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NEW INFORMATION ON *SEGISAURUS HALLI*, A SMALL THEROPOD DINOSAUR FROM THE EARLY JURASSIC OF ARIZONA

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ABSTRACT—Here we redescribe the holotype and only specimen of *Segisaurus halli*, a small Early Jurassic dinosaur and the only theropod known from the Navajo Sandstone. Our study highlights several important and newly recognized features that clarify the relationships of this taxon. *Segisaurus* is clearly a primitive theropod, although it does possess a tetanuran-like elongate scapular blade. Nonetheless, it appears to be a coelophysoid, based on the presence of a pubic fenestra, a long and ventrally curved pubis, and some pelvic (and possibly tarsal) fusion. *Segisaurus* does possess a furcula, as has now been observed in other coelophysoids, thus strengthening the early appearance of this 'avian' feature. The absence of an external fundamental system in bone histology sections and the presence of sutural contact lines in the caudal vertebrae, scapulocoracoid, and (possibly) between the pubis and ischium support the inference that this specimen is a subadult, neither a true juvenile nor at full skeletal maturity. A cladistic analysis confirms *Segisaurus* as a coelophysoid theropod. Poor resolution within Coelophysoidea makes speculation about evolution in this clade difficult, but *Segisaurus* apparently represents a lineage that had been distinct from *Coelophysis* and *Syntarsus* since at least the Carnian.

INTRODUCTION

The basal theropod *Segisaurus halli* Camp, 1936, is known from a single partial skeleton (UCMP 32101) from the Lower Jurassic Navajo Sandstone of Arizona (UCMP locality V3308). In his original description, Camp (1936) regarded *Segisaurus* as an unusual theropod, as illustrated by the possession of clavicles (then unknown in dinosaurs), seemingly solid centra and limb bones (atypical for theropods), and accessory fenestrae in the pubis and ischium. He placed it within the Coelurosauria, a taxon that at that time was used to accommodate most small theropods, and tentatively allied it with *Ornitholestes* and *Compsognathus*. However, Camp emphasized its distinctiveness from these and other known coelurosaurs by placing it in a new family, Segisauridae.

Segisaurus went largely ignored for the next fifty years, with most authors (e.g., Norman, 1985) commenting on its apparent distinctiveness when they bothered to discuss it at all. *Segisaurus* was most often cited in reference to its retention of clavicles (e.g., Blotzheim, 1966; Bryant and Russell, 1993; Padian, 1997), but until recently (e.g., Chure and Madsen, 1996; Tykoski et al., 2002) this was considered aberrant among theropods and dinosaurs. Welles (1984:174, 177) questioned even the theropod nature of *Segisaurus*. Little progress was made on its phylogenetic placement during this time.

More recently, *Segisaurus* has been recognized as a coelophysoid (Gauthier, 1984, 1986; Rowe, 1989; Rowe and Gauthier, 1990; Sereno and Wild, 1992) within the Ceratosauria (along with *Ceratosaurus* and abelisauroids), following several cladistic revisions of theropod phylogeny (Gauthier, 1986; Sereno, 1999; Rauhut, 2000, 2003). This assignment has been generally accepted, but the incomplete nature of the holotype and only specimen—in particular, the lack of any skull materials—has made more specific assignment difficult. Only Sereno (1999; see also Sereno and Wild, 1992) offered a more refined view, allying *Segisaurus* and the European *Procompsognathus* within the clade Procompsognathinae based on similarities in pelvic morphology.

Recently, new preparation work was undertaken on UCMP 32101, allowing an extensive reexamination of the specimen. This in turn has clarified previous observations and revealed new attributes of this enigmatic theropod. A renewed understanding of *Segisaurus*, one of the few dinosaurs from the Navajo Formation (Brady, 1935, 1936; Camp and Vander Hoof, 1935) and one of the latest Early Jurassic theropods from North America, is important for our broader understanding of early theropod evolution.

Here we redescribe the osteology of *Segisaurus*, supplementing and emending Camp's (1936) original work as necessary, along with new illustrations and extensive photographs of the holotype. We discuss some of the more critical morphological features in detail, and use these new observations to analyze the phylogenetic position of *Segisaurus*. Its potential bearing on early theropod evolution is then evaluated.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
NEOTHEROPODA Bakker, 1986
COELOPHYSOIDEA (Nopcsa, 1928) Holtz, 1994
SEGISAURUS HALLI Camp, 1936

Holotype—UCMP 32101, a partial postcranial skeleton lacking the skull.

Locality—UCMP V3308, 1 mile north of Keet Seel ruin, north branch of Segi Canyon, Navajo (Diné) Nation, Coconino County, Arizona. Coordinates given as "36°46′50″N and 110°31′30″E" (sic: W; Camp, 1936:39).

Horizon—Navajo Sandstone, approximately 154 m above its base.

Diagnosis—Small coelophysoid theropod dinosaur with a rectangular humeral deltopectoral crest, narrow scapular blade, and a large, rounded foramen in the proximoventral ischiadic plate (modified from Rauhut, 2003).

DESCRIPTION

Skull

No skull materials can be identified.

Axial Skeleton

Cervicals—The cervical series appears to be entirely missing.

Dorsals—The dorsal series is partially preserved, starting with dorsal 4 and continuing back to the sacrum. Camp (1936) identified the individual vertebrae based on their position relative to other elements in the semi-articulated specimen. Assuming there were 24 vertebrae anterior to the two primordial sacrals (as in most basal neotheropods), his identifications appear to be correct and are followed here.

Fragments of dorsals 4, 5, and 6 are preserved articulated in the block with the scapular blade. All lack most of their neural arches, but dorsal 5 is more complete, retaining a portion of the left transverse process. The centrum appears to be amphicoelous, with a dense, spongy internal structure that suggests minimal, if any, pneumatic invagination. It is relatively long, resembling the condition in coelophysoids and noasaurids more than in coelurosaurs. The proportions are correspondingly more cylindrical than hourglass-shaped. The transverse process is relatively wide and backswept along its distal two-thirds; it is somewhat downturned as well. A small, anteriorly facing process near the anteromedial junction of the transverse process and centrum may be the parapophysis, which would be in agreement with the post-'pectoral' position of this vertebra.

Dorsals 8 and 9 are similar in morphology, although perhaps more strongly amphicoelous (Fig. 1). The lateral surface of dorsal 8 is exposed enough to reveal the absence of a pleurocoelous fossa. Its transverse process is fairly slender, angled slightly anteriorly, and extends horizontally more than one centrum width outward.

One additional fragment appears to represent an isolated dorsal neural arch, with the underside of the transverse process and its three associated fossae. A fragment of prezygapophysis is attached. The arch is long, but the spine is missing. Its length corresponds well with several of the preserved dorsal centra, but it cannot be unequivocally associated with any of them specifically.

Sacrals—The two primordial sacrals are partly preserved, along with a portion of the second sacral rib in articulation with the medial ilium, just opposite the posterior part of the left acetabulum (Fig. 2). These sacrals are firmly articulated but not fused; although a suture is still visible, no disc space is visible between the centra along the broken horizontal surface. The posterior end of the second primordial sacral appears to be natural, implying that fusion was also absent with the subsequent vertebra. No pleurocoels are evident. Anterior to these sacrals, the impressions of two centra probably represent two dorsosacrals, based on their position between the pelvic elements. The first caudal is missing, but we (like Camp, 1936) would predict one caudosacral as well, given the extension of the iliac postacetabulum toward caudal 2 (see below). Thus *Segisaurus* appears to have had five sacrals, as in most neotheropods except coelurosaurs and ceratosaurs.

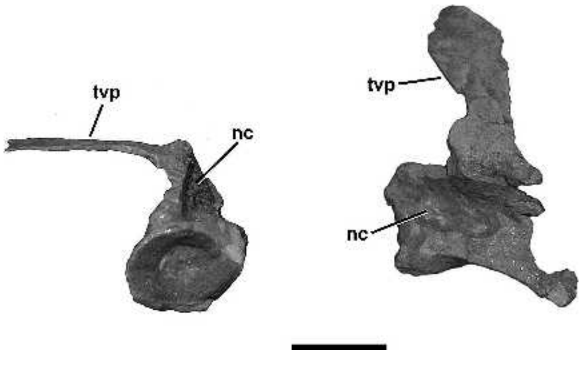

FIGURE 1. Dorsal vertebra 8 of *Segisaurus halli*, UCMP 32101. **A**, anterior view. **B**, dorsal view. **Abbreviations**: **nc**, neural canal; **tvp**, transverse process. Scale bar equals 1 cm.

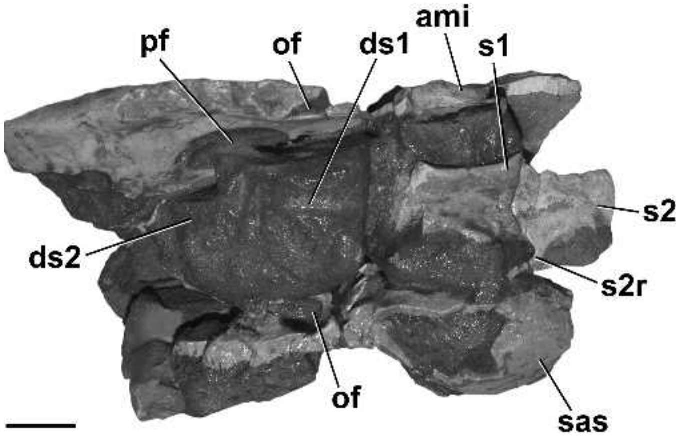

FIGURE 2. Sacrum and partial pelvis of *Segisaurus halli*, UCMP 32101 in dorsal view. **Abbreviations**: **ami**, acetabular margin of ischium (right); **ds1**, dorsosacral vertebra 1; **ds2**, dorsosacral vertebra 2; **of**, obturator foramen; **pf**, pubic foramen/fenestra; **s1**, sacral vertebra 1; **s2**, sacral vertebra 2; **s2r**, sacral rib 2; **sas**, supraacetabular shelf (left ilium). Scale bar equals 1 cm.

Caudals—After caudal 1, the next 21 caudal vertebrae are preserved in articulation, with fragments of several more (Fig. 3). The neurocentral sutures are not open, but are usually evident. Caudal 1 (= caudosacral 1?) is apparently not preserved. Most caudals are ventrally grooved, a feature typically considered synapomorphic of 'ceratosaurs' (e.g., Rowe and Gauthier, 1990) but actually more widespread among theropods (Rauhut, 2000, 2003).

Caudal 2 is represented by its neural arch, including postzygapophyses (situated close together near the midline), the base of the neural spine, and part of the upturned transverse process. The neural canal was apparently large and round, and the neural spine was anteroposteriorly long (as in many primitive theropods). A small pocket is present in the infradiapophyseal fossa, presumably indicating some sort of soft tissue association (e.g., respiratory, circulatory), although probably not a "lymph heart" (Camp, 1936:42).

The transverse processes of subsequent caudals are more horizontally oriented, although still upturned, and present a lobate (distally expanded) shape in dorsal view (Fig. 3B). No arch fossae are present, and the neural spines are posteriorly inclined. The centra are relatively long, even in the more anterior caudals, while the transverse processes persist to at least caudal 21. These become shorter anteroposteriorly in the distal caudals, but a distinct 'transition point' (Gauthier, 1986) is not evident in the preserved series. The neural spines appear to be thickened dorsally into a 'spine table', and most have an accessory anterior process as in many other theropods (Fig. 3; e.g., *Poekilopleuron*, Eudes-Deslongchamps, 1837; *Lourinhanosaurus*, Mateus, 1998).

The prezygapophyses of caudal 18 are preserved in articulation with the postzygapophyses of caudal 17. This articulation is strongly vertically inclined, and the prezygapophyses are not particularly elongate. A small bump anterior to the neural spine persists in these mid-caudal vertebrae.

The more distal caudals are preserved only as isolated, antero-

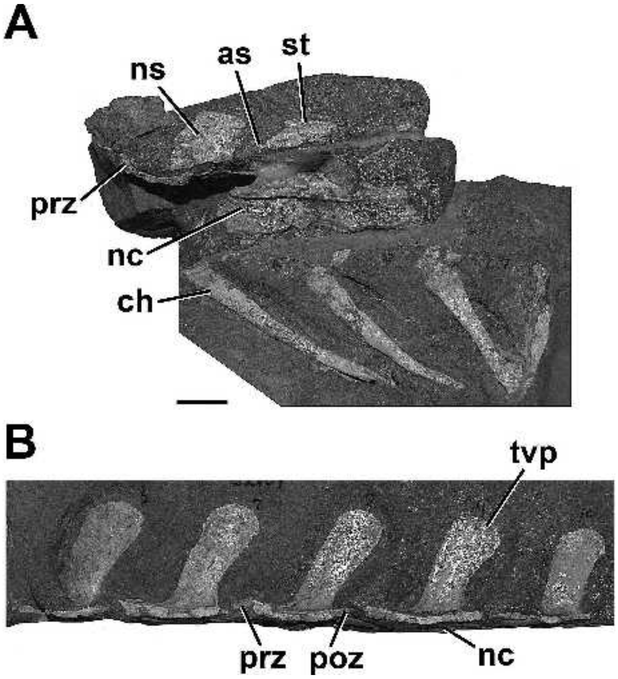

FIGURE 3. Caudal vertebrae and chevrons of *Segisaurus halli*, UCMP 32101. **A**, partly bisected caudal vertebrae 4 through 6 in left lateral view, showing articulated chevrons of vertebrae 4 through 7. **B**, dorsal view of caudal vertebrae 6–10. **Abbreviations**: **as**, anterior spine; **ch**, chevron; **nc**, neural canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **st**, spine table; **tvp**, transverse process. Scale bars equal 1 cm.

posteriorly elongate centra. Some have a distinct ventral groove; all are amphicoelous.

Cervical Ribs—As noted by Camp (1936:42), the cervical ribs are very long and thin, as is typical for most theropods. Only the posterior portions of the cervical ribs from the last four vertebrae are preserved. Nothing can be discerned regarding their potential pneumaticity. There is certainly no compelling evidence to infer the presence of a cervical patagium in *Segisaurus* as Camp fancifully did; elongate cervical ribs are common in basal theropods and other archosaurs.

Dorsal Ribs—Portions of many of the dorsal ribs are present, but only the fourth retains its proximal end with the capitulum and tuberculum. Most ribs present are from the right side, having collapsed obliquely onto the gastralia. The left ribs are largely absent from the anterior thorax, but are present more posteriorly alongside the left hind limb. All have a rather typical rib morphology, including a posterior groove for attachment of the intercostal muscles and placement of the costal neurovasculature.

Sternum and Gastralia—The ventral portion of the thorax and anterior abdomen is not well preserved. Anterior to the preserved gastralia, the sediment is discolored (gray instead of red) in the region that likely contained the sternum. A long, flat element here might be a sternal fragment. It might also be a portion of a rib, but it differs significantly from most of the preserved dorsal rib shafts. A second flat element is present anterior to dorsal rib 4, but cannot be further identified.

The gastralia (Camp's "parasternal apparatus") are well preserved and mostly articulated, but they do not appear to be preserved anterior to the level of the sixth dorsal vertebra. The gap between the most anterior gastralial row and the pectoral girdle may be genuine, as in some other theropods (e.g., *Compsognathus*, Bidar et al., 1972; *Scipionyx*, Dal Sasso and Signore, 1998). Although many elements are broken, their general arrangement within the abdominal cuirass conforms to the general theropod and prosauropod patterns (Fig. 4; Claessens, 1997, 2004): left and right paramedian elements imbricate along the midline, and each articulates in turn with one lateral segment. The lateral segment is longer than the medial one (Camp, 1936), as is typical for small, basal saurischians (Claessens, 2004). Approximately twelve rows are preserved, along with several small posterior gastralial fragments still in contact with the distal pubes (Fig. 7). Among them are a few swellings and fusions, which are common pathologies or variations among gastralia and other dermal bones (Claessens, 2004).

Chevrons—The chevrons are primitive in morphology, with very small anterior and posterior processes at their proximal ends (Fig. 3). Many are preserved in articulation. The haemal canal is closed dorsally throughout. The distal ends are thin and tapered, and lack any expansion back to at least chevron 11. Chevron 16 is slightly expanded distally, and chevron 17 is almost blade-shaped. They also decrease in length progressively after chevron 7. The apparent absence of chevrons on caudal vertebrae 1–3 is probably artifactual.

Appendicular Skeleton

Scapula—The left scapula is preserved, along with parts of both coracoids and the furcula (Fig. 5). The scapula has a very long, slender shaft, especially compared with that of coelophysoids and other primitive theropods (Fig. 5A; e.g., *Eoraptor*, *Ceratosaurus*). The shaft broadens along its length to reach a maximum at the distal end. It resembles the condition in coelophysoids such as *Coelophysis*, *Gojirasaurus*, and *Dilophosaurus* in having a curved anterior margin, a straight posterior margin, and an asymmetrically curved distal expansion. The acromion is well preserved, emerging gently from the curve of the shaft and articulating with the lateral tip of the furcula (Fig. 5A, B). The suture with the coracoid is partly fused but evident as it runs toward the midpoint of the glenoid. The glenoid is deep and narrow, but cannot be described in further detail. The scapula is 93 mm long, 8.5 mm wide at its midshaft, and expands to 20 mm distally.

Coracoid—The left coracoid is nearly complete, missing only the posterior process and part of the area beneath the glenoid (Fig. 5A, C). Laterally, the coracoid foramen is visible, leading into a dorsally directed passage through the bone. The bone is fairly deep and bears a rounded ventral edge. Distinct muscle scars are evident, paralleling the posteroventral edge. A small bump below the broken posterior portion could be construed as

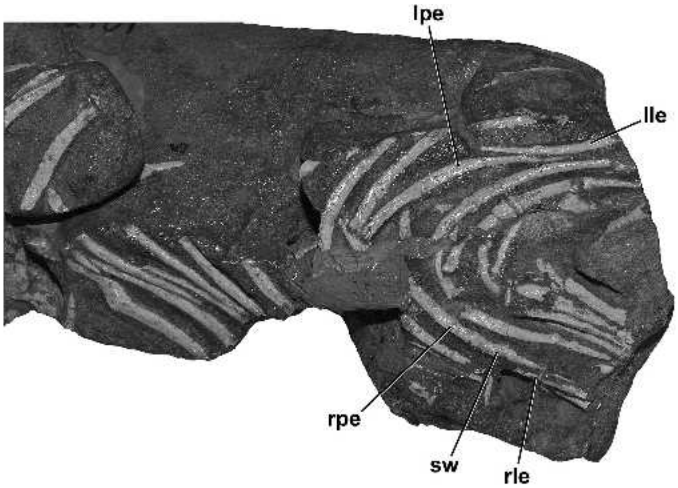

FIGURE 4. Gastralia of *Segisaurus halli*, UCMP 32101. Ventral view. **Abbreviations**: **lle**, left lateral element; **lpe**, left paramedian element; **rle**, right lateral element; **rpe**, right paramedian element; **sw**, swelling.

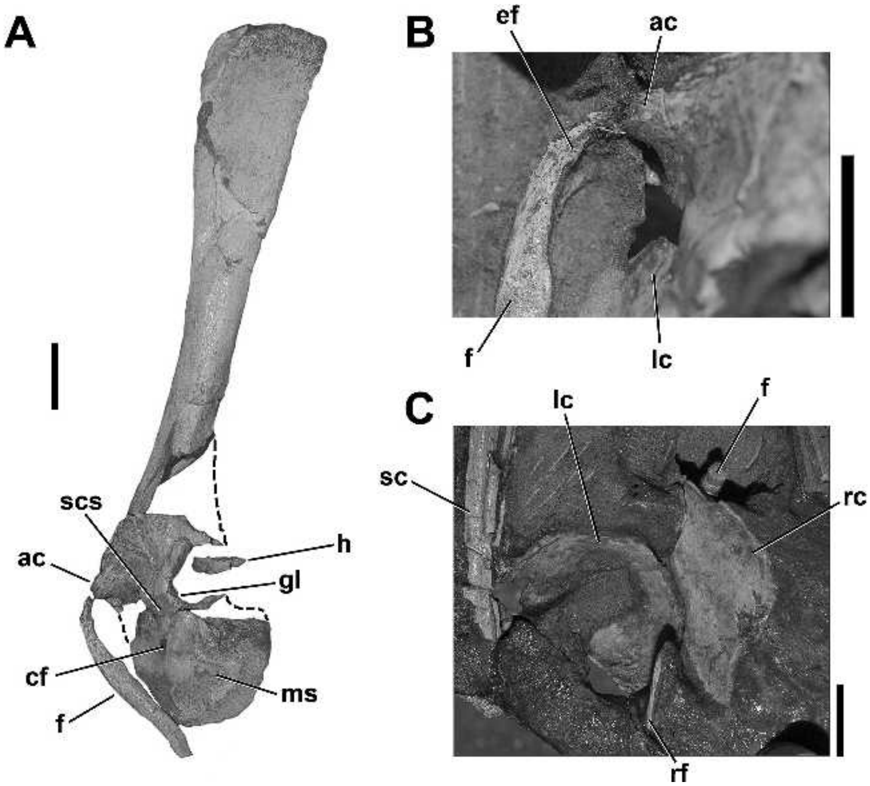

FIGURE 5. Left pectoral girdle of *Segisaurus halli*, UCMP 32101. **A**, lateral view of articulated elements. **B**, articulation of furcula and scapular acromion process. **C**, dorsal (internal) view of left and right coracoids, showing articulated furcula. **Abbreviations**: **ac**, acromion process; **cf**, coracoid foramen; **ef**, epicleidal facet; **f**, furcula; **gl**, glenoid; **h**, fragment of humerus; **lc**, left coracoid; **ms**, muscle scar ('biceps tubercle'); **rc**, right coracoid; **rf**, rib fragment; **sc**, scapula; **scs**, scapulocoracoid suture. Scale bars equal 1 cm.

a biceps tubercle, with a distinct facet ventrally, but the damaged posterior region renders such homologies uncertain.

Only the medial (sternal) half of the right coracoid is preserved (Fig. 5C). Its posterior end has rotated counterclockwise (dorsal view), unnaturally abutting the posterior end of the left coracoid and sitting where the anterior end of the sternum should be. However, the anterior right coracoid is articulated in its expected location. Given this, and the location of the median 'dip' of the furcula (see below), the relative positions of the furcula and anterior coracoids appears to be natural, not artifactual.

Furcula—UCMP 32101 has a furcula (Fig. 5). This element was described as a single clavicle by Camp (1936:44), who was followed by most subsequent authors (e.g. Blotzheim, 1966; Bryant and Russell, 1993; Padian, 1997; Makovicky and Currie, 1998). However, three lines of evidence reveal that the element is indeed a furcula. First, it is at least 50% longer than any linear dimension of the nearly complete left coracoid. In dinosaurs with separate clavicles, each element is shorter than the coracoid as measured from the anterior extremity of the scapulocoracoid suture to the tip of the posterior process (the longest linear dimension of the coracoid in most theropods) (Bryant and Russell, 1993; Chure and Madsen, 1996:fig. 1; Makovicky and Currie, 1998). Second, the element crosses the anterior ends of both coracoids, as do other furculae (Chure and Madsen, 1996; Norell et al., 1997; Clark et al., 1999). Finally, the bone 'dips' ventrally between the two coracoids, a product of the junction between the two sigmoidally curved clavicles (Makovicky and Currie, 1998). A single clavicle would be half as long, and therefore not cross the anterior ends of both coracoids. It also would lack this midline 'dip,' instead forming a single sigmoid curve. It is certainly not formed from fused gastralia, hyoids, ribs, or other bones because it lacks the diagnostic features of those elements, as detailed in other studies (Chure and Madsen, 1996; Makovicky and Currie, 1998; Tykoski et al., 2002; Claessens, 2004).

The furcula of *Segisaurus* apparently lacks a hypocleideum, although there seems to be a slight nubbin where the hypocleideum would be located. Furculae without prominent hypocleidea are known in other basal theropods (Chure and Madsen, 1996; Makovicky and Currie, 1998; Tykoski et al., 2002) as well as in oviraptorids (Clark et al., 1999) and *Archaeopteryx* (Owen, 1863). As is usual, there is no evidence of a suture at the midpoint of the furcula. The two rami diverge at an angle of about 140°. The furcula also possesses a modest swelling on the left side, as noted by Camp (1936:44). This asymmetry is atypical for theropod furculae (Chure and Madsen, 1996; Norell et al., 1997; Makovicky and Currie, 1998; Clark et al., 1999; Tykoski et al., 2002) and may be pathological (it does not appear on the right side). As in *Syntarsus* (Tykoski et al., 2002), the left ramus of the furcula has a striated, posterodorsally facing epicleidal facet (Fig. 5B). A similar morphology has been noted for *Allosaurus* (Chure and Madsen, 1996).

Humerus—Only the left humerus is present (Fig 6A). The proximal end is damaged, and lacks the head and greater tubercle, although a fragment of bone lodged in the left glenoid may represent part of these structures. The broken end clearly demonstrates that the humerus is hollow and thin walled. The internal tuberosity may be present along the edge of the proximal break. Below it, the deltopectoral crest extends as a rugose ridge to about the midshaft. The distal edge of the deltopectoral crest is distinct, emerging from the shaft nearly perpendicularly and much more abruptly than in *Dilophosaurus*. It is not clear whether the crest continues to the proximal end or terminates well below it, but some segregation of muscle insertion develop-

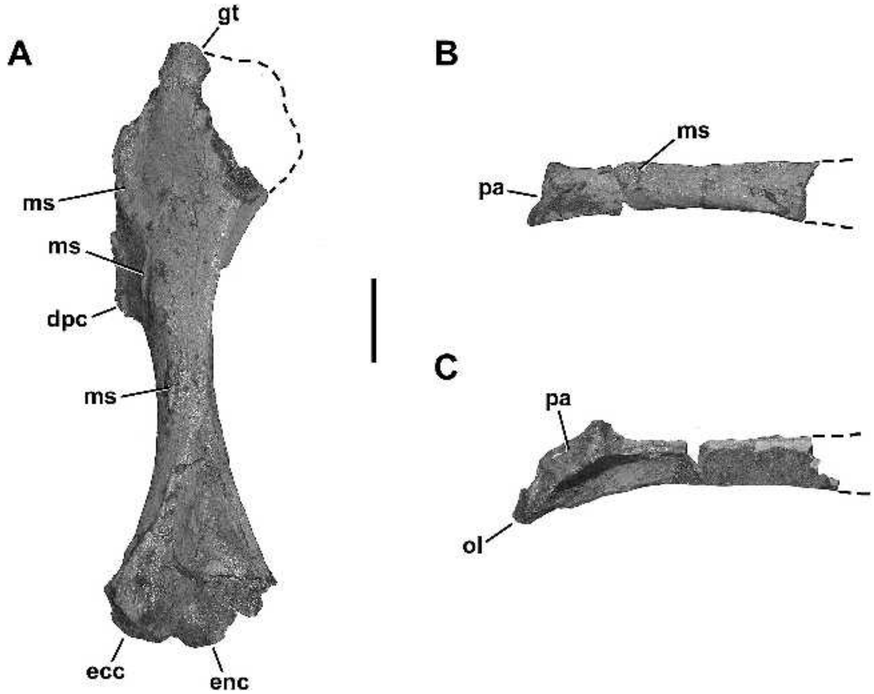

FIGURE 6. Left forelimb of *Segisaurus halli*, UCMP 32101. **A**, humerus, posterior view. **B**, radius, lateral view. **C**, ulna, medial view. **Abbreviations**: **dpc**, deltopectoral crest; **ecc**, ectepicondyle; **enc**, entepicondyle; **gt**, greater tubercle; **ms**, muscle scar (four different muscle attachments indicated); **ol**, olecranon; **pa**, proximal articular surface. Scale bar equals 1 cm.

ment along the crest accentuates its distal third. The deltopectoral crest and humerus are well marked with scars for the insertions of shoulder muscles such as the Mm. deltoidei and Mm. pectorales.

The proximal and distal ends of the humerus are twisted about 50°, demonstrating more torsion than in most coelophysoids but comparable to the condition in *Dilophosaurus* and basal tetanurans. The shaft is straight in mediolateral view, rather than sigmoid, and (as preserved) both ends expand to about 20 mm from the 7 mm wide midshaft. The distal end preserves the ectepicondyle and half of the entepicondyle; both are rounded.

Radius—Camp (1936:44) reversed the identifications of the radius and ulna. About two-thirds of the radius appears to be present (Fig. 6B), with the broken shaft revealing a hollow interior. The proximal articular surface is teardrop-shaped and distinctly concave, and remains in near articulation with the humeral ectepicondyle. The main shaft is substantially deeper than wide, although this may have been enhanced by crushing.

Ulna—The proximal two-thirds of the ulna are preserved, bearing a triangular expansion that includes the base of an olecranon process (Fig. 6C). The slightly concave medial surface has been exaggerated by crushing. Laterally, the radial articulation is obscured by matrix. The shaft is hollow at the broken end, and appears to have been somewhat more slender than the radial shaft. The ulna is preserved in a different block from the other forearm elements (along with the scapula and gastralia), but can be re-articulated into its natural position with the radius and humeral entepicondyle.

Carpus—Nothing of the carpus can be identified.

Manus—The manus is represented by several fragmentary phalanges and unguals of uncertain identity. At least two belong to the left manus, which Camp (1936:45) identified as digits II and III, apparently by comparison with *Compsognathus*; if this identification is correct, then digit II seems to be the longest in the manus, befitting a basal theropodan saurischian (Gauthier, 1984). Other, isolated fragments could pertain to elements of either manus. Most are unremarkable in morphology, tending to be rather slender. The unguals are strongly recurved, laterally compressed, and bear a distinct single vascular groove, resembling the condition in *Coelophysis*. The exact number of manual digits cannot be determined, but the phylogenetic position of *Segisaurus* (see below) suggests there should have been four.

Ilium—Parts are present of all the pelvic elements of both sides, but the ilia are particularly fragmentary. The left acetabulum is open medially and longer (30 mm) than tall (20 mm), with a large, hooded supraacetabular crest (Fig. 2). Its preserved margins do not show any evidence of sutures with either the pubis or ischium. A depression occurs within the acetabulum along its anterior margin, as in *Coelophysis* and many neotheropods.

The right ilium is represented only by a small sliver of bone alongside the right lateral edge of the second caudal vertebra. It is, however, sufficient to indicate that *Segisaurus* has an elongate postacetabulum that extended far past the ischial peduncle, as in other neotheropods.

Pubis—The pubis has two openings, as in most coelophysoids (Figs. 7, 8; e.g., *Syntarsus*, *Gojirasaurus*, *Procompsognathus*). The obturator foramen is the smaller and more dorsally situated of the two. Below it, a large pubic (or 'thyroid') fenestra faces ventrally. This fenestra is incomplete along its ventral margin, although it is difficult to determine whether this is natural or the result of breakage (Fig. 7). A potential suture is evident between the left pubis and ischium, directly below the acetabular opening where these two bones are laminar (Fig. 8A). Both pubes and ischia are preserved, clearly demonstrating that the puboischiadic plate was complete ventral to the acetabulum, although there may have been a diamond-shaped space at the junction of all four elements.

The proximal pubic shaft downcurves 35° ventrally, but the midshaft is broken and partly missing. The paired distal pubes are thickened distally but not expanded into a 'boot' or similar structure (Fig. 7B). There is a median gap below the pubic apron, as in *Procompsognathus* (Sereno, 1999) and many other coelo-

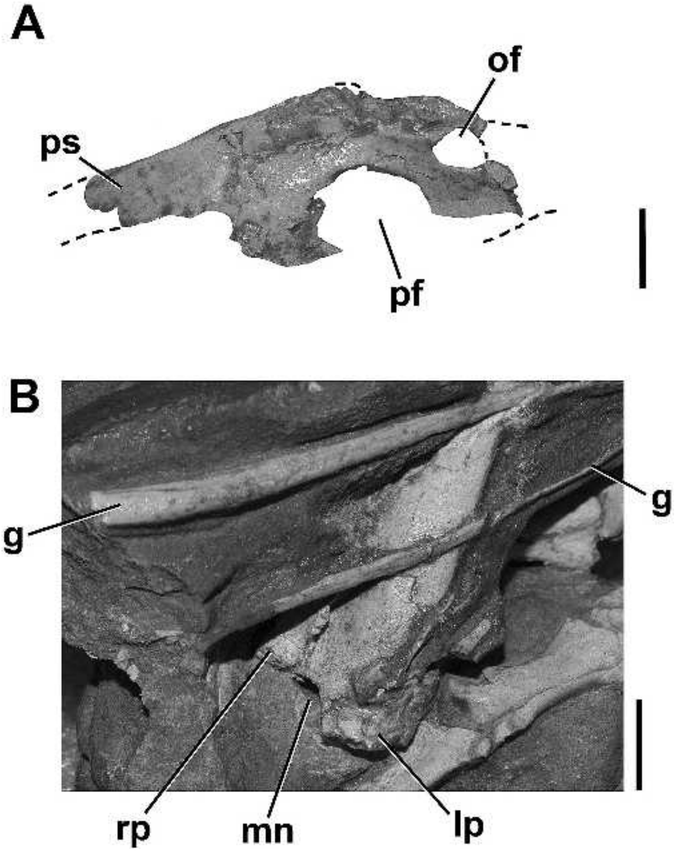

FIGURE 7. Pubis of *Segisaurus halli*, UCMP 32101. **A**, proximal end of left pubis in lateral view. **B**, distal pubes with associated gastralia in anterolateral view. **Abbreviations**: **g**, gastralia; **lp**, left pubis; **mn**, median notch; **of**, obturator foramen; **pf**, pubic fenestra/foramen; **ps**, pubic shaft; **rp**, right pubis. Scale bars equal 1 cm.

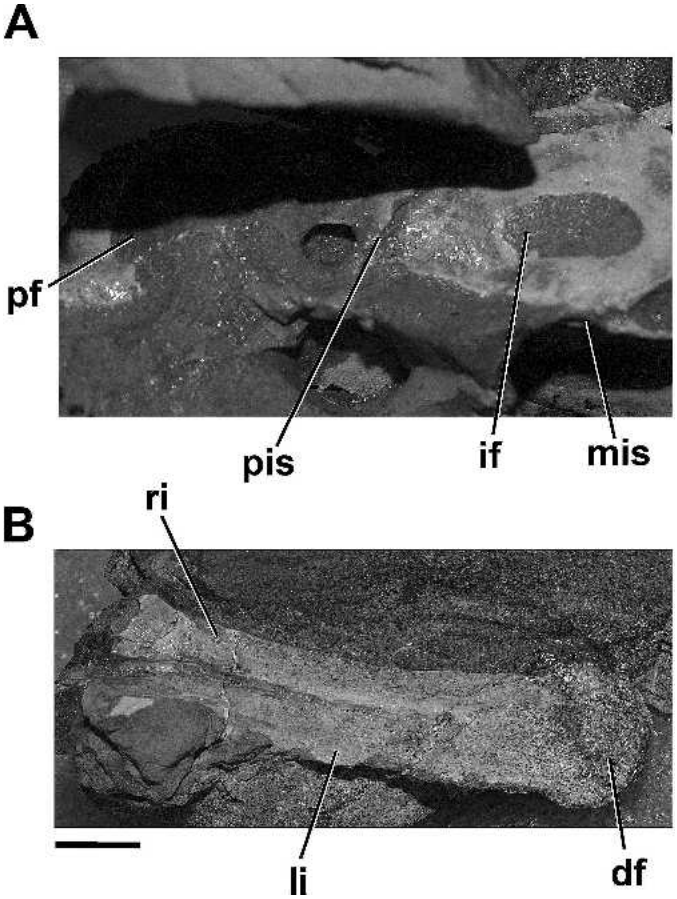

FIGURE 8. Ischium of *Segisaurus halli*, UCMP 32101. **A**, proximal end of left ischium in articulation with left pubis. **B**, distal ischia in left dorsolateral view **Abbreviations**: **df**, distal fusion; **if**, ischial foramen; **li**, left ischium; **mis**, median suture between left and right ischia; **pf**, pubic foramen; **pis**, puboischial suture; **ri**, right ischium. Scale bars equal 1 cm.

physoids (including *Dilophosaurus*, *Syntarsus kayentakatae*, and *Liliensternus liliensterni*; Huene, 1934; R. Tykoski, pers. comm.). This differs from the condition in basal tetanurans, where the distal pubes are slightly swollen and contact along their medial surfaces, leaving a more proximal gap. The apron in *Segisaurus* is beautifully preserved, the right having telescoped slightly dorsally over the left and slid proximally (Fig. 9B). It has a similar cross section to that of most primitive theropods, with a lateral rod-like portion that is distinct from the thin, medially sharpened apron itself. Based on their position relative to other articulated elements, at least 10 mm are missing from the pubic shaft; the estimated length is minimally 110 mm.

Ischium—The articulated ischia bear a large ischial foramen that appears to be diagnostic for *Segisaurus* (Fig. 8A; Camp, 1936; Rauhut, 2000, 2003). They are appressed throughout their lengths, and fused distally into a thin, flattened structure (Fig. 8B). Some compression is apparent along the midshaft, where the left and right ischia have collapsed mediolaterally and folded inward (Fig. 9A). Hence some distortion may have occurred post-mortem, but the midshafts seem to have been genuinely flattened (contra Rowe and Gauthier, 1990). Presumably the fused distal portions prevented the telescoping seen on the pubes. Somewhat more of the shafts seem to be missing as well (ca. 27 mm), but based on position we estimate their lengths as 96 mm. A faint pit on the posterolateral proximal right ischium corresponds to the ischial tuberosity, marking the origin of M. flexor tibialis internus 3 (Hutchinson, 2001b; Carrano and Hutchinson, 2002). The distal ischia are angled ventrally about 35°.

Femur—A fragment of the left femoral head remains in life position in the block close to the left acetabulum, connected to a larger, free fragment. It preserves the nearly complete left lesser trochanter, showing both a shelf laterally and a spike-like process more anteriorly. A marked groove along the anterior edge of the shelf indicates the insertion of M. ischiotrochantericus (Hutchinson, 2001a). More distally, a ridge-like fourth trochanter is bounded posterolaterally by a prominent facet for M. caudofemoralis brevis (Hutchinson, 2001a; Carrano and Hutchinson, 2002). The broken shaft is relatively solid, but does show some evidence of internal hollowing. The relatively complete distal end has a distinct fossa on the anterior surface of the fibular condyle; it bears prominent muscle striations for the origin of a distal part of M. femorotibialis externus (Hutchinson, 2001a; Carrano and Hutchinson, 2002). The fossa and extensor groove are more pronounced than in *Coelophysis*. The proximal ridges leading to the distal condyles are barely visible, along with the associated flexor groove.

The proximal right femur is better preserved. The greater trochanter is a long, flat facet along the lateral surface, marking the insertion of Mm. puboischiofemorales externii (Hutchinson, 2001a; Carrano and Hutchinson, 2002). A small, spike-like lesser trochanter is present on the anterolateral corner of the shaft, contiguous with a more lateral shelf as in *Coelophysis*, *Syntarsus*, and other coelophysoids. The orientation of the head cannot be observed, but its anteroposterior narrowness is consistent with

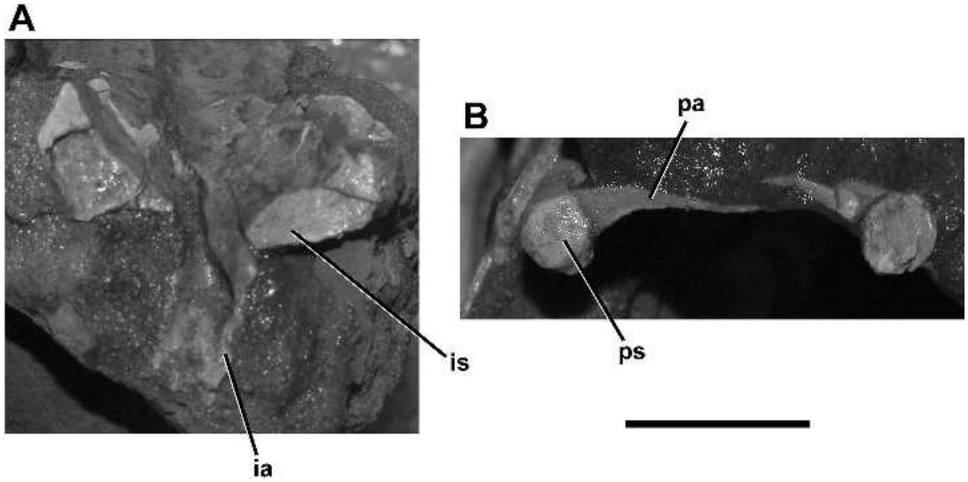

FIGURE 9. Pubis and ischium of *Segisaurus halli*, UCMP 32101. **A**, ischial midshafts in cross section, proximal view. **B**, pubic midshafts in cross section, proximal view. **Abbreviations**: **ia**, ischial apron; **is**, ischial shaft; **pa**, pubic apron; **ps**, pubic shaft. Scale bar equals 1 cm.

the coelophysoid condition, which would involve an anteromedial orientation of the head (Carrano, 2000). The lateral portion of the proximal end preserves part of the curved articular surface and sulcus that would have articulated beneath the prominent iliac supraacetabular crest. A hollow shaft section from what is probably the right femur can be seen to the right of the ischial shafts.

Tibia and Fibula—The left tibia is nearly complete (Fig. 10). It has a prominent cnemial crest that nonetheless does not extend significantly above the level of the proximal articular surface. The distal cnemial crest has a flat facet for insertion of the knee extensor tendon(s) and origin of at least part of M. tibialis cranialis (Carrano and Hutchinson, 2002). The medial surface of the tibial shaft is somewhat damaged and partly restored. Laterally, a marked fibular crest still clasps the fibula, demarcating a significant fossa anteriorly and proximally. The medial proximal condyle is prominent, but the lateral condyle cannot be seen. The tibia is closely appressed to the fibula for most of its length.

The right tibia includes the cnemial crest and much of the proximal end, along with approximately two-thirds of the shaft adjacent to the right fibula. The bone is broken beneath the cnemial crest, revealing the interior.

The left fibula is also mostly complete (Fig. 10). It is not fused to the tibia as Camp (1936) contended—its proximal end has been displaced slightly posteriorly, so that the shaft sits entirely posterior to the fibular crest, instead of alongside it. On the posteromedial surface, a distinct sulcus is present as in many coelophysoids (Rowe and Gauthier, 1990), delimited proximally by a faint tuber. The insertion for M. iliofibularis is marked and rugose, situated along the anterior edge of the shaft approximately one-third of the way down. A narrow, concave groove runs down the medial shaft from the level of this tubercle toward the distal end. Only the central portion of the right fibular shaft is present.

Tarsus—The tarsus is represented only by elements of the left side, specifically distal tarsal 4, a portion of the calcaneum, and possibly part of the astragalus (Fig. 11). Camp misidentified the latter as a "calcaneal tuber" (1936:48), but such a structure is unknown in theropods. This fragment is difficult to identify with certainty, but it may represent the posteromedial corner of the left astragalus, which is consistent with its original position amidst the articulated hind limb elements (Camp, 1936:pl. 3) and comparisons with the astragalus of other basal theropods such as *Coelophysis*. Gauthier (1984:217) seems to have misinterpreted Camp's description of the 'calcaneal tuber' as referring to distal tarsal 4, but Camp's illustration (1936:pl. 3) clearly associates the term with this fragment.

The calcaneum is articulated with the distal end of the fibula, which remains lodged in a distinct, dorsal cup with a semicircular lateral margin (Fig. 11). The medial articular surface for the astragalus appears to be partly intact, suggesting that these two elements were not fused. The medial wall of the fibular cup is missing, and would have been formed by the lateral part of the astragalus. In general the fibular cup is similar in shape to that of *Coelophysis*, although somewhat more elongate mediolaterally. The ventral portion of the calcaneum is roller shaped and ventrally (not anteroventrally) positioned, forming the lateral portion of the mesotarsal joint.

Distal tarsal 4 is flattened dorsoventrally, as in all dinosaurs, and is more triangular than trapezoidal, as in dinosaurs (Novas,

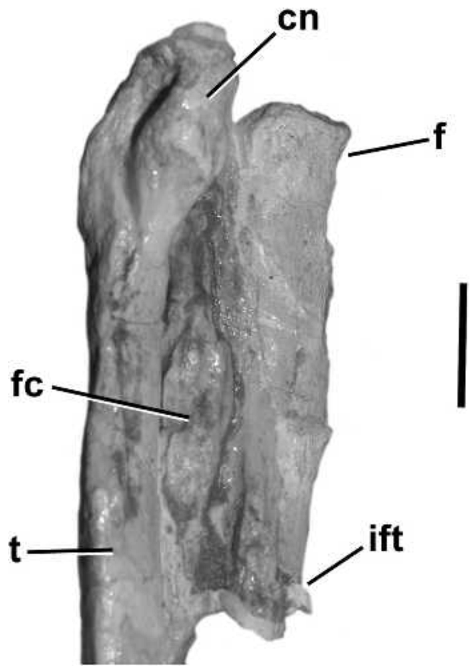

FIGURE 10. Proximal left tibia and fibula of *Segisaurus halli*, UCMP 32101, in anterior view. **Abbreviations**: **cn**, cnemial crest; **f**, fibula; **fc**, fibular crest; **ift**, M. iliofibularis tubercle; **t**, tibia. Scale bar equals 1 cm.

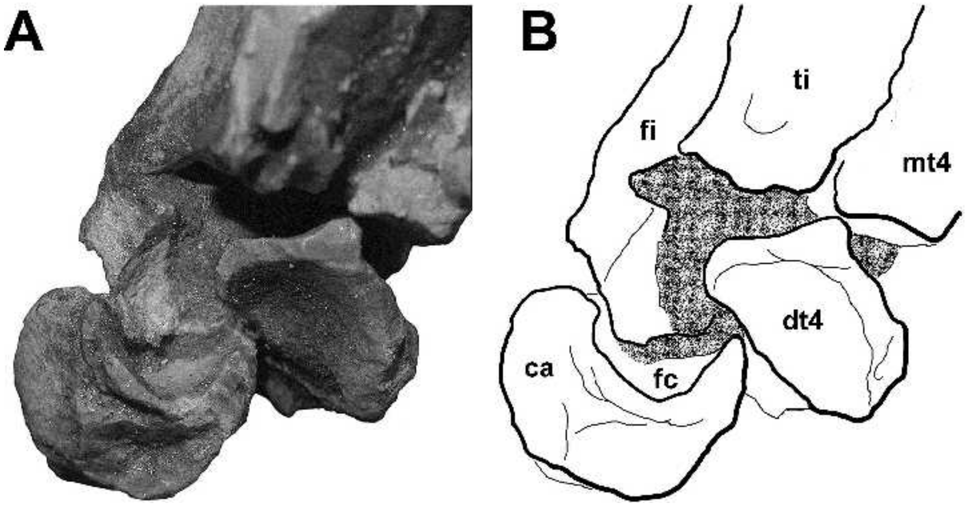

FIGURE 11. Left tarsus of *Segisaurus halli*, UCMP 32101, in oblique anteromediodistal view. **A**, photograph. **B**, interpretive drawing. **Abbreviations**: **ca**, calcaneum; **dt4**, distal tarsal 4; **fc**, fibular cup of calcaneum; **fi**, fibula; **mt5**, metatarsal V; **ti**, tibia. Shaded area indicates matrix.

1996). It has a slightly thickened lateral edge where it overlaps metatarsal V, which is preserved in near articulation. Its distal articular surface is approximately split between the articulations for metatarsals IV and V, as is typical for dinosaurs.

Pes—All the elements of the pes are preserved on at least one side. The left is more complete, including all five metatarsals and phalanges except for I-2. The right pes lacks metatarsals I and V, and phalanges II-1, III-4, and IV-3 through 5.

Metatarsal I is a thin splint articulated in situ along the medial surface of metatarsal II, and shifted slightly ventrally. It extends three-quarters of the length of metatarsal II, and bears an asymmetrical distal ginglymus that articulates with I-1. The proximal end is not well preserved, and although we cannot determine unambiguously whether it reached the ankle, it certainly approached this joint quite closely.

Metatarsals II-IV are long and slender, appressed, and resemble those of most other basal theropods. They are relatively unspecialized in either morphology or proportions. As in most theropods, metatarsal IV has a mediolaterally narrow distal end.

Metatarsal V is a long, triangular splint of bone that bears no phalanges. It articulates with distal tarsal IV and extends proximally above the articular plane of metatarsals II-IV. Its distal end reaches down along one-third of the length of metatarsal IV.

The pedal phalanges and unguals are typically theropod and bear few remarkable features. Collateral ligament pits and 'hyperextension' fossae are evident on most metatarsals and phalanges. The unguals bear a single vascular groove on each side, are only moderately recurved, and triangular in cross-section. At least one (left II-3) has a noticeable flexor tubercle ventrally.

DISCUSSION

Position of the Skeleton

The holotype specimen of *Segisaurus* is preserved in a crouched position, with the legs and feet tucked under the prone body. Camp (1936:50) likened it to that of "a sitting hen", and offered that such a posture would be useful "as a protection against sand blasts in storms, during sleep, and to elude enemies." It is strikingly reminiscent of nesting theropods buried quickly during sandstorms (e.g., Clark et al., 1999). Perhaps *Segisaurus* was similarly entombed by the slumps and shifting dunes known to be characteristic of the Navajo Sandstone (Loope et al., 2001). Here, however, we lack evidence of nest materials or sedimentologic information vital for further taphonomic inferences.

Internal Bone Structure

Camp (1936:39, 46, 49) claimed that the femur, tibia and centra of *Segisaurus* lacked the hollowed interior cavity that is typical of these bones in other theropods. This and other features led Welles (1984:174) to suggest that *Segisaurus* might not even be a theropod, and he doubted that any original bone was actually preserved. However, several broken long bone elements clearly preserve a hollow interior cavity, and some evidence of this is also present in the femur and tibia. These bones do not seem to have been much thicker than those of other primitive theropods, especially considering the amount of compression and diagenesis this skeleton has undergone (Gauthier, 1984; Rowe and Gauthier, 1990). In particular, the broken ends of the humerus reveal particularly thin-walled bone structure consistent with that seen in other theropods. In any case, histological analysis (see below) reveals that original bone material is indeed present, not a "chalky substance" as Welles (1984:161) inferred.

The centra, on the other hand, may well have been comparatively 'solid'. Only the posterior dorsals, sacrals, and caudals are preserved, and these vertebrae typically have non-pneumatic centra in most primitive theropods. Only the cervical and first four dorsal vertebrae show marked centrum pneumaticity in these taxa, and unfortunately these elements are not preserved in *Segisaurus*. Thus the presence of centrum pneumaticity should be regarded as undetermined in this taxon.

Clavicle Versus Furcula

The available information on the pectoral girdle of *Segisaurus* strongly supports identification of the clavicular element as a fused furcula. Positional, size, and morphological data conform to those expected for a furcula, and are inconsistent with a single clavicle. Thus we can confirm the presence of a derived 'avian' feature in this relatively primitive theropod.

Furculae are clearly present in other coelophysoids as well, specifically *Coelophysis* (Downs, 2000) and *Syntarsus* (Tykoski et al., 2002). Thus a furcula appears to have been present consistently in neotheropods, and its absence should conservatively be considered secondary or taphonomically influenced in this group. The purported presence of unfused clavicles in *Carnotau-*

rus (Bonaparte et al., 1990) could not be confirmed (pers. obs.) and has been questioned elsewhere (Rauhut, 2000).

The position of the furcula in the pectoral girdle of *Segisaurus* is instructive, as it is clearly directly attached to the scapular acromion at its lateralmost tip. Its general morphology is similar to that noted in other theropods (e.g., Chure and Madsen, 1996; Tykoski et al., 2002), and thus little modification of the furcula occurred until well within Maniraptora.

Ontogenetic Status

Histological examination of the right tibial shaft (Fig. 12) shows a bone structure suggestive of subadult status. In particular, there is a pattern of fast growth during early ontogeny, as seen in the central part of the cross-section. The bone here is fibrolamellar with several lines of arrested growth (LAGs) indicating that the specimen may have been in the fifth year of its life (e.g., Erickson et al., 2004), although given the amount of damage to the cortical region of the bone, this should be viewed as a minimum estimate. In addition, drift lines are visible that indicate a change in bone shape during ontogeny. Longitudinal vessels are widespread, whereas radial vessels are less common. LAG intervals decrease progressively towards the outer (periosteal) surface, which suggests rapid early growth followed by progressive slowing of growth. Although in some regions of the cortex the outermost LAG appears to be part of an external fundamental system, more complete regions show yet another LAG interval. Furthermore, there is some increase in the density of vascular canals toward the periosteal surface, which is inconsistent with a truncation of growth. Sections of a proximal left rib shaft show similar overall patterns, suggesting that these observations are not exclusive to the tibia and hence represent general skeletal ontogeny.

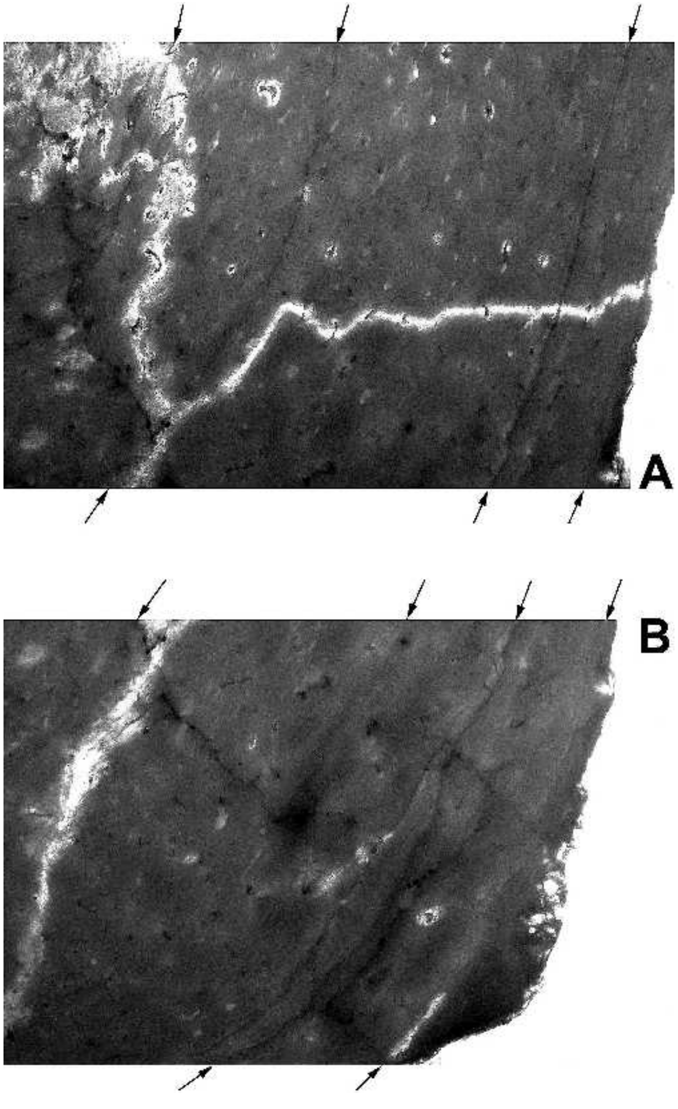

FIGURE 12. Bone histology of the distal tibial shaft from UCMP 32101. Two sections (**A**, **B**) are shown at 40x magnification under a light microscope. Arrows indicate preserved LAGs. Scale bar equals 0.25 mm.

The astragalus and calcaneum appear to have been unfused. Neurocentral sutures are visible on the caudal vertebrae, but the arches and centra are not separate (although Camp [1936] indicated obliterated neurocentral sutures in the dorsal vertebrae). If these tend to fuse earlier in ontogeny than the (missing) cervicals and anterior dorsals, this condition may indicate a relatively young animal. Partial fusion is evident in the pelvis, whereas the scapula and coracoid are tightly connected but a suture remains visible.

We acknowledge that skeletal fusion need not signal the cessation of growth. However, the sequence of ossifications and fusions (e.g., Brochu, 1996) is informative with respect to ontogenetic stage. In particular, the presence of visible neurocentral sutures in the caudal vertebrae is indicative of an earlier stage of growth. Although the pelvis is at least partly fused, a suture remains visible between the ischium and pubis. The scapulocoracoid suture likewise remains patent. Taken together, the balance of these observations suggests that the holotypic individual of *Segisaurus* died prior to reaching skeletal maturity.

This has some relevance for character codings. If the holotype of *Segisaurus* is not fully mature, then the absence of certain fusions in the adult state cannot be determined. Thus we code these features as uncertain in our phylogenetic analysis (e.g., Tykoski, 2004). One potential complication is that the skeleton seems to be of a ‘robust morph,’ common in basal theropods (Rowe and Gauthier, 1990), although correlation of skeletal robusticity in these forms with ontogenetic stage remains unclear (Colbert, 1990; Raath, 1990). However, we feel that the histological evidence speaks clearly that the specimen was subadult.

PHYLOGENETIC ANALYSES

We performed a phylogenetic analysis to determine the relationships of *Segisaurus* to other primitive theropods. We chose 15 taxa for the ingroup, representing putative coelophysoids (*Coelophysis*, *Dilophosaurus*, *Gojirasaurus*, *Liliensternus*, *Procompsognathus*, *Sarcosaurus*, *Segisaurus*, *Syntarsus*, and *Zupaysaurus*), ceratosaurs (*Carnotaurus*, *Ceratosaurus*, *Elaphrosaurus*, and *Majungatholus*), and tetanurans (*Allosaurus* and *Ornitholestes*). *Herrerasaurus* and *Eoraptor* were used as successive outgroups. We coded *Syntarsus* based on both *S. kayentakatae* and *S. rhodesiensis*, but note that these two taxa may not form a monophyletic group (R. Tykoski, pers. comm.). (We also retain this generic name pending resolution of discrepancies regarding its homonymy and proposed replacement.) The matrix included 145 characters, 131 binary and 14 multistate (unordered), and was analyzed with PAUP*4.0b10 (Swofford, 2002), using both heuristic and branch-and-bound searches.

These analyses produced 302 most parsimonious trees (MPTs) of 217 steps, with CI = 0.7327 and RI = 0.8284. In all trees, we recovered the clades Neotheropoda, Coelophysoidea, Ceratosauria, and Tetanurae, but no clades were present within Coelophysoidea in all MPTs (Fig. 13A). The placement of *Segisaurus* and *Procompsognathus* as sister taxa has been suggested elsewhere (Procompsognathinae; Sereno, 1999), but this clade was not supported here.

An Adams consensus (Fig. 13B) revealed significant addi-

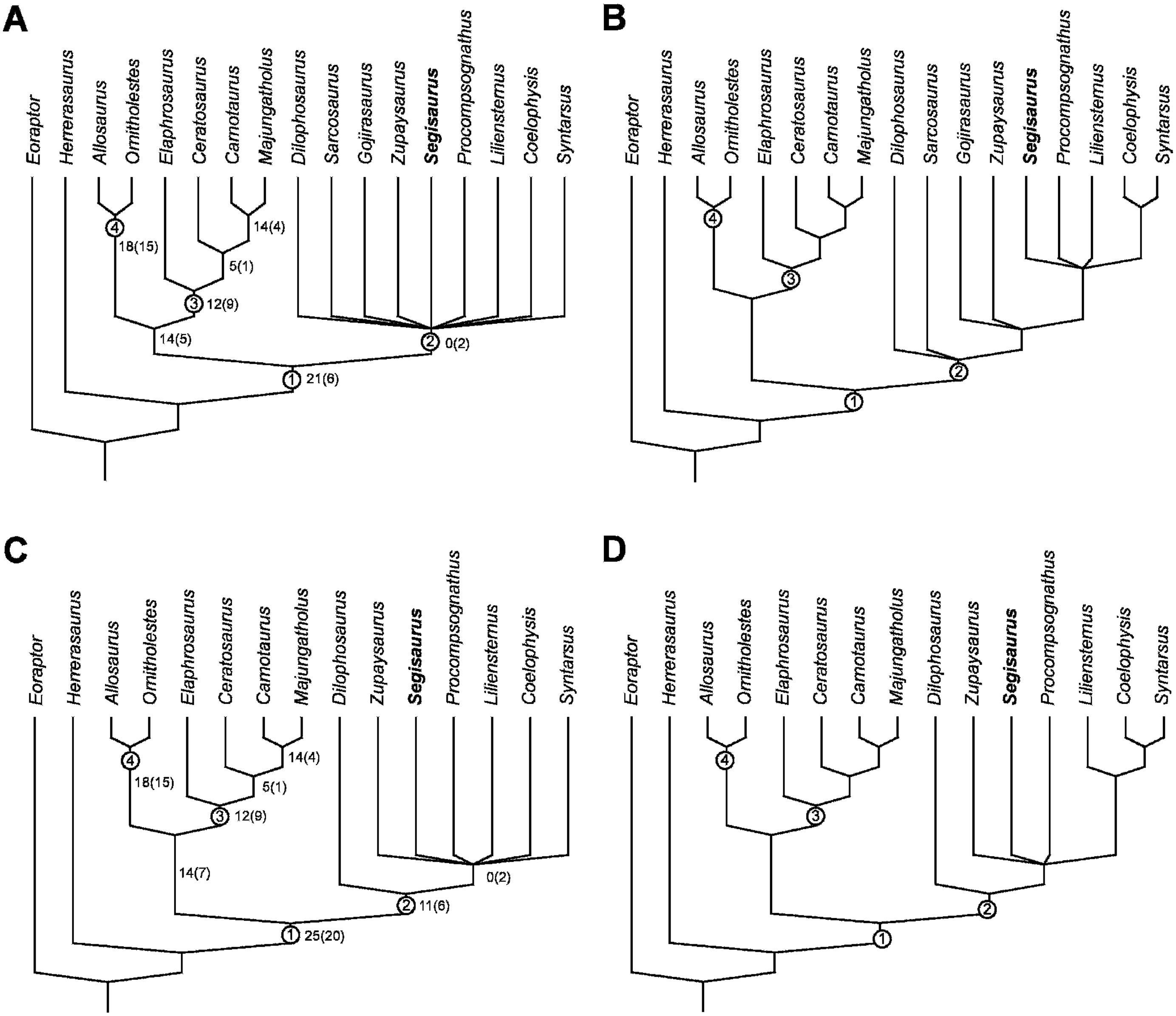

FIGURE 13. Phylogenetic results. **A**, strict consensus of 302 MPTs with all taxa included. **B**, Adams consensus of 302 MPTs. **C**, strict consensus of 42 MPTs obtained from analysis excluding *Gojirasaurus* and *Sarcosaurus*. Clade numbers (in circles): 1, Neotheropoda; 2, Coelophysoidea; 3, Ceratosauria; 4, Tetanurae. Numbers alongside each node indicate number of unambiguous characters supporting that node (outside parentheses), and decay indices (in parentheses).

tional resolution that had been obscured by the presence of two incomplete taxa (*Gojirasaurus*, *Sarcosaurus*) that acted as 'wild cards.' Specifically, we recovered a monophyletic clade composed of (*Liliensternus*, *Procompsognathus*, *Segisaurus* + (*Syntarsus* + *Coelophysis*)), followed by *Zupaysaurus* and *Dilophosaurus*.

When *Gojirasaurus* and *Sarcosaurus* were removed, only 42 MPTs were found (217 steps, CI = 0.7327, RI = 0.8242), with *Dilophosaurus* as the outgroup to all other coelophysoids (Fig. 13C). An Adams consensus of these trees (Fig. 13D) placed *Segisaurus*, *Procompsognathus*, and *Zupaysaurus* outside the *Liliensternus* + (*Syntarsus* + *Coelophysis*) clade. The position of *Zupaysaurus* as a coelophysoid is well supported here, contradicting its previous identification as the oldest known tetanuran (Arcucci and Coria, 2003).

Thus *Segisaurus* resides firmly within the Coelophysoidea, as has been suggested by numerous other workers. The few seemingly derived traits (e.g., slender scapular blade and humeral shaft torsion) are therefore homoplastic. In addition, most characters used to support the Procompsognathinae (Sereno, 1999) were found to have a wider distribution within coelophysoids.

Relationships within Coelophysoidea are poorly resolved due to the incompleteness of most constituent taxa, and therefore it is difficult to say much about evolution within this group. Nonetheless, it seems clear that basal taxa (such as *Dilophosaurus*) were relatively large, and that the comparatively small size of coelophysids is a derived trait (Carrano, in press). The apparent diversity of both European (Carrano and Sampson, 2004) and North American (Heckert et al., 2004) coelophysoids implies that multiple lineages were present in both regions for tens of millions of years (Fig. 14). The origins of the clade date back to at least the late Carnian, as represented by the poorly known

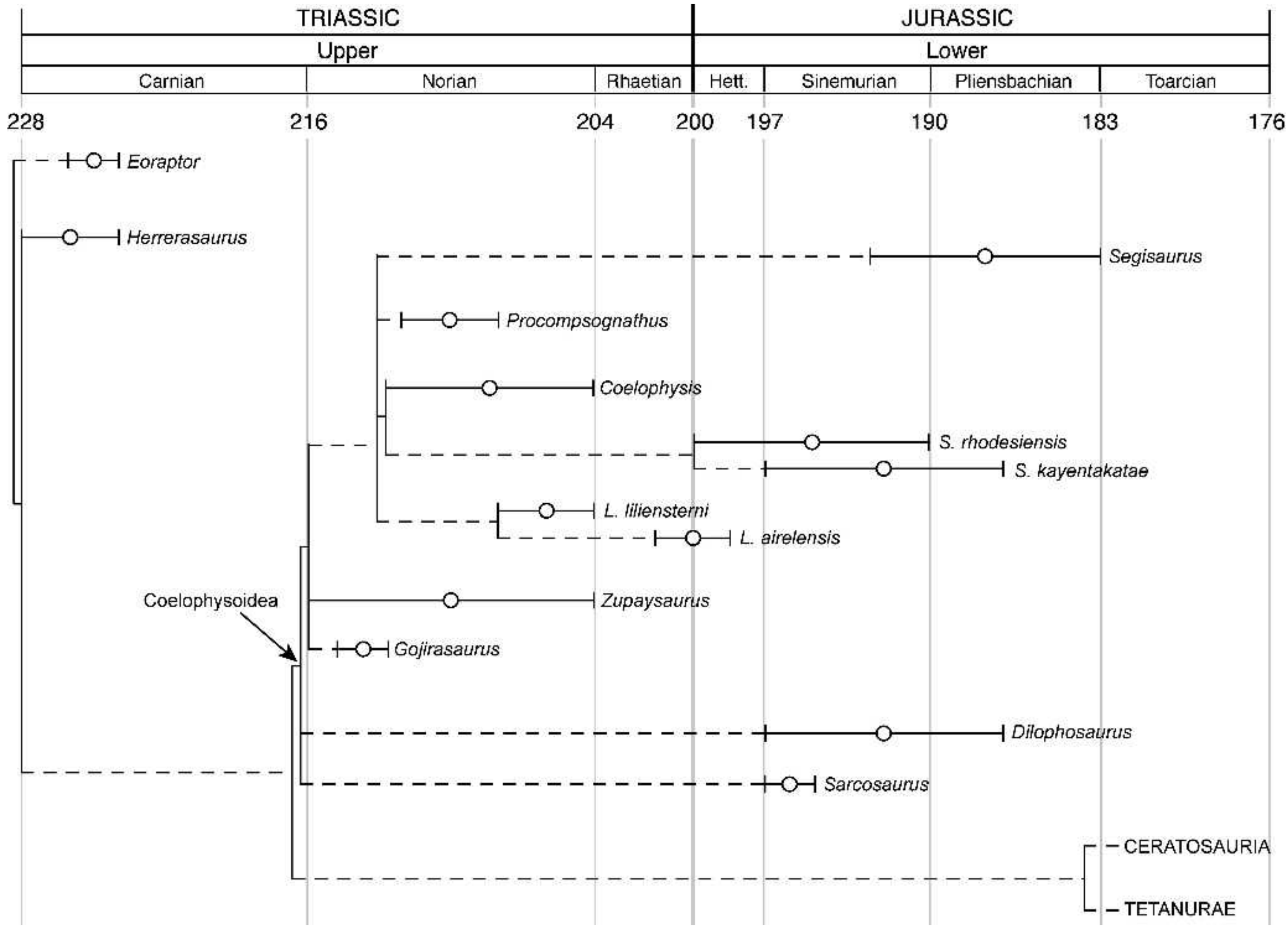

FIGURE 14. Stratigraphically calibrated phylogeny of Coelophysoidea and basal Theropoda, based on the results of the current study. The Adams consensus tree is used here; the placement of *Sarcosaurus* and *Gojirasaurus* are therefore maximally basal. Note that the monophyly of both *Liliensternus* (*L. liliensterni*, *L. airelensis*) and *Syntarsus* (*S. rhodesiensis*, *S. kayentakatae*) has been assumed. The 'error' bars shown reflect the temporal resolution of taxon occurrences, not true time ranges.

Camposaurus and *Shuvosaurus* (in part; Rauhut, 2003). The coelophysoid radiation may have been spent by the latest Early Jurassic (Carrano and Sampson, 2004), making *Segisaurus* and *Podokesaurus* among the latest surviving forms (Fig. 14).

CONCLUSIONS

Our re-study of the holotype and only specimen of *Segisaurus halli* Camp, 1936, has significantly enhanced our knowledge of the morphology of this taxon. Although incomplete and fragmentary, the holotype can be recognized as less than fully mature, yet probably deriving from a "robust" individual. *Segisaurus* appears to be diagnosable, and represents one of the latest North American coelophysoids.

We can confirm the presence of an articulated furcula in this taxon, as well as numerous other theropod synapomorphies. More specifically, the skeleton displays several coelophysoid features, including a pubic fenestra, separated distal pubes, and a ventrally curved pubis.

These observations are supported by a phylogenetic analysis, which confidently places *Segisaurus* within the Coelophysoidea. Ingroup relationships are difficult to resolve, but there is some support for a clade including *Coelophysis*, *Syntarsus*, and *Liliensternus*, as well as the basal position of *Dilophosaurus*. This implies the presence of several distinct coelophysoid lineages throughout the latest Triassic and Early Jurassic.

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APPENDIX 1

List of characters used in phylogenetic analyses. First cited use of character is given in parenthesis, followed by significant modifications (if any).

1. Subnarial gap and modified articulation between premaxilla and maxilla: absent (0), present (1) (Welles, 1984).
2. Subnarial foramen: small/absent (0), enlarged (1) (Novas, 1989).
3. Premaxilla height/length ratio ventral to external naris: 0.5–2 (0), < 0.5 (1), > 2 (2) (Paul, 1988; Novas, 1989).
4. Maxillary fenestra: absent (0), fossa (1), fenestra (2) (Gauthier and Padian, 1985).
5. Promaxillary fenestra: absent (0), present (1) (Sereno, 1999).
6. Rim along anteroventral edge of antorbital fossa: absent (0), present (1) (Rowe, 1989).
7. Shape of anterior end of antorbital fenestra: rounded (0), acutely angled (1) (Rauhut, 2000).
8. Ventral antorbital fossa on maxilla: substantial (0), absent (1) (Novas, 1989).
9. Anterior end of antorbital fossa: posterior (0), ventral (1) to external naris (Sereno, 1999).
10. Paired nasal-lacrimal crests: absent (0), present (1) (Holtz, 1998 [2000]).
11. Posterior narial margin: fossa (0), hood (1) (Sereno et al., 1994; Carrano et al., 2002).
12. Prefrontal: separate (0), fused (1).
13. Frontal exposure on orbital rim: broad (0), narrow/absent (1) (Gauthier, 1986).
14. Nuchal crest height: moderate (0), very tall (1) (Bakker et al., 1988; Sereno, 1999).
15. Postorbital suborbital flange: absent (0), present (1) (Gauthier and Padian, 1985; Novas, 1989).
16. Laterosphenoid contacts: frontal and postorbital (0), postorbital only (1) (Sereno, 1999).
17. Lacrimal anterior process length: < 65% (0), > 65% (1) ventral process length (Paul, 1984; Sereno et al., 1998).
18. Antorbital fossa on jugal: absent (0), present (1) (Rauhut, 2000).
19. Jugal-lacrimal overlap: absent or narrow rod (0), flange (1), socket (2) (Paul, 1988; Sereno, 1999).
20. Quadratojugal-squamosal contact: at tips (0), absent 1), broad (2) (Paul, 1984; Holtz, 1998 [2000]).
21. Squamosal contributing to nuchal crest: no (0), yes (1) (Novas, 1989; Sampson et al., 1998).
22. Quadrate foramen: present (0), absent (1) (Novas, 1989).
23. Interorbital region: unossified (0), ossified (1) (Paul, 1988; Sampson et al., 1998).
24. Shape of basisphenoid recess opening: ovoid (0), teardrop (1).
25. Indentation between tubera and basipterygoid processes in lateral view: shallow curve (0), deep notch (1).
26. Median basioccipital fossa ventral to occipital condyle: absent (0), present (1).
27. Basioccipital-basisphenoid suture: oblique (0), transverse (1) in posterior view.
28. Median supraoccipital ridge depth: < (0); ≥ (1) occipital condyle length (Holtz, 1998 [2000]; Carrano et al., 2002).
29. Foramen between supraoccipital and parietal knob: present (0), absent (1).
30. Palatine shape: triradiate (0), tetraradiate (1) (Harris, 1998).
31. Pocket in ectopterygoid flange of pterygoid: absent (0), present (1) (Gauthier and Padian, 1985).

32. Ventral fossa on ectopterygoid: absent (0), present (1), groove (2) (Gauthier and Padian, 1985).
33. External mandibular fenestra size: moderate/small (0), large (1) (Gauthier, 1986; Sampson et al., 1998).
34. Anterior end of external mandibular fenestra: posterior (0), ventral (1) to last dentary tooth (Sereno, 1999).
35. Horizontal shelf on lateral surangular: absent/weak (0), strong (1) (Gauthier, 1986).
36. Posterior edge of splenial: straight (0), curved or notched (1) (Sereno et al., 1994).
37. Dentary-surangular articulation: small notch (0), large socket (1) (Carrano et al., 2002).
38. Mediolateral width of anterior end of dentary: equal to that of posterior part (0), expanded (1).
39. Posteroventral process of dentary: far posterior (0), ventral (1) to poserodorsal process (Sereno, 1999).
40. Anterior serrations cover: all (0), 1/2 to 2/3 (1) of carina in maxillary and posterior dentary teeth (Paul, 1988).
41. Premaxillary tooth carinae: opposite sides (0), on lingual side (1) (Bakker et al., 1988).
42. Posterior end of maxillary tooth row: beneath (0), anterior (1) to orbit (Gauthier and Padian, 1985).
43. Number of maxillary teeth: > 17 (0), 11–17 (1) (Carrano et al., 2002).
44. Dentary tooth count: ≤ 25 (0), 25–29 (1) (Russell and Dong, 1993).
45. Paradental plates: obscured or moderate in height (0), very tall (1) (Carrano et al., 2002).
46. Paradental plates: smooth (0), striated (1) (Sampson et al., 1996).
47. Groove for replacement teeth: present (0), absent (1) (Currie, 1995).
48. Posterior face of anterior presacrals: flat (0), concave (1) (Gauthier, 1986; Carrano et al., 2002).
49. Pleurocoel posterior to parapophysis in anterior presacrals: absent (0), present (1) (Gauthier, 1986; Rowe, 1989).
50. Posterior pleurocoel in anterior presacrals: absent (0), fossa (1), foramen (2) (Gauthier, 1986; Rowe, 1989).
51. Vertebral centrum pneumaticity: absent (0), camerate (1), camellate (2) (Britt, 1993).
52. Axial neural spine: broad (0), invaginated laterally (1) (Molnar et al., 1990).
53. Axial parapophyses: moderate/large (0), reduced/absent (1) (Rowe, 1989).
54. Axial diapophyses: moderate (0), reduced/absent (1) (Rowe, 1989).
55. Axial pleurocoels: absent (0), present (1) (Rowe, 1989).
56. Cervical prezygapophyseal-epipophyseal lamina: absent/weak (0), marked (1) (Coria and Salgado, 1998 [2000]).
57. Cervical prespinal fossa width: narrow (0), broad (1) (Coria and Salgado, 1998 [2000]).
58. Anterior cervical epipophyses: low, blunt (0), long, thin (1), long, thick (2) (Novas, 1993).
59. Anteroposterior length of cervical neural spines: long (0), short (1) (Novas, 1992a).
60. Longest post-axial cervicals: first five (0), last five (1) (Gauthier, 1986; Novas, 1993).
61. Cervical centrum height: < 3 (0), ≥ 3 (1) times centrum length (Russell and Dong, 1993; Sereno, 1999).
62. Shape of dorsal transverse processes: rectangular (0), triangular (1) (Rowe, 1989).
63. Dorsal parapophysis position relative to centrum: close (0), far lateral/pedestal (1) (Currie and Zhao, 1993).
64. Dorsal parapophysis and transverse process: separate (0), connected by lamina (1) (Carrano et al., 2002).
65. Dorsal centrum length: 1–2.5 (0), ≤ 1 (1), ≥ 2.5 (2) times centrum height (Sereno, 1999).
66. Number of sacrals: 2 (0), +2d +1c (1), +3d +1c (2) (Gauthier, 1986; Carrano et al., 2002).
67. Mid-sacral centrum dimensions: normal (0), strongly constricted (1) (Sereno, 1999).
68. Ventral sacral margin: horizontal (0), arched (1) (Sereno, 1999).
69. Sacral spines coalesced and thickened dorsally: no (0); yes (1).
70. Sacral neural spines fused in adults: no (0), yes (1) (Rowe and Gauthier, 1990).
71. Sacral ribs: separate (0), fused together (1) in adults (Rowe and Gauthier, 1990).
72. Caudosacral attachment to ilium: ventral (0), posterodorsal (1) (Sereno, 1999).
73. Sacral rib depth relative to ilium height: ≥ 90% (0), < 85% (1) (Novas, 1992b).
74. Mid-caudal and distal chevrons: straight or gently curved (0), strongly curved (1) (Russell and Dong, 1993).
75. Anterior chevron process: small or absent (0), large (1) (Molnar et al., 1990).
76. Distal expansion of scapular blade: marked (0), weak/absent (1) (Novas, 1992b).
77. Shape of anterodorsal corner of distal scapular blade: rounded (0), acuminate (1).
78. Scapular blade height/width ratio: < (0), ≥ (1) 8.0 (Paul, 1984; Gauthier and Padian, 1985).
79. Dorsal lip of scapular glenoid: moderate (0), marked (1).
80. Posteroventral coracoid process: moderate (0), well developed (1) (Sereno et al., 1996).
81. Spacing between ventral glenoid and posteroventral coracoid process: ≥ (0), ≤ (1) dorsoventral depth of glenoid.
82. Humerus length: ≥ (0), < (1) 1/3 femur length (Novas, 1993).
83. Humeral head shape: elongate (0), globular (1) (Carrano et al., 2002).
84. Distal humeral condyles: rounded (0), flattened (1) (Carrano et al., 2002)
85. Humeral shaft torsion: absent (0), present (1) (Holtz, 1998 [2000]).
86. Humeral internal tuberosity: low/rounded (0), hypertrophied (1) (Russell and Dong, 1993).
87. Ulnar olecranon process: absent (0), present (1) (Sereno, 1999).
88. Distal carpals 1+2 fused in adults: no (0), yes (1) (Gauthier and Padian, 1985).
89. Extent of metacarpal I contact with metacarpal II: <1/3 (0), 1/2 (1) metacarpal I shaft length (Gauthier, 1986; Harris, 1998).
90. Manus length: < (0), ≥ (1) length of arm + forearm (Gauthier, 1986; Sereno, 1999).
91. Manus digit IV: present (0), absent (1) (Paul, 1984; Gauthier and Padian, 1985).
92. Manus digit V: present (0), absent (1) (Paul, 1984; Gauthier and Padian, 1985).
93. Metacarpal I length: ≥ (0), < (1) 50% of metacarpal II length (Gauthier and Padian, 1985).
94. Longest digit in manus: III (0), II (1) (Novas, 1993).
95. Metacarpal III width: > (0), < (1) 50% of metacarpal II width (Gauthier, 1986).
96. Fusion between pelvic elements in adults: absent (0), present (1) (Gauthier, 1986).
97. Posterior width of iliac brevis fossa: narrow (0), broad (1) (Molnar et al., 1990; Sereno et al., 1994).
98. Iliac supraacetabular crest and lateral edge of brevis shelf: gap between (0), continuous (1).
99. Iliac supraacetabular crest: large/pendant (0), reduced (1) (Gauthier and Padian, 1985).
100. Iliac pubic peduncle orientation: mostly ventral (0), mostly anterior (1) (Sereno, 1999).
101. Iliac M. iliofemoralis internus fossa: small (0), large, onto pubic peduncle (1) (Novas, 1991; Sereno, 1999).
102. Ilium-pubis articulation: ≤ (0), > (1) ilium-ischium articulation (Sereno et al., 1994).
103. Iliac ischial peduncle: rounded (0), acuminate (1).
104. Iliac pubic peduncle length: < (0), ≥ (1) twice width (Sereno et al., 1994).
105. Anteroventral iliac lobe: absent (0), present (1) (Sereno et al., 1994).
106. Shape of dorsal iliac margin: convex (0), straight (1) (Carrano et al., 2002).
107. Shape of posterior iliac margin: convex (0), concave (1) (Sereno et al., 1994).
108. Pubic apices: separate (0), contacting (1) (Holtz, 1998 [2000]; Rauhut, 2000, 2003).
109. Pubic symphysis: marginal (0), broad (1) (Sereno, 1999).
110. Pubic obturator opening: absent (0), closed (1), notch (2) (Sereno et al., 1994; Harris, 1998).
111. Pubic fenestra ventral to obturator foramen: absent (0), present (1) (Rowe, 1989).
112. Puboischial fenestra: closed (0), broadly open (1) (Sereno et al., 1998).

113. Distal pubis expanded posteriorly: no (0), yes (1) (Gauthier and Padian, 1985).
114. Ilium-pubis contact: undulating (0), peg-in-socket (1) (Carrano et al., 2002).
115. Proximal pubic shaft: straight (0), ventrally curved (1) (Rowe, 1989).
116. Notch ventral to ischial obturator process: absent (0), present (1) (Rauhut, 2000).
117. Shape of distal ischia: rounded (0), expanded/triangular (1), tapered (2)
118. Distal ischia: separate (0), fused (1) (Forster, 1999).
119. Cross-sectional shape of paired ischial midshafts: oval (0), heart-shaped (1), rectangular (2) (Sereno, 1999).
120. Ischial antitrochanter: large and notched (0), reduced (1) (Sereno, 1999).
121. Relative lengths of pubis and ischium: subequal (0), pubis much longer (1) (Gauthier and Padian, 1985).
122. Femoral head orientation: 45° anteromedial (0), medial (1) (Bonaparte, 1991).
123. Dimorphism in femoral morphology: absent (0), present (1) (Rowe and Gauthier, 1990).
124. Femoral head angle: ventral (0), horizontal (1) (Molnar et al., 1990).
125. Anterior M. iliofemoralis insertion: shelf (0), low lesser trochanter (1), aliform lesser trochanter (2) (Gauthier, 1986; Carrano et al., 2002).
126. Posterior M. iliofemoralis insertion: shelf (0), mound (1) (Gauthier, 1986; Carrano et al., 2002).
127. Femoral entepicondyle: rounded (0), ridge (1) (Forster, 1999).
128. Femoral tibiofibularis crest orientation in posterior view: longitudinal (0), oblique (1).
129. Tibial lateral malleolus: backs astragalus (0), overlaps calcaneum (1) (Sereno et al., 1994).
130. Tibial lateral malleolus edge: smoothly curved (0), tabular notch (1) (Sereno, 1999).
131. Distal tibial cnemial crest: rounded (0), expanded proximodistally (1) (Paul, 1984; Novas, 1992b).
132. Anteromedial buttress on distal tibia for astragalus: absent (= ventrally facing) (0), marked (= anteriorly facing) (1) (Molnar et al., 1996).
133. Size of M. iliofibularis tubercle on fibula: moderate (0), large (1) (Rauhut, 2000).
134. Orientation of astragalar condyles: ventral (0), anteroventral (1) (Sereno et al., 1994).
135. Astragalar ascending process: blocky (0), laminar (1) (Sereno et al., 1994).
136. Astragalar ascending process height: < (0), ≥ (1) depth of astragalar body (Welles and Long, 1974).
137. Anterior horizontal groove on astragalus: absent or faint (0), marked (1) (Welles and Long, 1974).
138. Round fossa at base of astragalar ascending process: absent (0), small (1), large (2) (Welles and Long, 1974; Holtz, 1994).
139. Astragalus facet for fibula: large and dorsal (0), reduced and lateral (1) (Sereno et al., 1994).
140. Astragalus and calcaneum fused in adults: no (0), yes (1) (Welles and Long, 1974; Rowe, 1989).
141. Metatarsal I length: ≥ (0), < (1) 50% metatarsal II length (Gauthier and Padian, 1985; Novas, 1996).
142. Proximal metatarsal III shape: rectangular (0), notched (1) (Paul, 1984; Sereno et al., 1996).
143. Metatarsal IV distal end: broader than tall (0), taller than broad (1) (Sereno, 1999).
144. Metatarsal V distal end: articular (0), non-articular (1) (Gauthier, 1986).
145. Metatarsal V length: > (0), < (1) 50% metatarsal IV length (Gauthier, 1986; Harris, 1998).

APPENDIX 2

Taxon-character matrix used in phylogenetic analyses. 0, 1, 2 = character states; ? = could not be observed. Character states in parentheses indicate uncertainties.

Allosaurus
01021 00000 00100 11112 00000 10011 11001 10001 11101 00110 11001
00211 00001 10000 01111 10100 00001 11111 11111 00010 11111 00112
01100 10001 01012 10010 01011 11210 11111

Carnotaurus
00201 00100 11111 11021 111?0 01111 ??111 1101? 10101 11112 21001
11211 01111 21111 011?0 10011 01111 00??0 ????? 11100 010?1 11111
001?0 11?00 00?01 111?? 1?1?? ????1 ?????

Ceratosaurus
01211 00000 10100 11011 01111 00111 12001 1?0?0 10101 01112 21001
00211 01101 201?1 01100 10011 01001 01?10 01??? 11100 01001 01111
00110 11100 0010(01) (01)1110 11111 11211 ?01??

Coelophysis
11100 11010 00000 ?1001 000?1 ??01? 0?000 0000? 00010 00011 10110
00101 11002 10001 11100 01000 10000 0(01)111 01010 11001 00000 11001
10001 10010 10101 (01)0101 01000 0(01)101 10110

Dilophosaurus
11101 01001 00000 1101? 00001 10010 ??000 00100 00&1100 00111 10110
00001 11100 10011 11100 01000 10001 00?11 01010 11001 00000 00101
?0000 10000 1010(01) (01)(01)001 01000 11101 10110

Elaphrosaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ??011 (12)????
00?01 11102 21111 011?? ???11 10111 0???? ????? 01100 01001 111?(12)
???00 11100 ?0?01 11?10 0110? ?0??1 ?0???

Eoraptor
01000 10100 00000 00000 00?0? ?0000 10000 00001 00000 ?0000 0????
00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 001?1
00000 000?0 00?00 00000 00000 00000 00000

Gojirasaurus
????? ????? ????? ????? ????? ????? ????? ????1 ????? ????? ?????
????? ?1000 ????? ???0? 0100? ????? ????? ????? ????1 ????? ??101
1?001 ????? ????? ???0? 01??? ????? ?????

Herrerasaurus
01000 00100 00000 00100 000?1 00000 00100 00001 00000 00000 00010
00000 0000? 00000 00000 1000? 00000 00001 00000 00000 00000 00100
00100 00000 00000 00000 00000 10000 00000

Liliensternus
?1??? 1101? ???0? ???0? ?0??? ??0?? 1???? 0?1?? ???00 00011 1????
0010? 1?000 1000? 111?? 01000 10000 00?11 010?? ?1001 00000 1100(12)
?0001 ?0010 10?01 10001 01000 00101 ?01??

Majungatholus
00201 00100 11111 11021 11110 01111 12111 11010 10101 11112 21001
11211 01111 ?1?11 01100 10011 0?111 0???? ????? ?1100 01001 11???
???1? ????? ?0??1 11?10 11111 11211 ?01??

Ornitholestes
01021 00000 ?0?00 ?1112 0???? ??01? ??000 ?000? 11100 ??110 (12)????
00?0? 0?000 100?? 01111 ????? ?0001 1??1? 11111 00010 11111 00??2
01?00 00001 11?12 100?? ??0?? ????? ?11??

Procompsognathus
????? ????? ????? ????? ????? ????? ????? ????? ????? ???1? (12)????
?0101 11??2 ????? ???00 ????? ????? ????? ?1??? ???0? ????? ??0?1
1?001 ????? ?0??? 00?0? 0?0?0 ????? ?????

Sarcosaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ??0?0 ????? ?11?? ????? ????? ????? ????? 11001 00000 00??1
?0??0 ????? ?0??1 00??? ????? ????? ?????

Segisaurus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ??0?0 ????? ?11?? ????? ????? ????? ????? 11001 00000 00??1
?0??0 ????? ?0??1 00??? ????? ????? ?????

Syntarsus
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ?1??2 100?? ?1100 0?10? ?0001 ?1??? ????? 1??0? ????? ??001
100?1 ?012? 1???1 00??? 0?0?? ????? 1?111

Zupaysaurus
?1?11 11001 00000 ?1012 00??? ??01? ??000 ?010? ?000? ??0?? ?0???
????? 1???? ????? ????? ????? ????? ????? ????? ????? ????? ?????
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