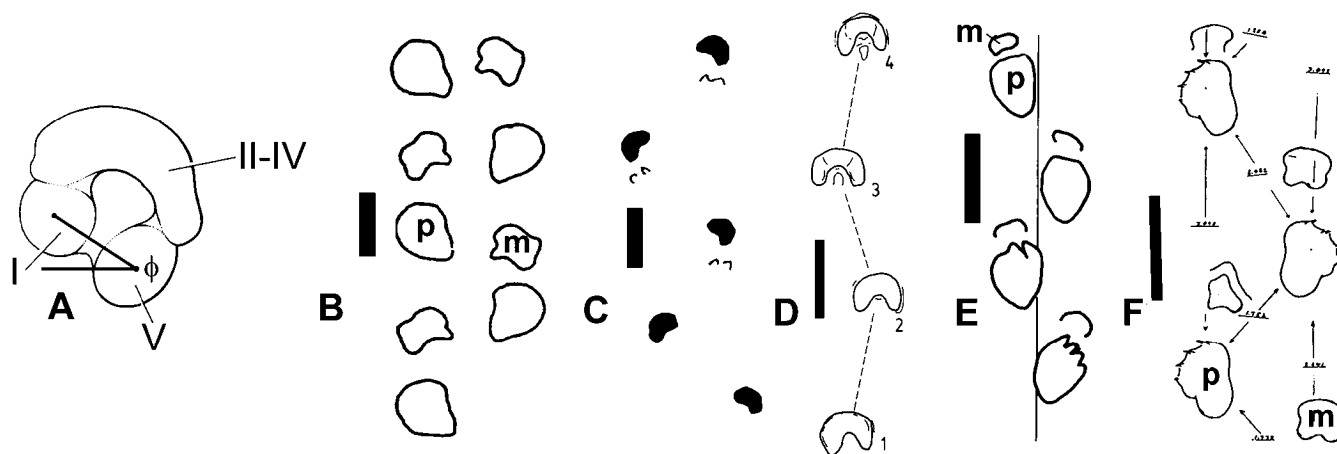


FIGURE 4. Sauropod manus orientation in trackways. **A**, *Brontopodus* stylized right manus print showing “typical” anterolateral orientation and “supination” angle (25–30°)—the “supination” angle was measured off the figures as an angle between a line connecting the centers of the digit I and V prints and a line perpendicular relative to the direction of travel. **B**, Middle Jurassic sauropod trackway from Portugal with manus and pes impressions. **C**, Middle Jurassic manus-dominated sauropod trackway from Portugal showing large degree of manus “supination” (~55°). **D**, Middle Jurassic manus-dominated sauropod trackway from Japan. **E**, Late Jurassic sauropod trackway from Colorado, USA—due to the poor manus preservation in this trackway, manus orientation was estimated here but was never used to determine “typical” orientation. **F**, Early Cretaceous sauropod trackway from Texas, USA, showing well-developed manus pronation (~5–10°). **A**, modified from Wilson and Sereno (1998); **B**, **C**, extracted from Santos et al. (1994); **D**, extracted from Ishigaki (1989); **E**, extracted from Lockley and Hunt (1995); **F**, extracted from Farlow et al. (1989). Scale bars equal 1 meter. **Abbreviations**: **m**, manus; **p**, pes; **φ**, “supination” angle. Roman numerals denote digits.

and ulna of sauropods would not have allowed full pronation of the manus. Instead, it appears that the radius was positioned lateral to the ulna at the elbow and anterior to the ulna at the wrist. This resulted in a manus that was (permanently) laterally rotated (supinated) relative to the direction of travel. . . .

Although never explicitly stated by Wilson and Sereno (1998) or Wilson and Carrano (1999), such a forearm orientation would be similar to those of other saurischians and was likely suggested by these authors because it is most parsimonious.

Thus, there appears to be a strong correlation between forearm orientation and manus pronation in sauropods and various interpretations have been proffered to account for pronated manus tracks despite the lack of radial crossover. Moreover, any changes in the orientation of the radius in relation to the ulna might also correlate with changes in manus shape. Therefore, reconciling sauropod forearm orientation with manus pronation may also elucidate the evolution of sauropod manus shape. Re-study of manus and forelimb osteology in North American neosauropod taxa suggests that manus shape, manus orientation, and forelimb posture were temporally linked in all sauropods. Here, I present data that suggest the development of a digitigrade and semi-tubular metacarpus in sauropods was probably correlated with forelimb modifications that resulted from reversion to quadrupedal locomotion during early sauropod evolution. Furthermore, osteological evidence presented here suggests that the unique shape of the sauropod manus may have arisen within the basal sauropods prior to the evolution of the Eusauropoda or Neosauropoda.

Institutional Abbreviations—**AMNH**, American Museum of Natural History; **BYU**, Brigham Young University; **CEU**, College of Eastern Utah, Price; **CM**, Carnegie Museum of Natural History; **DNM**, Dinosaur National Monument; **FMNH**, Field Museum of Natural History; **HMNS**, Houston Museum of Natural Science; **KUVP**, University of Kansas Vertebrate Paleontology Museum; **MWC**, Museum of Western Colorado; **NMNH**, National Museum of Natural History; **OMNH**, Oklahoma Museum of Natural History; **TATE**, Tate Geological

Museum; **UC**, University of Chicago; **UMNH**, Utah Museum of Natural History; **YPM**, Yale Peabody Museum.

MATERIALS AND METHODS

Materials and Manipulation

The forelimb and manus of several neosauropods were examined at the fifteen North American collections listed above. *Apatosaurus*, *Diplodocus*, and *Camarasaurus* comprise a majority of the observational and articular data presented here because their postcrania are numerous in North American collections, their phylogenetic relationships are clear, and these taxa represent two major branches of Neosauropoda (*Apatosaurus*, *Diplodocus*: Diplodocoidea [Upchurch, 1998; Wilson and Sereno, 1998]; *Camarasaurus*: “Brachiosauria” [of Upchurch, 1998]) or Macronaria [of Wilson and Sereno, 1998]). The forelimb and manus of additional sauropod and saurischian taxa were examined to provide a broader functional perspective and to frame the functional hypotheses presented here in a phylogenetic framework (see below): *Herrerasaurus* (basal dinosaur/theropod), *Allosaurus* (theropod), *Plateosaurus* (prosauropod), *Barosaurus lentus* (diplodocid), “*Pleurocoelus*” (brachiosaurid), *Alamosaurus sanjuanensis* (saltasaurid titanosaur), and “*Pelorosaurus becklesii*” (titanosaur?). Finally, the forelimbs and manus of the African elephant (*Loxodonta africana*) and the Indian elephant (*Elephas maximus*) were also examined because these mammals have typically been used as analogs for sauropods (e.g., Bakker, 1986; Paul, 1987; Jensen, 1988; Colbert, 1993).

Examination involved articulation and manipulation of forelimb and manus elements. Manipulation of sauropod forelimbs is difficult because of their mass and size, and certain manipulations required the assistance of museum staff and the use of heavy lifting equipment. Therefore, lightweight forelimb casts of *Apatosaurus yahnahpin* (TATE 001) and “*Pelorosaurus becklesii*” (YPM 5727), as well as juvenile sauropod forelimb material from CM and OMNH, supplemented manipulations of original adult material and provided additional opportunities to

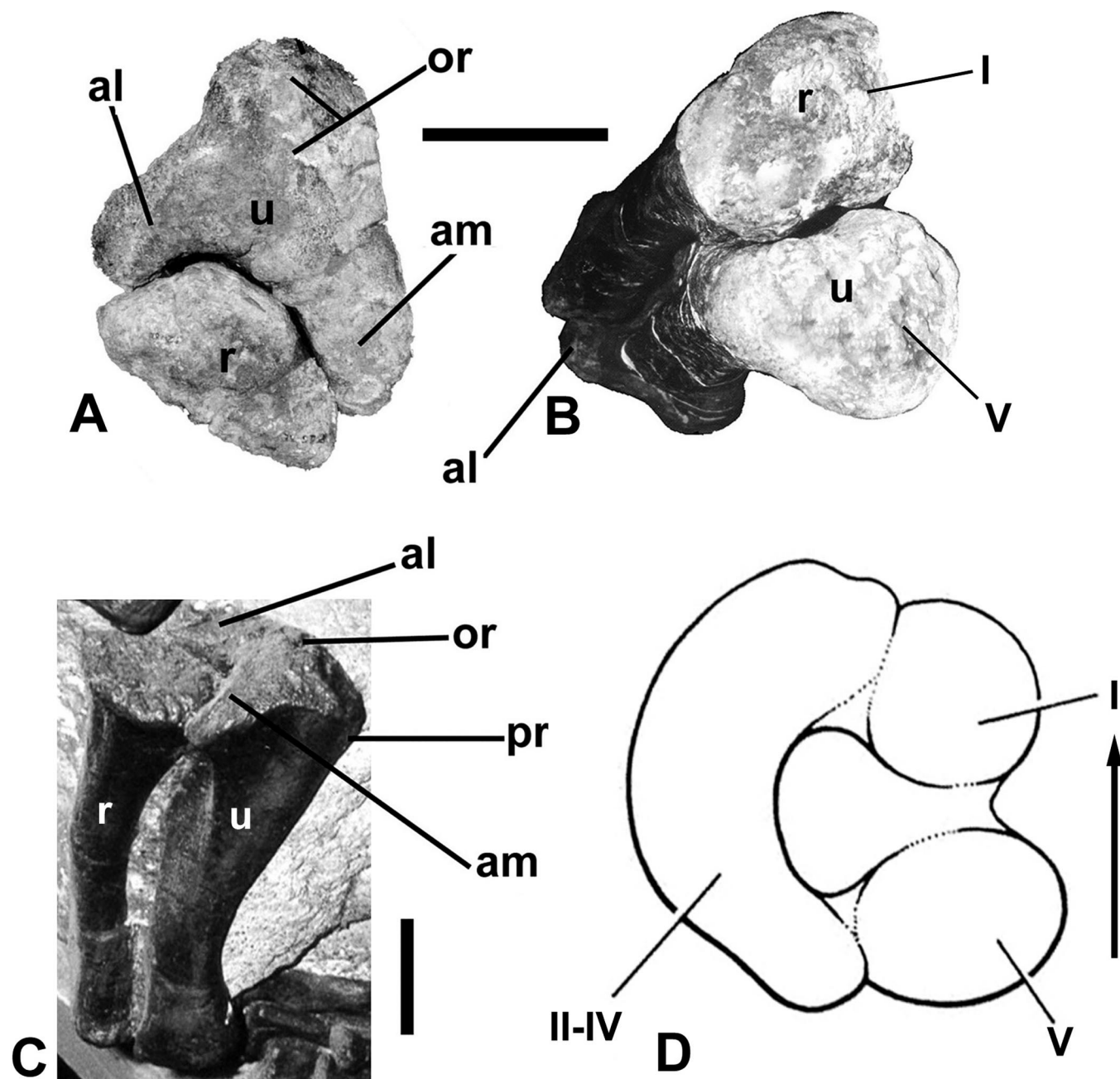


FIGURE 5. Forearm articulation in a neosauropod and its effect on manus orientation. *Camarasaurus grandis* (FMNH P6668) right radius and ulna in articulation in **A**, proximal and **B**, distal views; lateral is left and anterior is down in **A** but right and up in **B**. The forearm is oriented here as would be typical of other saurischians (i.e., the radius is anterior and lateral to the ulna proximally, and anterior to the ulna distally). Notice that the radius does not cross the ulna distally as it would in proboscideans and that, with the exception of a gentle bowing of its shaft, the radius parallels the ulna. With minor variation, the relationships of the ulna and radius depicted here are similar in other sauropods for which the forearm is known and articulated (Fig. 10). **C**, Lateral view of the articulated forearm of *Camarasaurus lentus* (CM 11338) showing a similar relationship between the radius and ulna as observed in *C. grandis* (FMNH P6668) above. **D**, Hypothetical orientation of manus print that would be formed by a sauropod with the radius and ulna oriented as in other saurischian dinosaurs—manus is semi-supinated, arrow indicates direction of travel; modified from Wilson and Sereno (1998). Scale bars equal 10 cm. **Abbreviations:** as for Figures 3 and 4 except: **al**, anterolateral process; **am**, anteromedial condyle; **or**, olecranon region; **pr**, posterior ridge of the ulna.

manipulate and articulate sauropod forelimbs. Allometric differences between juvenile and adult sauropod limbs appear to have been slight (Carpenter and McIntosh, 1994), and Wilhite (1999) has even suggested that limb growth in *Camarasaurus* was essentially isometric. Examination and manipulation of juvenile and adult sauropod limbs suggests that the range of mo-

bility observed in juvenile limbs does not appreciably differ from that of adults.

In addition to manipulating original or casted fossil material, two scale models were utilized to simultaneously manipulate and articulate the scapulocoracoid, humerus, forearm, and manus of a juvenile and adult *Apatosaurus*. The juvenile model

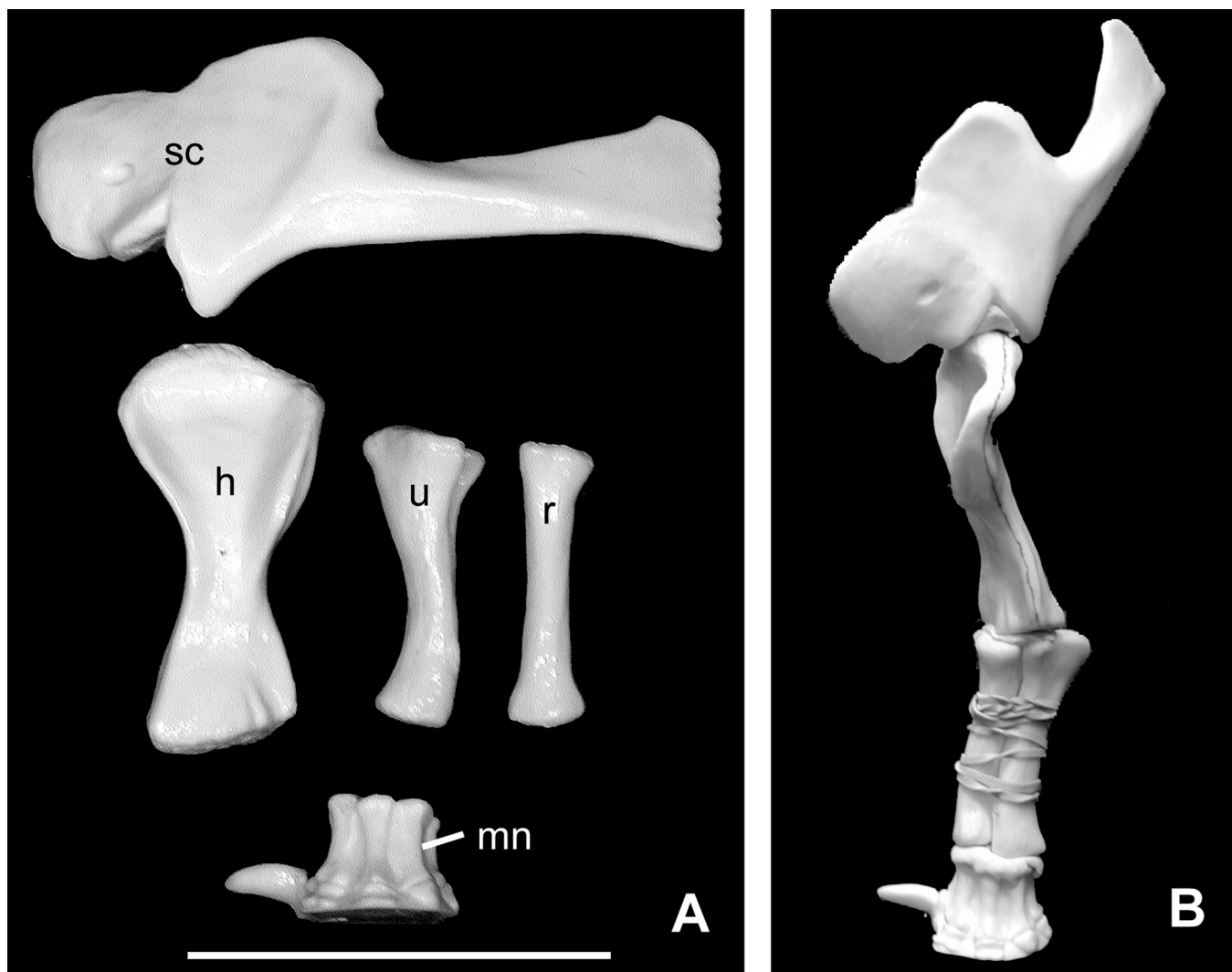


FIGURE 6. Platt model of *Apatosaurus louisae* (CM 3018). The model was constructed at 1/12th scale based on Gilmore (1936) and measurements by Platt. **A**, disarticulated view of model showing scapulocoracoid in lateral view, humerus, radius, and manus in anterior view, and ulna in oblique medial view; **B**, articulated model in oblique lateral view held together with a thin layer (~5 mm) of modeling clay between the joints. See Materials and Methods for more information on positioning and articulating the model. Scale bar equals 10 cm. **Abbreviations:** as for Figure 3 except: **mn**, manus; **sc**, scapulocoracoid.

was sculpted by the author using Sculpey[®] modeling compound, and was based on personal examination and measurement of the *Apatosaurus excelsus* CM 566 forelimb (Peterson and Gilmore, 1902; McIntosh, 1981; see Bonnan [2001] for details). Although this model was used in the initial stages of this research, it was based on an incomplete specimen without a coracoid, radius, or manus (these elements were modeled after published and examined adult *Apatosaurus excelsus* specimens and scaled accordingly). Therefore, a 1/12th scale model of the complete *Apatosaurus louisae* (CM 3018) (Gilmore, 1936) forelimb sculpted by Phillip R. Platt was used here to more precisely determine the relationships among the scapulocoracoid, humerus, forearm, and manus (Fig. 6). The Platt model was not constructed under the author's supervision, but it is an accurate three-dimensional facsimile based both on Platt's personal observations and measurements of the original material in combination with published figures and measurements by Gilmore (1936). The Platt model is illustrated here and was used to complement the observations and manipulation of sauropod forelimb and manus material.

Interpretation of Joint Surfaces

The ends of sauropod limb bones have a rugose and deeply pitted texture that does not represent the actual living articular surface (Wilson and Sereno, 1998). Instead, unlike the well-defined articular surfaces of adult mammalian long bones that articulate in precise ways in the absence of cartilage (Hildebrand, 1995), an unknown portion of the actual articular surface morphology is unpreserved in sauropod long bones. Holliday et al. (2001) suggest 10–20% of limb-bone size, as well as major articular surface features, are severely truncated or lost during skeletonization in extant archosaurs. They further suggest an appreciable amount of morphological data may be absent in dinosaur skeletons as well, although birds showed less dramatic changes than alligators (Holliday et al., 2001). Therefore, it is difficult to estimate the natural spaces formed between sauropod limb bones. However, the sculpted and grooved articular surfaces of sauropod bones may not necessarily indicate the presence of thick hyaline cartilage. In most tetrapods, hyaline cartilage on the epiphyses is usually relatively thin (Chris-

tiansen, 1997). This is because cartilage is poorly vascularized tissue and chondrocytes obtain nutrients mostly via diffusion (Currey, 1984). Because diffusion of nutrients limits the physical thickness of hyaline cartilage, Christiansen (1997) suggested that the pitted epiphyses of sauropods were more likely covered by a thin layer of hyaline cartilage, with additional joint support deriving from one or more fibrocartilaginous menisci as observed in both mammals and birds. Moreover, the grooved and pitted articular surfaces of the long bones in extant archosaurs and other sauropsids are remnants of the finger-like, calcified cartilage projections of the growth zone between the bone surface and the articular cartilaginous epiphysis (Haines, 1969). For example, as the cartilaginous epiphyses continue to migrate distally throughout the life of extant crocodylians, the growth zone of calcified cartilage continuously grows into these epiphyses because the growth zone never overtakes the epiphysis (Haines, 1969). Therefore, although the presence of rugose and pitted articular surfaces in sauropod long bones is assumed to correlate with thick cartilaginous epiphyses (Hotton, 1980:342–343; Wilson and Sereno, 1998:57), this morphology may instead simply reflect the absence of ossified epiphyseal plates in sauropods.

Whereas the precise thickness and shape of long bone articular cartilages are unknown for sauropods, it does not follow that the relationships of the forelimb bones to one another are unintelligible in the absence of cartilage. Although the range of forelimb flexion, rotation, abduction, and adduction in sauropod forelimbs are difficult to constrain without soft tissue parameters, the relationships of the forelimb bones to one another in a support posture can be constrained on the basis of biomechanical considerations. The mechanical properties of bone make it strongest under compression, weaker under tension, and weakest under shear (Currey, 1984). Hence, the columnar limb posture of elephants and other graviportal mammals acts to restrict flexion and rotation of the limb during the support phase of locomotion to subdue tensile and torsional forces (Hildebrand, 1995; Ramsay and Henry, 2001). In elephants, a ventrally directed scapular glenoid and dorsally facing humeral head act to orient the humerus vertically (Sikes, 1971). Furthermore, the posteriorly deflected olecranon process of the ulna allows the forearm to extend completely against the distal end of the humerus without interference (pers. obs.). Finally, antebrachial flexion is restricted during the support phase (Ramsay and Henry, 2001) and only occurs during the recovery stroke as the forelimb is lifted off the ground and swung forward (see Muybridge, 1957:pls. 110, 112). Therefore, the relative positions and associations of the forelimb bones in elephants do not change appreciably during the support phase of locomotion.

The forelimb posture of sauropods was probably columnar during the support phase of locomotion based on similar biomechanical constraints. As in elephants, the sauropod glenoid faces ventrally, and the humeral head faces mostly dorsally, which would have allowed the humerus to assume a vertical orientation (see below). The humeral condyles of sauropods are directed mostly ventrally and thus, regardless of cartilage shape or thickness at this joint, such an orientation would have restricted flexion at the elbow (and see below). Moreover, the olecranon process of the ulna is very reduced or absent, which suggests the forearm was capable of full extension against the humerus (and see below). Furthermore, recent work by Erickson et al. (2002) on femora has shown that the biomechanical properties of long bones in all vertebrates are similar. Thus, the support posture of the sauropod forelimb was probably columnar on the basis of known bone mechanics in other graviportal vertebrates. In other words, there was a limited range of possible articulations and associations between the bones of the forelimb and manus during the support phase of locomotion in sauropods regardless of articular cartilage shape or thickness.

For the purposes of the present study, only the relationships of the forelimb and manus during the support phase of locomotion will be considered because this is when manus prints were formed.

Evaluating Forearm Orientation

Based on previous discussion in the literature regarding the relative positions of the humerus, radius, and ulna, two functional hypotheses are presented here that may account for the manus pronation observed in sauropod trackways. The null hypothesis is the parsimonious assumption that the orientations of the sauropod humerus, radius, and ulna were similar to those of theropods and prosauropods. The null hypothesis would require active pronation of the manus through movements at the carpus, elbow, and gleno-humeral joint during the support phase of locomotion in order to match available trackways. The alternative hypothesis is the assumption that some transformation in the relationships of the humerus, radius, and ulna occurred, and that manus pronation was accomplished through such a transformation.

These functional hypotheses were evaluated within the context of the two most recent and comprehensive sauropod systematic studies by Upchurch (1998) and Wilson and Sereno (1998). In both phylogenies, Prosauropoda and Theropoda are consecutive monophyletic outgroups used to infer ancestral posture and forelimb orientation in the Sauropoda (Upchurch, 1998; Wilson and Sereno, 1998). Although the monophyly of Prosauropoda is debated (Galton, 1990a; Benton, 1997; van Heerden, 1997; Sereno, 1997, 1999), monophyly was assumed in the present study to simplify outgroup comparisons. Bipedalism in basal dinosaurs, theropods, and prosauropods is strongly supported by fossil evidence and phylogenetic analyses (Novas, 1996; Sereno, 1993, 1997, 1999; Sereno and Arcucci, 1993, 1994; Benton, 1997), and this study follows Upchurch (1998) and Wilson and Sereno (1998) in assuming quadrupedalism was acquired secondarily in sauropods. Current phylogenetic studies suggest birds and crocodylians form the two closest extant outgroups to dinosaurs (e.g., Sereno, 1999), and these archosaurs form an Extant Phylogenetic Bracket within which inferences regarding soft tissue in sauropods and their outgroups can be evaluated (Witmer, 1995). Although the forelimbs of many neosauropods were examined, manipulated, and photographed for this research (Bonnar, 2001), this paper will focus on the osteology of *Apatosaurus* in particular because it is the only sauropod whose forelimb was manipulated as original material, in life-sized casts (*A. yahmahpin* [TATE 001]), and as a scale model (*A. louisae* [CM 3018]) by the author. This allows both functional hypotheses of manus pronation to be tested on a single sauropod genus that is well known. These data will be supplemented by the observed orientations and articulation of the forelimb in other sauropods and outgroup taxa, and exceptions or significant differences will be discussed.

An inverted approach to analyzing the sauropod forelimb is adopted in this study: the mobility of the manus is examined first, followed by examination of the forelimb. This approach was taken for two reasons. First, the orientation of the manus during the support phase of locomotion is known from many sauropod trackways and represents the only portion of the forelimb whose living orientation is known. Second, the anatomy and inferred range of motion in the manus, coupled with known manus print orientations, provide a primary source of both osteological and biological data from which to infer and constrain the relative positions and orientations of the forelimb bones. Therefore, by addressing the anatomy and orientation of the manus first, the orientation of the forelimb is rooted in, and constrained by, primary data from a walking sauropod.

RESULTS

Functional Morphology of the Sauropod Manus and Carpus

The sauropod manus probably functioned as a single, rigid, block-like structure. Intermetacarpal movements were eliminated by the angular and close-fitting proximal articular surfaces of the metacarpals (McIntosh, 1990; Upchurch, 1994). In addition, the extremely foreshortened phalanges of digits II–V appear to have had very restricted movements: their broad, flat, and undivided proximal articular surfaces, in articulation with poorly developed, ventrally facing distal articular surfaces on the metacarpals, allow for very limited flexion and almost no extension without disarticulation (Christiansen, 1997; Bonnan, 2001). In many sauropods, a pollex claw of varying size was present that may have possessed a limited range of flexion and extension (Thulborn, 1989; Upchurch, 1994). However, apart from pollex claw movement, the sauropod manus appears to have functioned as a rigid and block-like weight-supporting unit.

The manus of elephants is encased in a fleshy pad that supports and restricts the movements of metacarpals and phalanges (Mariappa, 1986; *Elephas maximus*; Shoshani, 1996; pers. obs.: *Loxodonta africana*). The proximal ends of the metacarpals interlock tightly with the distal row of carpals, preventing movement at this juncture. In elephants, the eight block-like carpals are locked together into a single functional unit by a complex series of ligamentous bands that prevent intercarpal movements (Mariappa, 1986; *Elephas maximus*, figs. 2–3; Sikes, 1971, and pers. obs.: *Loxodonta africana*; contra Jensen, 1988). Flexion and extension only occur between the proximal row of carpals and the distal ends of the radius and ulna. Thus, the manus of elephants cannot rotate or abduct at the wrist (Ramsay and Henry, 2001), and is restricted to flexion and extension in an anteroposterior plane.

The carpus of most sauropods consists of three or fewer ossified carpal elements (McIntosh et al., 1997), and neosauropods typically retained two or fewer (McIntosh, 1990; Upchurch, 1998; Wilson and Sereno, 1998). The odd nature and shape of sauropod carpal bones has led to difficulties in interpreting their orientation and articulation, and even their identity. For many sauropod taxa, it remains unclear whether the ossified carpal elements were proximal or distal because their articular surfaces are poorly defined and very rugose and pitted (McIntosh, 1990), although Wilson and Sereno (1998:39) suggest the three carpals present in the most primitive sauropods were probably distal carpals. Among the three genera that were the main focus of this study, *Apatosaurus* and *Camarasaurus* are known to have ossified carpal elements. No ossified carpal elements have been reported for *Diplodocus* (McIntosh, 1990). Although the carpi of *Apatosaurus* and *Camarasaurus* cannot represent the complete spectrum of carpus function and mobility in all sauropods, carpal elements of both genera are well known and provide two distinct morphological models of carpus function in neosauropods.

A single carpal element is known for *Apatosaurus*. Both Hatcher (1902:pls. 19, 20) and Gilmore (1936) have shown that the carpal bone was located close to the distal end of the radius and ulna in *Apatosaurus excelsus* (CM 563) and *Apatosaurus louisae* (CM 3018) (Fig. 7). A number of morphological features of the *Apatosaurus* carpal bone suggest that it is a proximal carpal. The carpal element has a disc-like outline proximally. The proximal articular surface of the carpal possesses two articular facets, one larger than the other, divided by a low and broad ridge. Hatcher (1902), and later Gilmore (1936), found that the larger facet articulated with the radius, whereas the smaller facet articulated with the ulna. Examination of the mounted CM 3018 material, the cast of CM 563, and other

Apatosaurus carpals supports this interpretation. If the large proximal facet articulated with the radius, this facet was medial and the smaller facet was lateral, and the low anteroposterior ridge between the facets articulated between the radius and ulna. The carpal element has a shallowly convex distal articular surface and, if articulated in the orientation described above, aligns with the proximal ends of metacarpals II, III, and IV (Hatcher, 1902; Gilmore, pers. obs., 1936).

The proximal articular surfaces of metacarpals II–IV in *Apatosaurus* are convex anteroposteriorly and mediolaterally. The combined proximal articular surfaces of metacarpals II–IV in articulation with the very gently convex distal articular surface of the carpal allow the central metacarpals to roll posteriorly approximately 20–30° from vertical in “flexion.” If metacarpals II–IV articulated directly with the carpal element, metacarpals I and V may have articulated directly with the radius and ulna, respectively, as described by Hatcher (1902:pls. 19, 20, fig. 4). The proximal articular surfaces of metacarpals I and V are shallow and cup-shaped, and metacarpals I and V articulate with metacarpals II and IV, respectively, such that their proximal articular surfaces lie several centimeters above the central three metacarpals. Articulation of metacarpals I and V with the distal ends of the radius and ulna in *Apatosaurus* specimens showed that these metacarpals were capable of anteroposterior flexion against the forearm. If the articulation between metacarpals II–IV and the carpal bone, and metacarpals I and V with the radius and ulna, reflect the actual articulation of the manus with the radius and ulna, flexion and extension occurred in a single plane in *Apatosaurus*. A similar functional arrangement may have been present in *Diplodocus*.

Two ossified carpals are known in *Camarasaurus* (Osborn, 1904). Carpal 1 is wedge-shaped, and its distal articular surface is composed of two smooth and gently concave facets separated by a thin ridge. These facets articulate tightly with the proximal ends of the first two metacarpals, demonstrating that carpal 1 is a distal carpal (Fig. 8A, B). A shallow but distinct ovate fossa occupies much of the proximal surface of carpal 1 and slopes approximately 30° posteriorly (Fig. 8). The shape of this fossa is similar in morphology to the distal end of the radius in *Camarasaurus*, and Osborn (1904) had suggested that the radius may have articulated directly with carpal 1 in this genus. Although it remains unclear whether a proximal row of unossified carpals were present in *Camarasaurus* (McIntosh, 1990), articulation of the radius with carpal 1 in two *Camarasaurus* specimens (AMNH 711/712 and KUPV 129716) showed a surprisingly good fit (Fig. 8).

Because the distal articular surface of the radius is convex, when the manus is assembled and oriented in pronation the radius easily rolls anteroposteriorly along the shallow ovate fossa of carpal 1 until it is angled approximately 30–40° from vertical in “flexion” (Fig. 8C, D). Disarticulation of the radius from the ovate fossa of carpal 1 results if the distal radius rolls past vertical anteriorly, or tilts more than a few degrees medially or laterally. Thus, if the radius articulated directly with carpal 1, the manus was only capable of flexion and extension. Such “flexion” was probably restricted further by cartilage, ligaments, menisci, and other soft tissues. Carpal 2 is disc-shaped and articulates with the proximal end of metacarpal V. The cup-shaped and concave proximal articular surface of carpal 2 can articulate with the hemispherical distal articular surface of the ulna. By itself, the ulna can be made to “flex” anteroposteriorly, as well as rotate slightly medially or laterally about the long axis of its shaft. However, in articulation with the radius, the movements of the ulna are constrained to anteroposterior flexion and extension. Again, soft tissues probably acted to constrain these motions. Therefore, when the ends of the radius and ulna are articulated with carpals 1 and 2, the manus can only flex and extend in a single, anteroposterior plane. Hence,

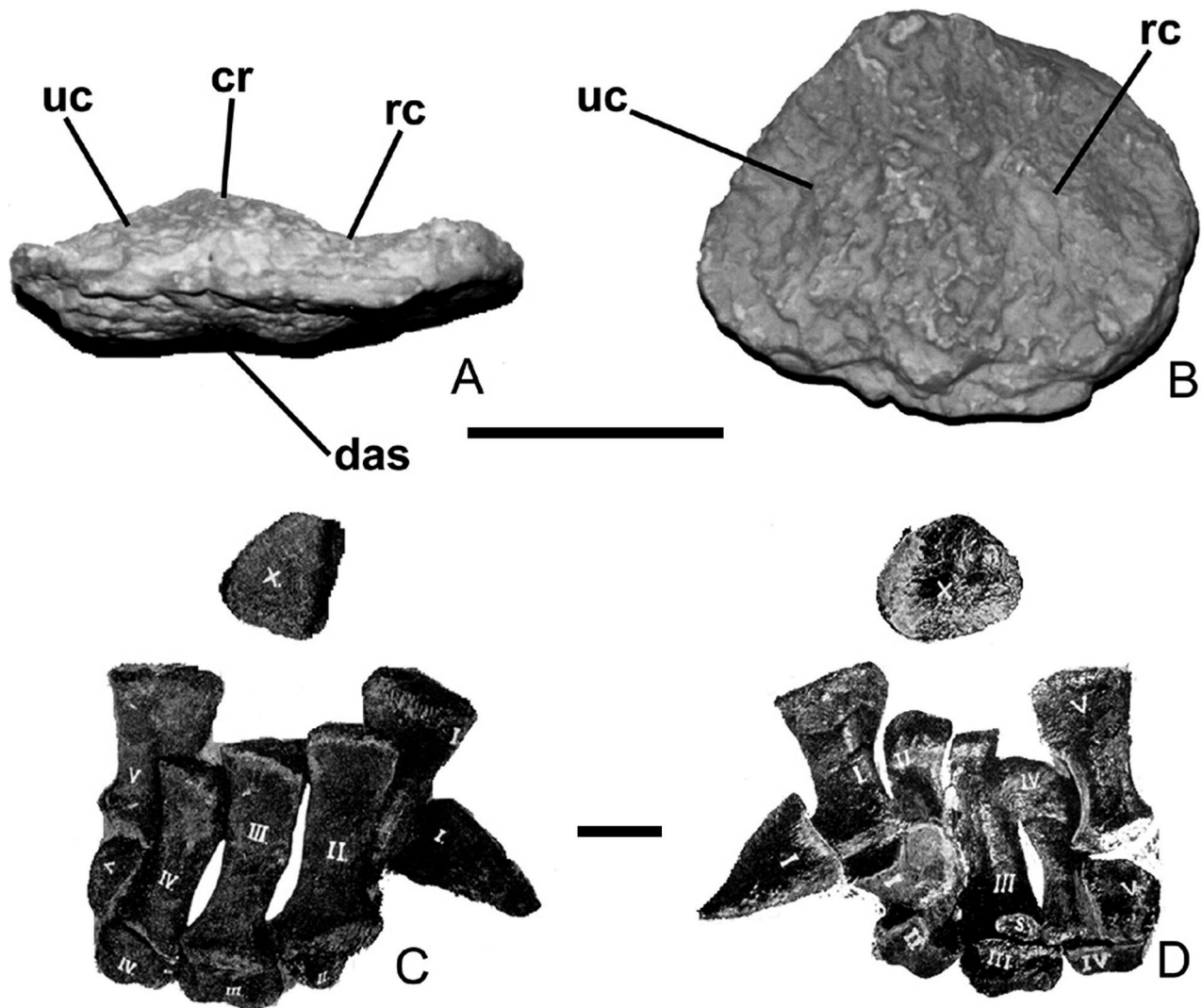


FIGURE 7. Carpus anatomy in *Apatosaurus*. **A**, *A. excelsus* right carpal CM 563 (cast from YPM) in anterior view and, **B**, proximal view; **C**, *A. excelsus* CM 563 manus in anterior and, **D**, posterior views as found by Hatcher (1902), showing the position of the carpal (labeled X). **C** and **D** from Hatcher (1902). Scale bars equal 10 cm. **Abbreviations:** cr, central ridge; das, distal articular surface; rc, radial condyle; uc, ulnar condyle. Roman numerals indicate metacarpals of same number.

the manus would have to be pronated to flex and extend anteroposteriorly with the pes in *Camarasaurus*.

These observations of manus anatomy in *Apatosaurus* and *Camarasaurus* are significant. First, to flex and extend in the same anteroposterior plane as the pes during locomotion, the manus must be pronated. If the manus were semi-supinated, its articulation with the carpus, radius, and ulna would have caused it to flex and extend mediolaterally, a range of movement that was orthogonal relative to forward travel. Second, although cartilaginous or undiscovered additional ossified carpal elements may have been present in the carpus of *Apatosaurus*, *Camarasaurus*, or other sauropods, manus rotation was unlikely because the flat articular surfaces of all known sauropod carpal bones suggest such movements were minimized. Third, restriction of wrist mobility to anteroposterior flexion and extension acts to limit the development of twisting forces through the carpus and manus during locomotion. Finally, the apparent degree of manus flexion and extension in both *Apatosaurus* and *Camarasaurus* was much less than the apparent wrist mobility of theropods, prosauropods, or even elephants. All of these ob-

servations suggest manus pronation could not be achieved through carpal movements in sauropods.

The Null Hypothesis Considered

Forelimb Movement at the Gleno-Humeral Joint—The scapulocoracoid glenoids of most sauropods are V- or U-shaped in lateral view and face almost directly ventrally (McIntosh, 1990:fig. 16.8). The head of the humerus in *Apatosaurus* is hemicylindrical and convex anteroposteriorly and mediolaterally. In articulation with the glenoid, the humerus in the model can achieve an arc of approximately 60° in anteroposterior (parasagittal) flexion-extension; this range of movement was probably restricted further by soft tissue constraints. Furthermore, the model showed that abduction and rotation at the gleno-humeral joint, although possible, were probably not well-developed actions because as the humeral head rotates obliquely in relation to the glenoid it becomes more difficult for the humerus to flex or extend without dislocation. Although additional cartilaginous extensions of the glenoid or humeral head

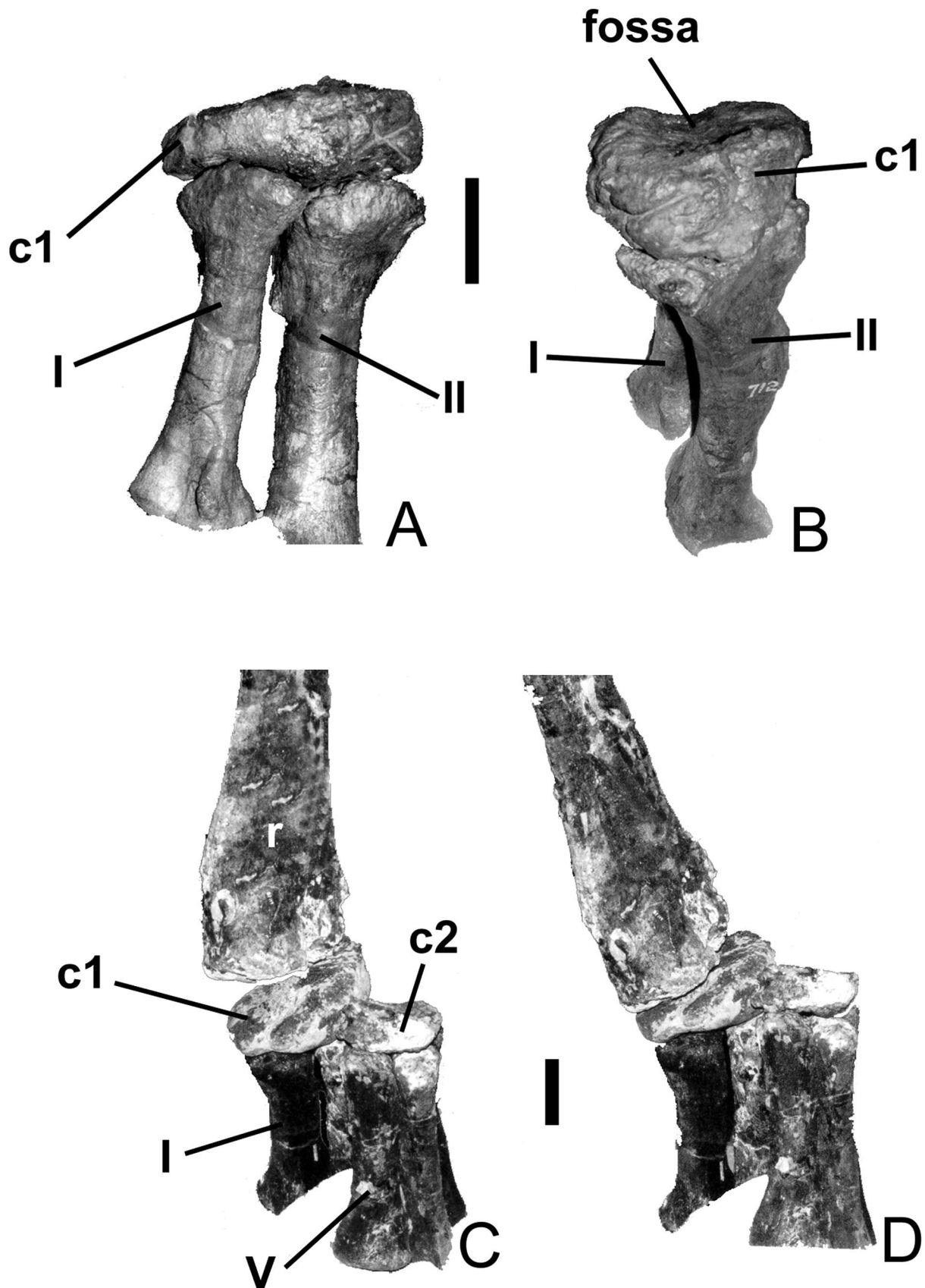


FIGURE 8. Carpus anatomy and articulation in *Camarasaurus*. **A**, *C. supremus* (AMNH 711) left carpal 1 articulating proximally with metacarpals I and II in medial view, and **B**, anterior view; **C**, articulated right manus of *C. sp.* (KUV 129713) in oblique lateral view showing the range of manus “extension” and, **D**, “flexion” if the radius articulated directly with carpal 1 (approximately 30–40°). Note that the metacarpals were placed in sand in all photos and thus the distal ends of these bones are obscured. Scale bars equal 10 cm. **Abbreviations**: as for Figure 3 except: c1, carpal 1; c2, carpal 2. Roman numerals indicate metacarpals of same number.

could probably have facilitated a greater range of humeral abduction and axial rotation than simple bone to bone contact suggests in the model, just how much non-parasagittal movement was possible at this joint is difficult to estimate. However, regardless of how much long axis rotation or abduction was possible at the gleno-humeral joint, if the forelimb was to assume a columnar posture during the support phase of locomotion then non-parasagittal movements were likely restricted as they are in proboscideans (Ramsay and Henry, 2001). Thus, the humerus was probably limited to parasagittal flexion and extension during manus contact with the substrate.

It has been difficult to establish the orientation and mobility of the scapulocoracoids in sauropods (Gilmore, 1925; Borsuk-Bialynicka, 1977; McIntosh, 1990; Filla and Redman, 1994; Parrish and Stevens, 1998). Most reconstructions incline the scapulocoracoid between 30° and 40° from horizontal, and the extent to which shoulder movement, if any, played a role in locomotion has not yet been established. Most restorations of mobile scapulocoracoids in dinosaurs assume a large, cartilaginous episternum was present anteriorly, and are patterned after the motion of the scapulae in mammals or chameleons (e.g., Bakker, 1986, 1987; Paul, 1987, 1988). It has been argued that the scapulocoracoids of sauropods and other dinosaurs were mobile in order to extend the range of limb extension and flexion, as in mammals. Although the functional morphology of sauropod scapulocoracoid movement is beyond the scope of this paper, any shoulder movements that may have occurred would have caused forelimb movement in a parasagittal plane only. Whereas scapulocoracoid movements could have improved the range of forelimb flexion and extension, they could not have caused medial rotation of the humerus under any interpretation of the osteology.

Viewed ventrally, the coracoid portion of the scapulocoracoids of *Apatosaurus* bend approximately 30° in medially from the thorax. In other words, regardless of the height or orientation of the scapulocoracoid against the thorax, the scapular blade must have assumed a relatively parallel and straight orientation against the ribs, but the coracoid portion bends inwards towards the sternum, orienting the glenoid anteromedially relative to the direction of travel. Thus, in articulation with the scapulocoracoid, the cranial face of the humerus could not have been oriented directly anterior but was oriented some 30° anteromedially in *Apatosaurus*.

Forearm Movement at the Elbow—The humeri of crocodylians, theropods, prosauropods, and avians have radial and ulnar condyles that expand onto the anterior face of the distal humerus (Reese, 1915; Romer, 1956; Proctor and Lynch, 1993). In theropods and prosauropods, the anterior expansion of these condyles and the presence of a deep cuboid fossa suggest a considerable amount of forearm flexion was possible. Although the radius cannot move independently of the ulna, abduction of the humerus in theropods and prosauropods will cause long-axis forearm rotation and orient the palmar side of the manus further ventrally in pronation (pers. obs.). Whether the forearm could rotate about its long axis at the elbow in theropods and prosauropods is uncertain. The radial condyle is greatly expanded both anteriorly and medially in *Allosaurus* and *Plateosaurus*, and the radius appeared to follow the radial condyle medially as the forearm was flexed in articulated specimens, imparting some long-axis rotation to the forearm. Although the fused radioulna of many amphibians will rotate about its long axis to pronate the manus (Haines, 1952), support for this type of movement in archosaur forearms has not been reported or demonstrated. The radial condyle of crocodylians and avians is more expanded than the ulnar condyle, and articulation and manipulation of *Alligator mississippiensis* forearms suggests a small amount of long-axis rotation may occur during flexion. However, in the absence of more thorough musculoskeletal

studies, the presence of forearm rotation at the elbow during flexion in theropods and prosauropods remains uncertain.

Two osteological features suggest that flexion and rotation of the forearm were restricted in *Apatosaurus* and most other sauropods. First, the distal articular surface of the humerus is gently convex and faces almost directly ventrally, and distinct and separate condyles are absent in all sauropods except titanosaurs (see discussion). Because no condyles expand anteriorly onto the humerus in *Apatosaurus*, and because a cuboid fossa is absent, the range of forearm flexion does not appear to have been great. Furthermore, the lack of radial condyle expansion in *Apatosaurus* and most other sauropods suggests any long-axis rotation of the forearm against the humerus was severely limited or absent. A second osteological feature that suggests reduced flexion in the forearm of *Apatosaurus* and most sauropods is the almost complete absence of the olecranon process. In most dinosaurs and mammals, the olecranon process prevents the complete extension of the forearm because it abuts the olecranon fossa of the humerus during extension. Absence of an olecranon process in *Apatosaurus* and other sauropods would allow the forearm to extend completely against the humerus (Wilson and Sereno, 1998), but why this process was not simply redirected posteriorly, as in elephants (Sikes, 1971), is not entirely clear. Perhaps a cartilaginous olecranon process was retained in sauropods and assumed a posteriorly directed orientation similar to that of proboscideans. However, unlike chelonians or lepidosaurs in which ulnar patellae form in the tendons of forearm extensors, no such sesamoids form in *Alligator* or other crocodylians (Haines, 1969:fig. 13). No cartilaginous extensions of the olecranon process or ulnar patellae have been reported for birds. Thus, because both extant outgroups to sauropods do not possess a cartilaginous extension of their olecranon regions, it appears unlikely that sauropods retained a cartilaginous olecranon process or ulnar patellae.

Even if flexion of the forearm were considerable and caused medial long-axis rotation of the forearm in sauropods, these movements would have had to occur during the support phase because that is when the pronated manus prints were made. However, flexion of the forelimb at any point during the support phase seems highly unlikely in such heavy animals simply on the basis of bone mechanics (see above). Moreover, because the forelimbs of extant graviportal mammals do not flex or rotate during the support phase, it is considered even more remote that *Apatosaurus* or most other sauropods ever walked with flexed or rotated forelimbs during the support phase of locomotion. Finally, in well preserved sauropod manus prints there appears to be little or no “smearing” of the prints, and this is yet another piece of evidence which strongly suggests the manus was not being pronated actively during the support phase of locomotion.

In summary, the sauropod manus probably functioned as a rigid block-like unit that could only flex and extend in single plane between the proximal carpus and the distal radius and ulna; it is unlikely that the manus could have been rotated or abducted. The humerus was probably restricted to movement in a parasagittal plane, and rotational movements or abduction were probably reduced during the support phase of locomotion. The forearm cannot flex in such a way that the manus is pronated distally, and even the slight degrees of pronation apparently accomplished through flexion in other saurischian dinosaurs would be impossible. Flexion during the support phase of locomotion was probably minimized to ensure the columnar orientation of the forelimb. Thus, the null hypothesis, that manus pronation was accomplished actively during the support phase of locomotion, is rejected.

Orientation of the Manus in the Articulated Model

Based on the osteological constraints of the gleno-humeral, elbow, and wrist joints described above, the Platt *Apatosaurus*

was assembled using a thin layer of modeling clay to temporarily position and hold the forelimb elements together. The scapulocoracoid was oriented such that the scapular blade was angled approximately 40° from horizontal, and this oriented the glenoid almost directly ventrally as in previously published estimations of scapular blade position (see above). Next, the scapulocoracoid was oriented such that it was directed anteriorly as if it were lying against the ribcage of *Apatosaurus*, and thus the coracoid portion of the scapulocoracoid was oriented 30° anteromedially relative to the direction of travel. Articulation of the humerus with the glenoid rotated the cranial face of this bone 30° anteromedially.

Next, the radius and ulna were articulated against the distal end of the humerus in the two ways suggested in the literature previously. Beginning with the most parsimonious orientation suggested by Wilson and Sereno (1998) and Wilson and Carrano (1999), the radius and ulna were articulated against the distal end of the humerus such that the radius articulated with the anterolateral corner of the humerus and the ulna articulated with the posterior and medial portion of the humerus. As much as possible, this was done relying on the suggested orientations of the radius and ulna described by Wilson and Sereno (1998) and Wilson and Carrano (1999). Because these authors provide no figure of an articulated radius and ulna from any sauropod, it was difficult in some respects to evaluate their proposed forearm orientation and articulation. This is not a criticism because neither article dealt with forelimb orientation specifically, and Wilson and Sereno (1998:foldout 1) did include two-dimensional skeletal silhouettes of five sauropods showing the radius positioned anterior and lateral to the ulna and the manus rotated such that its anterior (dorsal) surface faces laterally. The illustration of *Apatosaurus* in Wilson and Sereno (1998:foldout 1) is based on *Apatosaurus louisae* (CM 3018) (Wilson, pers. comm.).

If the radial head articulates with the anterior and lateral corner of the distal end of the humerus as Wilson and Sereno (1998) and Wilson and Carrano (1999) suggest, the forearm is oriented such that the medial “condyle” of the humerus lies over and articulates with the olecranon process of the ulna (Fig. 9A). Although the olecranon process of *Apatosaurus* is very reduced, articulation of the humerus and ulna in this fashion was very unlikely because such an orientation would interfere with the insertion of antibrachial extensor musculature (e.g., *M. triceps brachii*). Regardless of anatomical constraints, if the radius did articulate with the anterior and lateral portion of the distal end of the humerus, then the manus would be “supinated” approximately 70–80° in relation to the direction of travel (Fig. 5). Such a manus orientation has never been reported for any sauropod trackway and is at least 15–25° more supinated than the most supinated tracks yet reported (e.g., Santos et al., 1994: 55°; see above). Therefore, if the forelimbs of sauropods were columnar and incapable of all but a small degree of rotation or flexion at the gleno-humeral, elbow, and wrist joints during the support phase of locomotion, the forearm orientation and articulation suggested by Wilson and Sereno (1998) and Wilson and Carrano (1999) for sauropods is here considered unlikely.

An Alternative Hypothesis—Following Hatcher (1902), Gilmore (1936), and personal observations, the radius and ulna were oriented in the *Apatosaurus* model such that the ulna completely supported the humerus posteriorly and the radius articulated anterior and internally with the humerus. In this arrangement, the olecranon process of the ulna emerges posterior to the humerus as it does in all known saurischians, and this would allow the forearm to completely extend against the humerus without interfering with the insertion of extensor musculature. This forearm orientation, coupled with the 30° of anteromedial humeral rotation, results in manus pronation: the “supination”

angle was approximately 25–30° in the model, well within the range of reported sauropod manus tracks (Fig. 9B). Articulation of other neosauropod specimens with the radius anterior and internal relative to the ulna proximally and distally resulted in similar outcomes: the manus would be pronated as observed in most sauropod trackways. A major difficulty in accepting this forearm orientation is that it is unparsimonious: the radius does not assume a more internal position (anteromedial) relative to the ulna proximally in other saurischians or any other known fossil or extant tetrapods. It should be emphasized that this is not to suggest the radius and ulna literally “switched” places (i.e., the radius became medial and the ulna became lateral). Instead, whereas the ulna remained posterior to the radius in sauropods, the radius would have shifted from a lateral position to a more internal or medial position relative to the ulna. If this alternative hypothesis of sauropod manus pronation is correct, evidence for an internal shift of the radius relative to the ulna should be reflected in the morphology of the proximal ulna, the distal ends of the radius and ulna, and the manus itself.

There are two distinct processes that radiate from a central olecranon region in all known sauropod ulnae: a narrow, flattened, shelflike anteromedial (AM) condyle, and an anterolaterally-oriented (AL) process that is convex and usually shorter than the medial condyle (Hatcher, 1902; Gilmore, 1936; Raath, 1972; Cooper, 1984; McIntosh, 1990; the directional terms used here assume one is viewing the proximal end of the ulna such that the olecranon region is pointing directly posteriorly). In the earliest known sauropod with a preserved forelimb, *Vulcanodon*, the AL process is present as a small but distinct convexity (Raath, 1972; Cooper, 1984); the AL process is expanded in other known sauropods (see Fig. 10). The deep radial fossa results from the space formed between these two processes. The AL process of the proximal sauropod ulna is a unique development among saurischians. In basal dinosaurs, theropods, and prosauropods the proximal articular surface of the ulna is triangular with a single condyle that articulates with the medial or ulnar condyle of the humerus (Fig. 10).

The triradiate shape of the sauropod ulna could have developed through an internal shift in the radius relative to the ulna proximally. Shifting the radius medially would require the ulna to support the lateral, distal end of the humerus. In elephants, the radius has shifted from a primitively lateral to an anterolateral orientation (Wilson and Sereno, 1998). The proximal articular surface of the elephant ulna is triradiate, and the lateral portion of its proximal articular surface is expanded, supporting the posterior aspect of the radial condyle of the humerus (Sikes, 1971; pers. obs.: *Loxodonta africana*). This observation suggests that changes in the proximal orientation of the radius can have a morphological effect on proximal ulna morphology. Moreover, comparison of the proximal surface of the ulna in theropods, prosauropods, and sauropods suggests that the AL process is a new development in sauropods correlated with a medial shift in the radius relative to the ulna (Fig. 10). The presence of a unique convex anterolateral process in all known sauropod ulnae suggests it is a new condyle necessary for supporting the lateral, distal end of the humerus in the absence of the radius from this region. Furthermore, articulation and manipulation of the anterolateral process of the ulna with the distal end of the humerus in the Platt model and other sauropods support this proposed condyle-like function: both the AL process and AM condyle support and cradle the distal end of the humerus in this orientation.

Distally, the radius has shifted medially relative to the ulna such that the articulated distal ends of the radius and ulna form a strong arch in all sauropods where their distal ends are known (Fig. 10). This morphology differs from the condition observed in theropods and prosauropods where the radius articulates anterior to the ulna distally, forming a linear or gently cambered

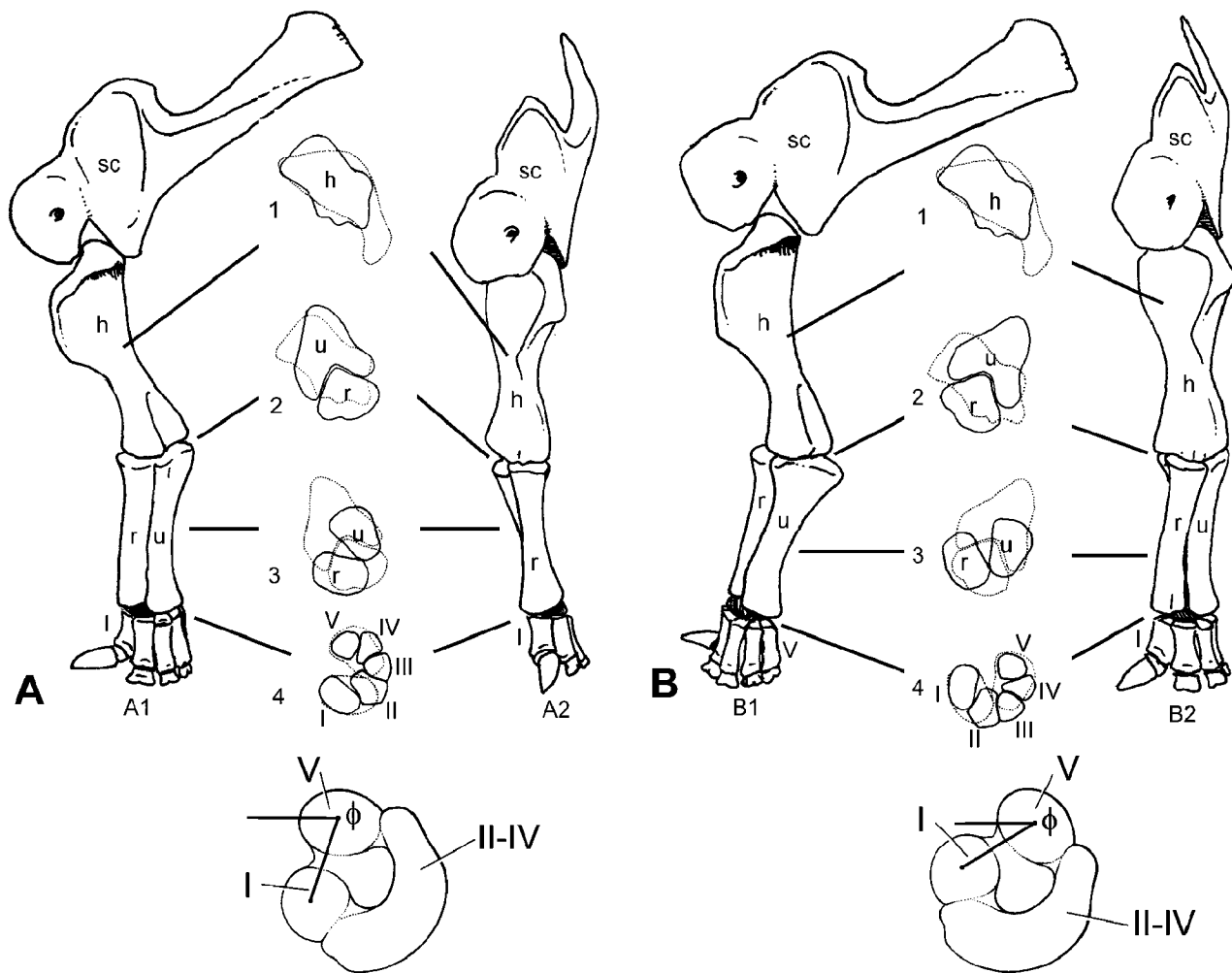


FIGURE 9. Articulation of the forelimb in the Platt *Apatosaurus* model and its effect on manus orientation. **A**, model articulated as a typical saurischian, as suggested by Wilson and Sereno (1998) and Wilson and Carrano (1999), with the radius anterior and lateral to the ulna proximally and anterior to the ulna distally in A1, lateral and A2, anterior views. **B**, model articulated as suggested by Hatcher (1902), Gilmore (1936), and the author with the radius anterior and medial relative to the ulna proximally and distally in B1, lateral and B2, anterior views. For A and B, outlines of the articular surface of 1, the humerus, 2, the distal humerus in articulation with the radius and ulna, 3, the orientation of the distal ends of the radius and ulna in relation to their proximal ends, and 4, the orientation of the metacarpals in relation to the distal ends of the radius and ulna (solid lines indicate distal surfaces, stippled lines indicate proximal surfaces). Directly below each series of articulations is a hypothetical manus print (modified from Wilson and Sereno [1998]) that reflects the orientation of the manus, with lines (as described in Fig. 5) indicating the degrees of manus "supination" in relation to the direction of travel (downward). Note that for A, manus "supination" is approximately 70° and for B, "supination" is approximately 25°. Compare these orientations to the trackways illustrated in Figure 4. **Abbreviations:** as for Figures 3 and 4. Roman numerals indicate metacarpal of same number.

arch (Fig. 10). This difference in distal forearm morphology from other saurischians further supports the hypothesis that the radius shifted internally relative to the ulna in sauropods during their evolution. Significantly, the morphology of the distal sauropod forearm corresponds with the shape of the proximal metacarpus. In other words, the strong arch observed in the articulated radius and ulna distally is reflected in the strongly arched proximal shape of the metacarpus (compare Figs. 1 and 10).

Recent paleontological and embryonic evidence shows that most carpals and all metacarpals in amniotes develop in a digital arch which originates from the ulnar axis of the forearm and sweeps over to terminate at the radial axis (Shubin, 1995). During embryonic forearm development in tetrapods, condensations along the ulnar (postaxial) axis form the ulna, all the digits, and distal carpals, whereas condensations along the radial (preaxial) axis form the radius and an unbranched column

of elements that may include the radiale and occasionally other carpals (Shubin, 1995; Shubin et al., 1997). Although the basic pattern of limb development in tetrapods is conservative (Shubin, 1995), variation in the timing of regulatory gene expression, the sequence of structural differentiation, and environmental modification of structures caused by embryonic movements can all cause variation in limb and foot morphology (Müller, 1990; Sordino et al., 1995; Shubin, 1995; Shubin et al., 1997; Gardiner et al., 1998). Moreover, Newman and Müller (2000) have even suggested that epigenetic mechanisms, not genotypes, have been the generative agents of morphological character origins. In most dinosaurs, the metacarpals and phalanges are arranged in a relatively straight sequence or slightly cambered arch that corresponds to the flat plane formed by the articulated radius and ulna distally (compare Figs. 1 and 10). However, in saurischian dinosaurs, the proximal ends of metacarpals IV and V lie on the palmar surfaces of metacarpals III

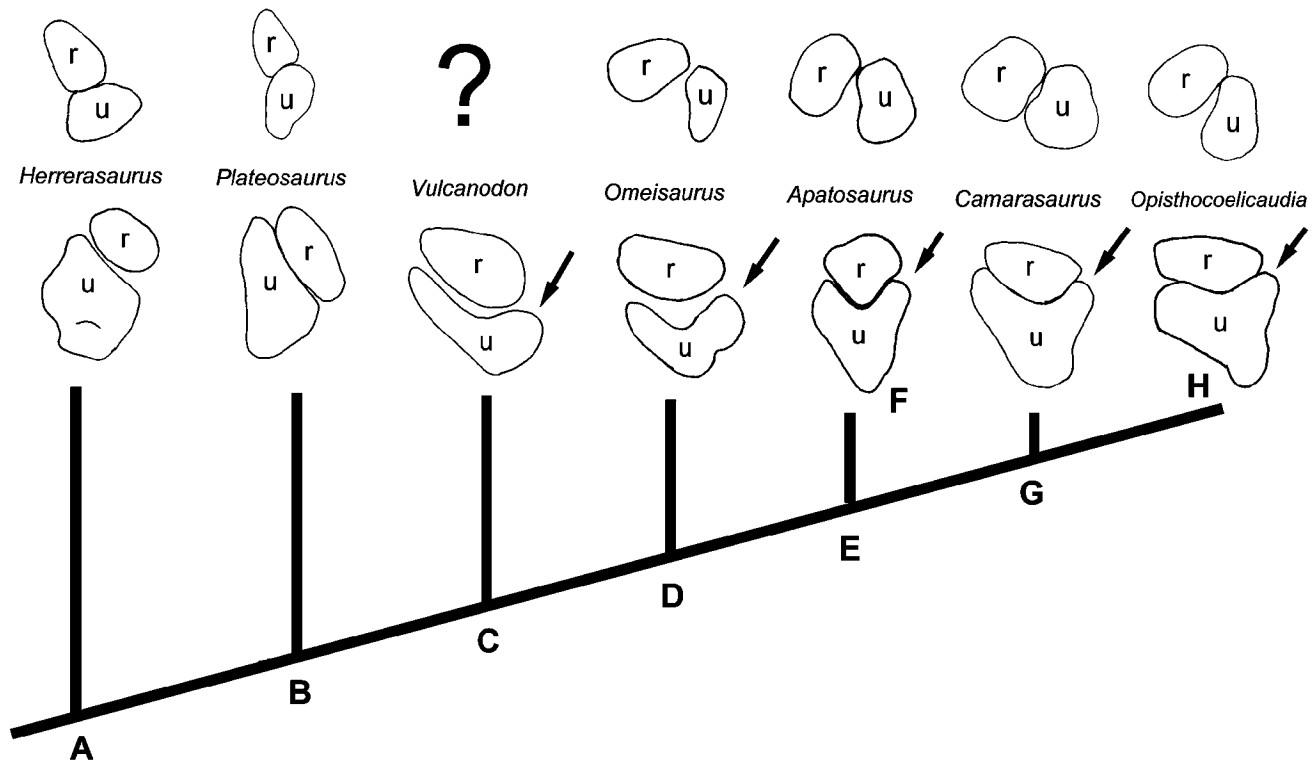


FIGURE 10. Phylogenetic diagram of the proximal and distal articulated right radius and ulna of sauropods and outgroups. Cladogram and lettering as for Figure 1. Outlines below taxon name are proximal; outlines above taxon name are distal. Anterior is up, posterior is down, medial is left, and lateral is right. Arrow indicates the presence of a new anterolateral (AL) process. Note that the ulnae of *Herrerasaurus* and *Plateosaurus* lack the AL process, whereas all sauropod taxa depicted here possess an AL process. The AL process appears to be correlated with an internal shift of the radius relative to the ulna proximally and distally in sauropods. Note also that whereas the radius of *Herrerasaurus* and *Plateosaurus* articulates anterior to the ulna distally, the radius in sauropods is shifted such that it articulates with the ulna internally (medially). Compare distal outlines of the radius and ulna with manus shape in Figure 1. Line drawings based on the following sources: *Herrerasaurus* (pers. obs. UC PR1806, photographically reversed), *Plateosaurus* (pers. obs. AMNH 2104), *Vulcanodon* (modified from Raath, 1972: note that Raath labels lateral as anterior, medial as posterior, anterior as medial, and posterior as lateral [fig. 11F]), *Omeisaurus* (modified from He et al., 1988, photographically reversed; the radius and ulna were not articulated in the original diagram—they were “articulated” here based on condition observed in other sauropods and on inferred manus shape [see Discussion for more details on manus shape]), *Apatosaurus* (modified from Gilmore [1936] and Platt model, photographically reversed), *Camarasaurus* (pers. obs. FMNH P6668), *Opisthocoelicaudia* (modified from Borsuk-Bialynicka, 1977). Not to scale. **Abbreviations:** as for Figure 3 except: ?, distal ends of radius and ulna unknown for *Vulcanodon*.

and IV, respectively (Benton, 1990). Thus, the lateral portion of the saurischian manus was primitively “cupped.”

Alteration of the primitive saurischian manus into the semi-tubular manus of sauropods may have resulted from shifting the radius internally in relation to the ulna, thus altering the preaxial axis and modifying the termination point of the digital arch. In other words, because the digital arch of all amniotes culminates with the alignment of digit I and the radius (Shubin, 1995), shifting the radius internally in relation to the ulna before or during the development of the digital arch might alter manus shape. The striking similarity between the shape of the proximal sauropod metacarpus and the combined distal ends of the radius and ulna suggests reorientation of the radius was the mechanism that produced a semi-tubular manus (compare Figs. 1 and 10). This scenario further suggests that this unique manus shape resulted from acquiring a quadrupedal posture secondarily. Competing functional constraints between the necessity of manus pronation and a columnar forelimb orientation on the framework of a saurischian forearm forced an alternate solution to radial crossover: radial migration. Because the proximal ends of metacarpals IV and V lay on the palmar side of the primitive saurischian manus, a medial shift in the distal position of the radius would have altered a gently cupped manus into an arch. In essence, the digital arch followed the radius as it migrated

medially, producing the characteristic semi-tubular manus of sauropods.

DISCUSSION

Functional Implications

Shifting the radius internally relative to the ulna so that both bones were more or less parallel to one another might have augmented the forelimb of sauropods to reduce shear stress during the support phase. If the radius were crossed over the ulna, its angled orientation might have subjected the radial shaft to shear forces great enough to damage this bone. By shifting the radius internally, the shaft of the bone would be loaded such that tensile and shear stresses were reduced, perhaps providing a more structurally stable configuration for bearing weight. If the alternative hypothesis is correct, the evolution of a semi-tubular manus was a fortuitous side effect or exaptation that arose out of the constraints imposed by the saurischian forelimb, a columnar limb posture, and the necessity of manus pronation. However, once acquired, the semi-tubular sauropod manus was an ideal weight-supporting structure whose tubular shape would have provided resistance to shear and tensile stresses by distributing them through five vertical columns of bone. Thus, the combination of an anteromedial radius, the al-

most parallel orientation of the radius and ulna to one another, and a semi-tubular manus may have contributed, in part, to the attainment of large size in sauropod dinosaurs. Perhaps, among several features, having a forelimb in which all the long bones were oriented to reduce tension and shear allowed sauropods to achieve the sizes and masses they did. Whereas various paleobiological factors surely contributed to the successful attainment of gigantic size in sauropods (e.g., Farlow et al., 1995; McIntosh et al., 1997), the historical constraints of saurischian forelimb structure and functional morphology appear to have played a significant role in the evolution of sauropod gigantism.

In the derived forelimbs of titanosaurids, the olecranon region is greatly expanded superiorly and the humerus bears distinct distal condyles (Wilson and Sereno, 1998). These two features suggest that titanosaurid forearms had a greater range of flexion than that of most neosauropods, and Wilson and Carrano (1999:264) have suggested that in saltasaurid titanosaurs (e.g., *Alamosaurus*, *Opitshocoelicaudia*, *Saltasaurus*) the forelimbs may have had a less columnar posture. Furthermore, as Wilson and Carrano (1999) suggest, the wide-gauge sauropod trackways that predominate during the Cretaceous may have been mostly titanosaurid in origin. Both the broad thorax and potentially angled limbs of saltasaurid titanosaurs were suggested as a means of producing wide-gauge trackways (Wilson and Carrano, 1999:256). It is significant that the best known wide-gauge trackways, *Brontopodus birdi* (Farlow et al., 1989), appear to be the most pronated, with a supination angle of less than 10° (see above). This “improved” pronation of the manus might result from a more angled forelimb posture during the support phase of locomotion in saltasaurid titanosaurs (as suggested by Borsuk-Bialynicka [1977:46]) that would further rotate the manus medially in relation to the direction of travel. This observation, although preliminary, bolsters the titanosaurid origin hypothesis of the wide-gauge trackways and would explain the greater pronation observed in the *Brontopodus birdi* tracks.

Phylogenetic Implications

All sauropods with known forearm material have a triradiate proximal ulna, a novel, convex AL process, and an arched distal forearm (Raath, 1972; Cooper, 1984; McIntosh, 1990; Bonnan, 2001). If the attainment of an anteromedial radius subsequently shaped the sauropod manus, the presence of these shared, derived morphological forearm features in the earliest known sauropods suggest manus shape and reversion to quadrupedal locomotion are linked, and that a semi-tubular manus was present in the most basal sauropods (contra Upchurch, 1998:Eusauropoda; contra Wilson and Sereno, 1998:Neosauropoda). Unfortunately, little is known about the early sauropod manus.

Only metacarpals III, IV, and V were reported for *Vulcanodon* (Raath, 1972), and these elements alone cannot establish its manus shape. *Shunosaurus* and *Omeisaurus* are the earliest known sauropods in which manus material is available and figured (Zhang, 1988:fig. 4; He et al., 1988:fig. 41, pl. 14, figs. 4–6). However, as noted by both Wilson and Sereno (1998) and Upchurch (1998), the metacarpals are arranged in a horizontal plane in the available figures. This arrangement does not appear to reflect the actual articulated metacarpus (Wilson and Sereno, 1998), but instead was probably done to facilitate illustration of the bones (Upchurch, 1998). Wilson and Sereno (1998:48) concluded that, whereas the figures did not represent the actual arrangement of the metacarpus, the metacarpals of *Shunosaurus* and *Omeisaurus* cannot be arranged such that they form a semi-tubular manus. However, this interpretation appears to be based on simply bringing the proximal ends of the metacarpals into closer contact in *Omeisaurus* (Wilson and Sereno, 1998:48, fig. 40) without considering the relationship between proximal

metacarpal shape and orientation. In other words, the proximal ends of the metacarpals of *Omeisaurus* are not figured in their articulated orientation (He et al., 1988:fig. 41A), so simply bringing the shapes of the proximal ends into closer contact will not reflect the actual arrangement of the metacarpals. For example, if the metacarpals of a neosauropod such as *Apatosaurus* or *Brachiosaurus* are oriented as they are illustrated for *Omeisaurus* and then brought closer together without regard for their proximal shape or orientation, a flattened manus results (Fig. 11). When the proximal ends of the metacarpals figured for *Omeisaurus* are arranged in accordance with basic orientations and articulations displayed in other known neosauropod manus, the manus shape is much more tubular than that proposed or figured by Wilson and Sereno (1998:fig. 40).

The line drawings of the proximal ends of the metacarpals in *Shunosaurus* are difficult to interpret because they contain no shading or other indicators of what was being traced (Zhang, 1988:fig. 4). However, examination of the *Shunosaurus* manus by Upchurch (1998) showed that the metacarpals did indeed articulate such that they formed a semi-tubular arc, and he suggested that the metacarpus of *Omeisaurus* was probably similar. Because *Omeisaurus* and *Shunosaurus* are placed by both Upchurch (1998) and Wilson and Sereno (1998) into the outgroup Eusauropoda, the presence of a supposedly derived neosauropod character state in eusauropod taxa suggests that a semi-tubular manus was present in sauropod outgroups to the Neosauropoda and perhaps the Eusauropoda as well. Therefore, although uncertainty still surrounds manus shape in various basal sauropods, the presence of a semi-tubular manus in all sauropods for which the manus is known and has been articulated suggests that this character may have been present in the earliest sauropods as well.

If manus shape and radius position are linked to quadrupedal posture in sauropods, then the following characters all form an integrated functional suite: obligatory quadrupedal posture with columnar limbs (Wilson and Sereno, 1998); ulna proximal end triradiate with deep radial fossa (Wilson and Sereno, 1998); radial distal condyle subrectangular with flat posterior margin for ulna (Wilson and Sereno, 1998); metacarpals, proximal ends subtriangular, composite articular surface U-shaped (McIntosh, 1990; Upchurch, 1995, 1998; Wilson and Sereno, 1998). Although some of these characters have been suggested as synapomorphies for clades beyond the basal Sauropoda, each has functional and osteological correlations with other characters that suggest they were present in the earliest sauropods instead. For example, the presence of a proximally triradiate ulna in a basal sauropod such as *Vulcanodon* where the manus is poorly known suggests, by correlation with other sauropods, that its manus was semi-tubular. Although a phylogenetic analysis of the suggested redistribution of these characters is beyond the scope of this paper, the apparent correlation between quadrupedal posture and the presence of specific morphological features in the ulna, radius, and manus offer compelling evidence that manus orientation, manus shape, and forelimb posture are linked in sauropods. Ultimately, the alternative hypothesis predicts that when the complete manus of a basal sauropod is discovered, it will be semi-tubular.

CONCLUSIONS

Osteological and functional data presented here provide compelling evidence that the development of the semi-tubular sauropod manus was intimately linked with forelimb posture. As the bipedal sauropod ancestor reverted to a quadrupedal posture, the columnar orientation of the forelimb and the necessity of manus pronation altered the primitively anterior and lateral position of the radius proximally by shifting it internally relative to the ulna. The mechanism that transformed a relatively

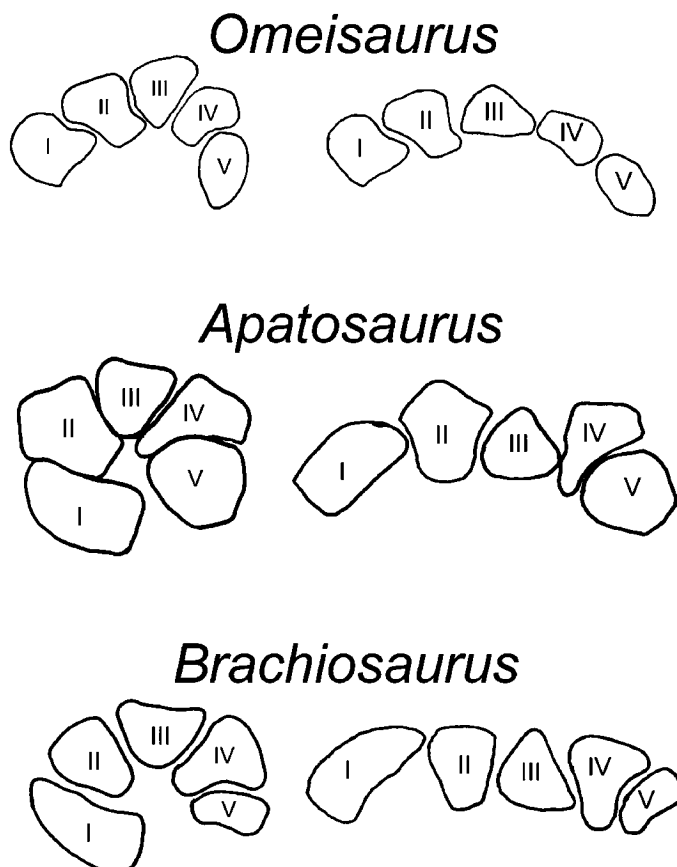


FIGURE 11. Varied interpretation of proximal manus shape in *Omeisaurus*. The proximal shape of the manus in the eusauropod *Omeisaurus* (modified from He et al. [1988]) and the neosauropods *Apatosaurus* (after Gilmore [1936]) and *Brachiosaurus* (after Janensch [1922]) when the metacarpals are articulated with regard for their proximal shape and orientation (left) and when they are laid flat and simply brought closer together (right). *Omeisaurus* manus configuration on right after Wilson and Sereno (1998:fig. 40). Notice that the typically U-shaped manus of both *Apatosaurus* and *Brachiosaurus* become flattened if articulated as suggested and illustrated by Wilson and Sereno for *Omeisaurus* (1998:48, fig. 40). The metacarpals of *Omeisaurus* have similar proximal shapes to those of neosauropods (compare especially the proximal outlines of metacarpals II, III, and IV in *Omeisaurus* to those of *Apatosaurus* and *Brachiosaurus*, as well as *Camarasaurus* and *Opisthocoelicaudia* in Fig. 1), and *Omeisaurus* probably possessed a more tubular manus than suggested and illustrated by Wilson and Sereno (1998). Roman numerals indicate metacarpal of same number.

flat basal dinosaurian manus into a digitigrade and semi-tubular structure was a shift in the position of the radius relative to the ulna that subsequently altered the shape of the digital arch. Thus, although the shape of the sauropod manus was likely an ideal tension and shear reducing structure, its initial development was probably less tied to weight-distributing factors and more the result of achieving pronation within the historical constraints of the saurischian forelimb: in other words, an exaptation. Functionally, a semi-tubular manus and a parallel radius and ulna may have limited tensional stresses in the forearm, and might constitute part of a larger number of mechanisms responsible for gigantism in sauropods. Phylogenetically, the columnar forelimb posture, proximally triradiate ulna, subrectangular distal condyle of the radius, and semi-tubular manus of sauropods form a functional suite that suggests a semi-tubular manus was present in basal sauropods. Ultimately, future phylogenetic studies of sauropods must consider the significance and complementary data functional analyses provide.

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