Scapular Position and Function in the Sauropodomorpha (Reptilia: Saurischia)

Matthew F. Bonnan[1], J. Michael Parrish[2], Kent A. Stevens[3], Jeanne P. Graba[4], Phil Senter[5]

[1]Dept. Biological Sciences, Western Illinois University, Macomb, IL 61455; [2]Dept. Biological Sciences, Northern Illinois University, DeKalb, IL 60155; [3]Dept. Computer and Information Science, University of Oregon, Eugene, OR 97403; [4]Deceased; [5]Dept. Math and Science, Lamar State College at Orange, Orange, TX 76630

ABSTRACT

The feeding range of sauropod dinosaurs was constrained by the height of the base of the neck, which was itself constrained by the nature of the articulation between the scapulocoracoid and the trunk. Sauropod scapulocoracoid orientation and mobility remain controversial because no tight, bony articulations were present between these bones and the vertebral column, and few osteological markers are available to constrain shoulder orientation. Previous hypotheses of scapulocoracoid orientation in sauropods were inferred from the death poses or through simple goodness-of-fit criteria, but were not developed within a phylogenetic context. We examined the scapulocoracoids, ribcage, and sterna of several neosauropods, basal sauropodomorphs, and extant archosaur and lepidosaur taxa to: 1) assess the soft tissue contributions to scapulocoracoid orientation and mobility; and 2) determine osteological correlates associated with shoulder position. Archosaurian scapulae vary in position from nearly parallel to the vertebral column (birds) to nearly vertical (crocodylians) but in all cases the scapular blade is nearly coincident with the top of the neural spines along its distal extent, suggesting a similar orientation in dinosaurs. Positions and homologies of the musculature associated with supporting the scapulocoracoid were conservative within extant taxa. Scapulocoracoid movements against the sternum, affected by the Mm. serratus, levator scapulae, and sternocoracoideus groups, become more restricted in archosaurs, particularly in birds. Flattened areas on the external surfaces of the dorsal ribs ('facets') are present in birds, sauropods, and other dinosaurs but are absent in crocodylians. Dissection and CT-scan data show that the scapular blade bows away from the dorsal ribs in *Alligator* whereas it lies in close contact with the dorsal ribs in birds, which may explain the lack of 'facets' in crocodylians. Rib facets correlate with the neutral orientation of the scapular blade in birds. We suggest that the presence of rib 'facets' and the more restricted movements of the scapulocoracoid in diapsid outgroups support a constrained, sub-vertical orientation of the pectoral girdle in sauropods.

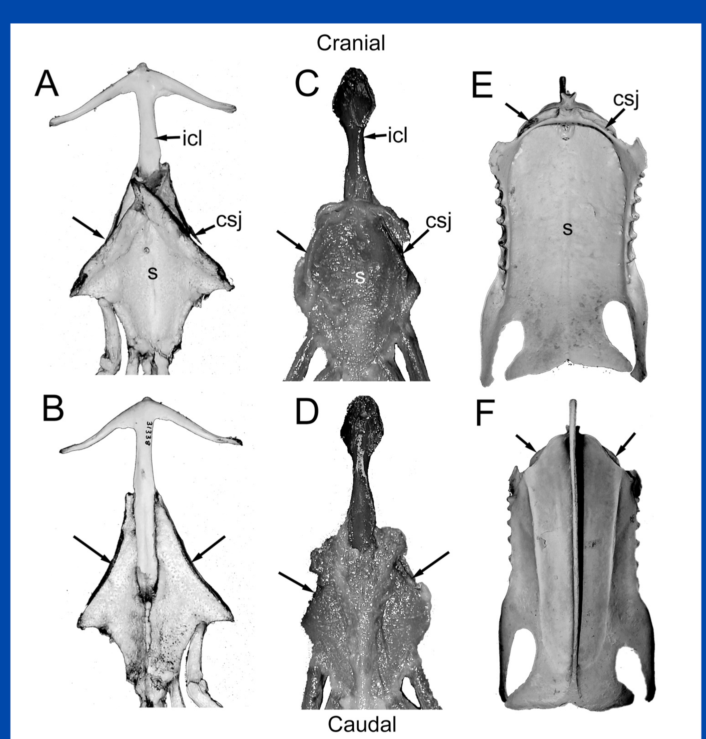

FIGURE 1. Sterna of *Varanus salvator* (FMNH 31338), *Alligator mississippiensis* (RWR specimen), and *Anser* sp. (WIU NSF1G) in dorsal (A, C, E) and ventral (B, D, F) views. Notice that the coracosternal joints (csj) are more laterally facing in *V. salvator* and *A. mississippiensis* than in *A.* sp, which, like most birds, has cranially oriented coracosternal joints (see also Fig. 5 for this articulation in the ostrich). Abbreviations: **csj**, coracosternal joint; **icl**, interclavicle; **s**, sternum. Arrows indicate position and orientation of the coracosternal joints.

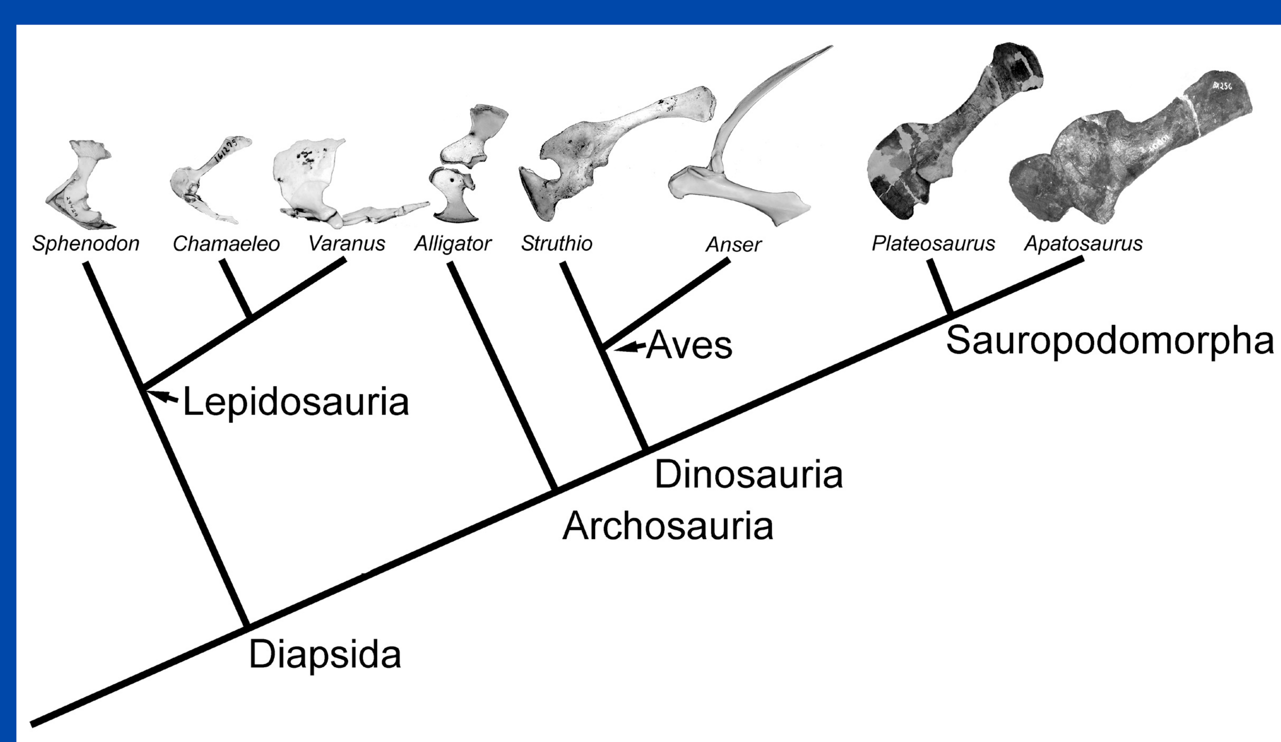

FIGURE 2. Comparative lateral view of left scapulocoracoids in lepidosaurs and archosaurs. Specimens are from the following collections: *Sphenodon* (USNM 29429), *Chamaeleo* (USNM 161279), *Varanus* (USNM 290873), *Alligator* (WIU NSFG2), *Struthio* (WIU NSFG1), *Anser* (WIU NSFG3), *Plateosaurus* (SMNS F50), *Apatosaurus* (CM 10004). Cranial (coracoid) ends face left in the figure. All scapulocoracoids are posed in neutral orientation or inferred neutral orientation (sauropodomorphs). Notice that in the flightless bird, *Struthio*, the coracoid is shorter, hatchet-shaped, and dorsoventrally tall at its cranial end whereas in the flying taxon, *Anser*, the coracoid is elongate and strut-like. With some modification, the morphology observed in *Struthio*, an archosaur taxon with limited scapulocoracoid mobility, is reflected in the scapulocoracoids of the sauropodomorph taxa, *Plateosaurus* and *Apatosaurus*.

Table 1. Major muscles affecting the movement and orientation of the scapulocoracoid in extant lepidosaurs, crocodilians, and avians. * Actions described here are known from electromyographic studies on *Varanus* and *Sternus* (except Mm. rhomboids) (Jenkins and Goslow 1983; Jenkins et al. 1988; Dial et al. 1991), and are inferred to be similar in the other taxa. ** This particular action occurs only in non-avian taxa. Taxa examined: *Sphenodon*, *Iguana*, *Varanus*, *Chamaeleo*, *Alligator*, *Columba*, *Anser*, *Struthio*.

Muscle	Actions*
M. trapezius	Anterior bracing / stabilization of the scapulocoracoid
M. levator scapulae	Anterior bracing / stabilization / protraction of the scapulocoracoid
M. serratus anterior	Posterior bracing / stabilization of the scapulocoracoid; suspension of body trunk on scapulocoraoid **
Mm. rhomboids	Superior bracing / stabilization of the scapulocoracoid
M. sternocoracoideus	Translation of scapulocoracoid along the sterno-coracoid joint

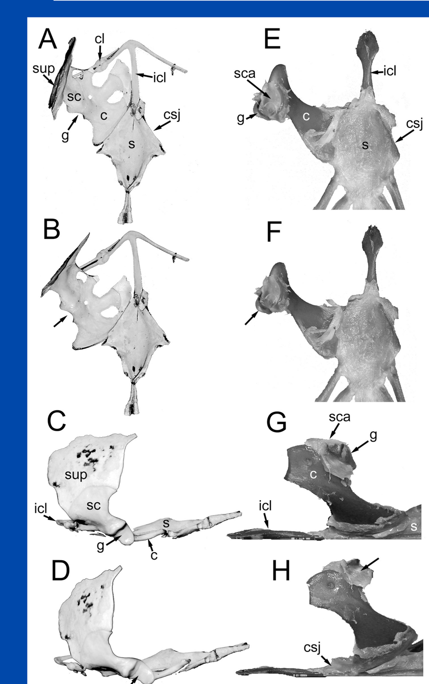

FIGURE 3. Articulation and movements at the coracosternal joint in *Varanus salvator* (USNM 290873) and *Alligator mississippiensis* (WIU NSF2G) in dorsal (A, B, E, F) and lateral (C, D, G, H) views. In *V. salvator*, starting from a neutral orientation (A, C), retraction of the scapulocoracoid (B, D) in the coracosternal joint results in marked cranial (B) and dorsal (D) rotation of the glenoid, a rotational movement that augments that sprawling gait of this lepidosaur. In *A. mississippiensis*, starting from a neutral orientation (E, G), retraction of the coracoid (F, H) results in some rotational and transitional movements, but none as pronounced as in *V. salvator* or other lepidosaurs. Unlabeled arrows indicate position of the glenoid. Abbreviations as per Figs. 1 & 3 except:**c**, coracoid; **csj**, coracosternal joint; **g**, glenoid; **sc**, scapula; **sca**, articular surface for attachment of scapula; **sup**, suprascapular cartilage.

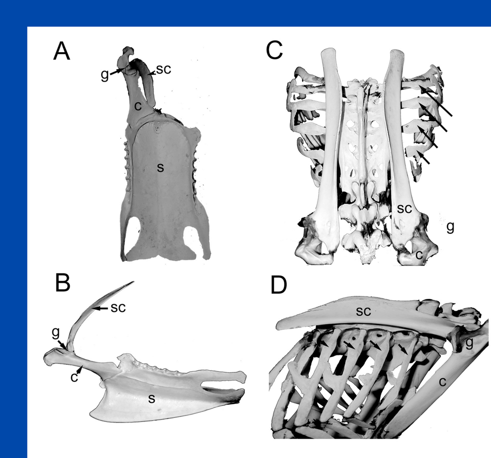

FIGURE 4. Articulation of the scapulocoracoid with the coracosternal joint and the presence of rib 'facets' in birds. Scapulocoracoid articulated with the sternum in *Anser* sp. (WIU NSF1G) in (A) ventral and (B) lateral views; small, lateral movements are possible at the coracosternal joints in most birds (see Jenkins et al. 1988). The presence of rib 'facets' in *Meleagris gallopavo* in (C) dorsal and (D) lateral view with arrows indicating their location. Note that in this specimen, the scapulocoracoid is articulated in a very retracted position such that the rib 'facets' are exposed; in neutral position, the scapular blade lies over and in close contact with the 'facets.' Abbreviations as per Fig. 3.

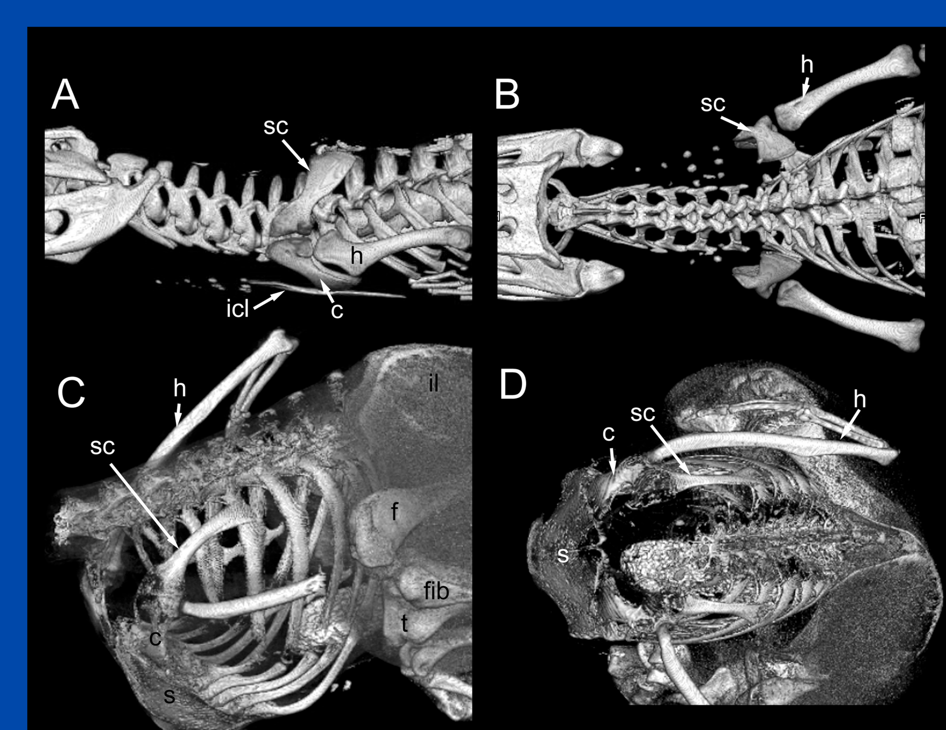

FIGURE 5. CT scans of *Alligator mississippiensis* and *Struthio camelus* showing relationship of the scapulocoracoid to the ribs in (A, C) lateral and (B, D) dorsal views. Note that the scapulocoracoids of *A. mississippiensis*, which have some mobility, do not make contact with the ribs and 'float' away from the body trunk. In contrast, the scapular blade of *S. camelus*, which has very limited movement, lies in close contact with the ribs and body wall. Abbreviations as per Figs. 1 & 3, except: **f**, femur; **fib**, fibula; **il**, ilium; **t**, tibia.

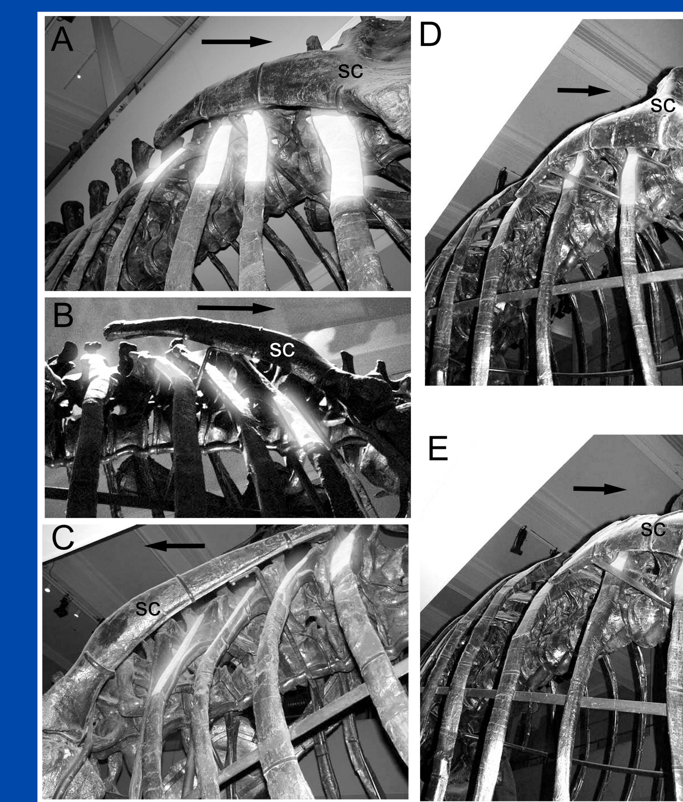

FIGURE 6. Lateral and oblique views of skeletal mounts of *Apatosaurus louisae* (CMNH 3018; A-C) and *Diplodocus carnegii* (CMNH 84; D-E), with the positions of the flattened rib facets highlighted. Arrows indicate cranial direction.

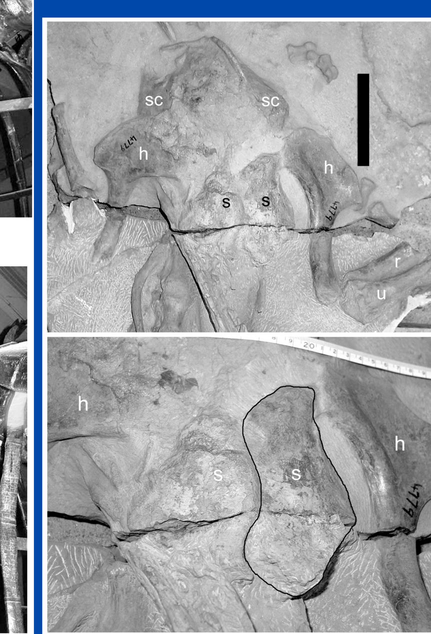

FIGURE 7. Sternal morphology and orientation in *Massospondylus carinatus* (BPI 4776). Wide (A) and close-up (B) ventral views of the sternal plates, scapulocoracoids, and forelimbs *in situ* of the basal sauropodomorph *Massospondylus*. The sternal plates are observed to lie caudal to the scapulocoracoids and humeral heads. The thickest edges of the sternal plates lie cranially and the plates broaden and thin out caudally. The humeri have rotated more laterally than was probably normal during the life of the animal probably due to taphonomic effects. In close-up (B), the left sternal plate is outlined to emphasize its shape; compare this morphology to the sternal plates of neosauropods (Fig. 8). Abbreviations as per Figs. 1 & 3, except: **h**, humerus, **r**, radius; **u**, ulna. Scale bar equals 10 cm.

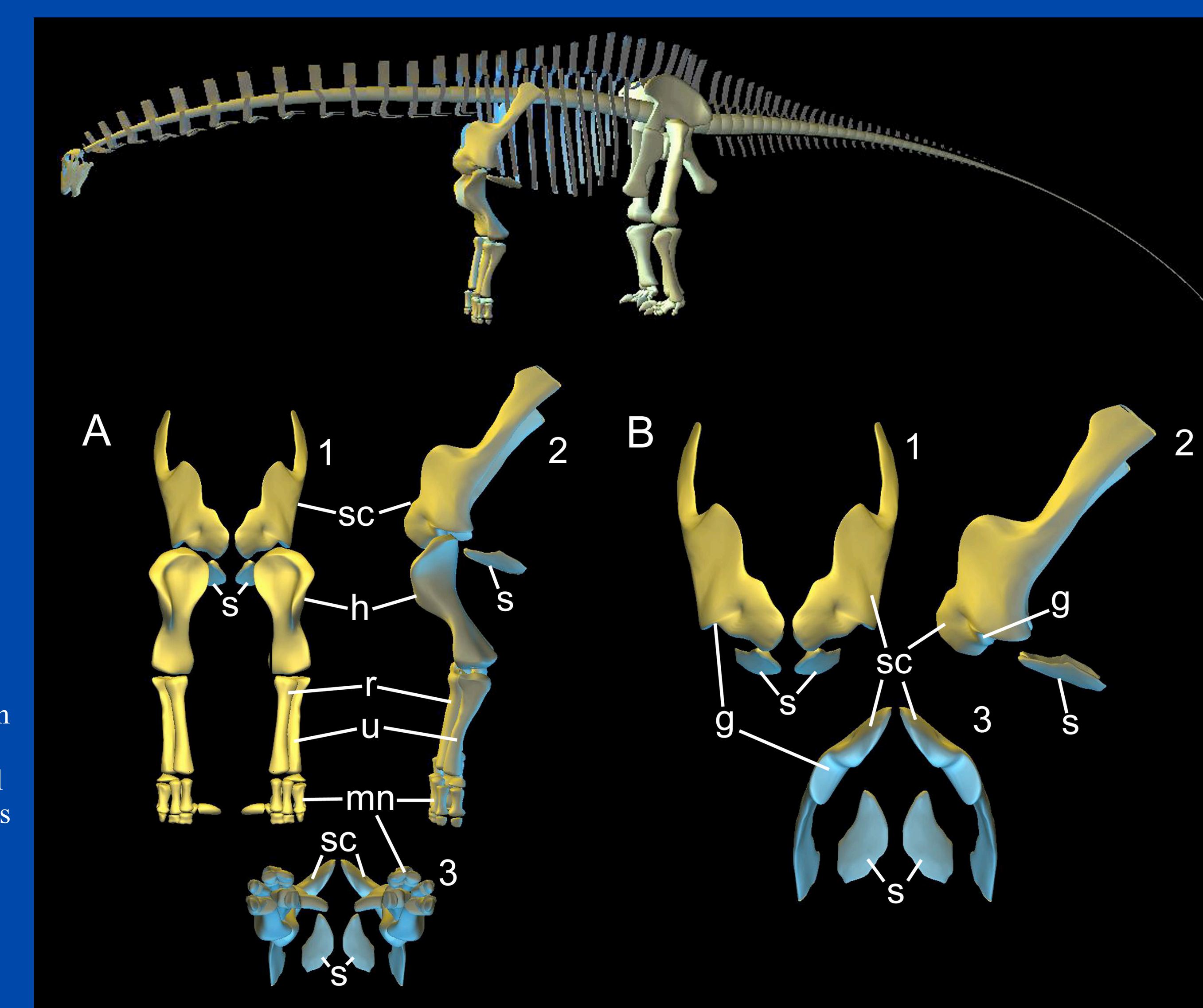

Figure 8. DinoMorph™ reconstruction of *Apatosaurus louisae* (CM 3018) showing neutral position of scapulocoracoid on ribcage based on outgroup comparison. (A) Isolated close-up of forelimb and (B) isolated close-up of scapulocoracoid and sternal plates. In each close-up: 1, cranial view; 2, lateral view; 3, ventral view. It is most parsimonious to place the sternal plates caudal to the scapulocoracoids. When the scapular blades are oriented with the rib 'facets,' the coracoids nearly articulate with one another cranially. An unossified cartilaginous sternum probably occupied the region cranial to the sternal plates based on outgroup comparison. Clavicles or furcula, if present, would have articulated with the acromion processes of the scapulae. Our proposed orientation of the pectoral girdle and the presence of well-defined rib facets suggests there was limited scapular mobility in neosauropods. Abbreviations: h, humerus; g, glenoid; mn, manus; r, radius; s, sternal plates; sc, scapulocoracoid; u, ulna.

ACKNOWLEDGMENTS

For help with various aspects of this project, the authors wish to acknowledge several individuals for their assistance with fossil and extant reptile skeletons: M. Raath, A. Yates, and B. Rubridge (Bernard Price Institute of Palaeontology and Palaeoanthropology, Johannesburg, South Africa); J. Ladonski, A. Resetar, H. Voris, and M. Kearney (Field Museum of Natural History); D. Berman, A. Henrici, M. Lamanna, and Z. Luo (CMNH); A. Chinsamy, S. Kaal, and staff (Iziko South African Museum); D. Unwin and staff (Humboldt Museum für Naturkunde, Berlin); P. Barrett, A. Milner, and S. (Natural History Museum, London); R. Schoch and staff (Staatliches Museum für Naturkunde); and R. Crombie and A. Wynn (U. S. National Museum of Natural History). R. Elsey (Rockefeller Wildlife Refuge, Louisiana) and R. Wilhite (Louisiana State University, Baton Rouge) provided MFB with *Alligator* specimens. R. Wilhite generously provided 3D scans of an *Apatosaurus* sternal plate. CT Scans were performed at the Department of Radiology, University of Iowa. We thank S.L. Masters for help with the ostrich. Funding was provided through NSF grant 0093929, received by J. M. Parrish and K.A. Stevens, a University Research Council grant 3-30135 from Western Illinois University (MFB), and National Geographic grant #7713-04 award to Adam Yates on which MFB is a recipient participant. Jeanne Graba passed away at a very early age in 2003. The surviving authors dedicate this work to her memory.