

A JUVENILE SPECIMEN OF THE SAUROPOD DINOSAUR *ALAMOSAURUS SANJUANENSIS* FROM THE UPPER CRETACEOUS OF BIG BEND NATIONAL PARK, TEXAS

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ABSTRACT—A juvenile specimen of the titanosaurid sauropod *Alamosaurus sanjuanensis*, recovered from just below the Cretaceous/Tertiary boundary horizon in Big Bend National Park, Texas, is from an individual less than half the size of adult specimens referred to this species. The disarticulated skeleton was preserved in deposits of a shallow flood-plain pond and includes elements not previously described, allowing for an improved diagnosis for this species. The elongate opisthocoelous cervical vertebrae have non-bifid posteriorly deflected neural spines with deep postspinal fossae. The dorsal vertebrae have wide spatulate neural spines with strong prespinal laminae, and lack hyposphene-hypantrum articulations. *Alamosaurus sanjuanensis* exhibits a unique morphology of the ischium, evident even in this juvenile specimen. Comparison with other titanosaurid species suggests that *A. sanjuanensis* is most closely related to an unnamed titanosaur from Peiropolis, Brazil and *Neuquensaurus australis* from Argentina.

INTRODUCTION

REMAINS OF the sauropod dinosaur *Alamosaurus sanjuanensis* are the most common fossils found in continental strata of latest Cretaceous (Middle to Late Maastrichtian) age in the southwestern United States (Lehman, 1987). Nevertheless, this species remains poorly known because most specimens consist of isolated limb and girdle elements, or caudal vertebrae; and several partial skeletons that have been collected have yet to be completely prepared for study. The presacral vertebrae of *A. sanjuanensis* have not been described, and these are among the most important skeletal elements in assessing phylogenetic relationships among sauropods.

Moreover, *Alamosaurus sanjuanensis* represents a widespread but enigmatic group of sauropod dinosaurs included among the Titanosauridae of Lydekker (1885) or more broadly the Titanosauria of Bonaparte and Coria (1993). Until Powell (1992) published a description of *Saltasaurus loricatus*, *Alamosaurus sanjuanensis* was one of only a few titanosaurid sauropods known from multiple skeletal elements. As the youngest North American sauropod, the osteology of *A. sanjuanensis* needs to be better documented for purposes of comparison with other species. This is especially important considering the discovery of new titanosaurid species in recent years (e.g., Jacobs et al., 1993; Jain and Bandyopadhyay, 1997).

Alamosaurus sanjuanensis was first described by C. W. Gilmore in 1922. The type specimen was collected from the Ojo Alamo Sandstone (now part of the Naashoibito Member of the Kirtland Shale, Kues, et al., 1980) in New Mexico, and consists of a left scapula (USNM 10486) found near a right ischium, which was designated a paratype (USNM 10487). In 1946, Gilmore described a more complete specimen collected from the North Horn Formation in Utah (USNM 15560). This specimen consists of a nearly complete tail, the right forelimb complete through the metacarpals, both sternal plates, and both ischia. In 1940, B. Brown (1941) collected a vertebra from the Javelina Formation in Texas, and from the 1960s to the present time W. Langston, Jr. collected numerous specimens from the same deposits, a few of which were described by D. Lawson (1972). Of

the many fragmentary specimens that have been referred to *A. sanjuanensis*, few have been adequately described. Remains of *A. sanjuanensis* have been collected from sites throughout the southwestern United States and this species characterizes a unique southern latitude latest Cretaceous fauna (distribution reviewed by Lehman, 1987).

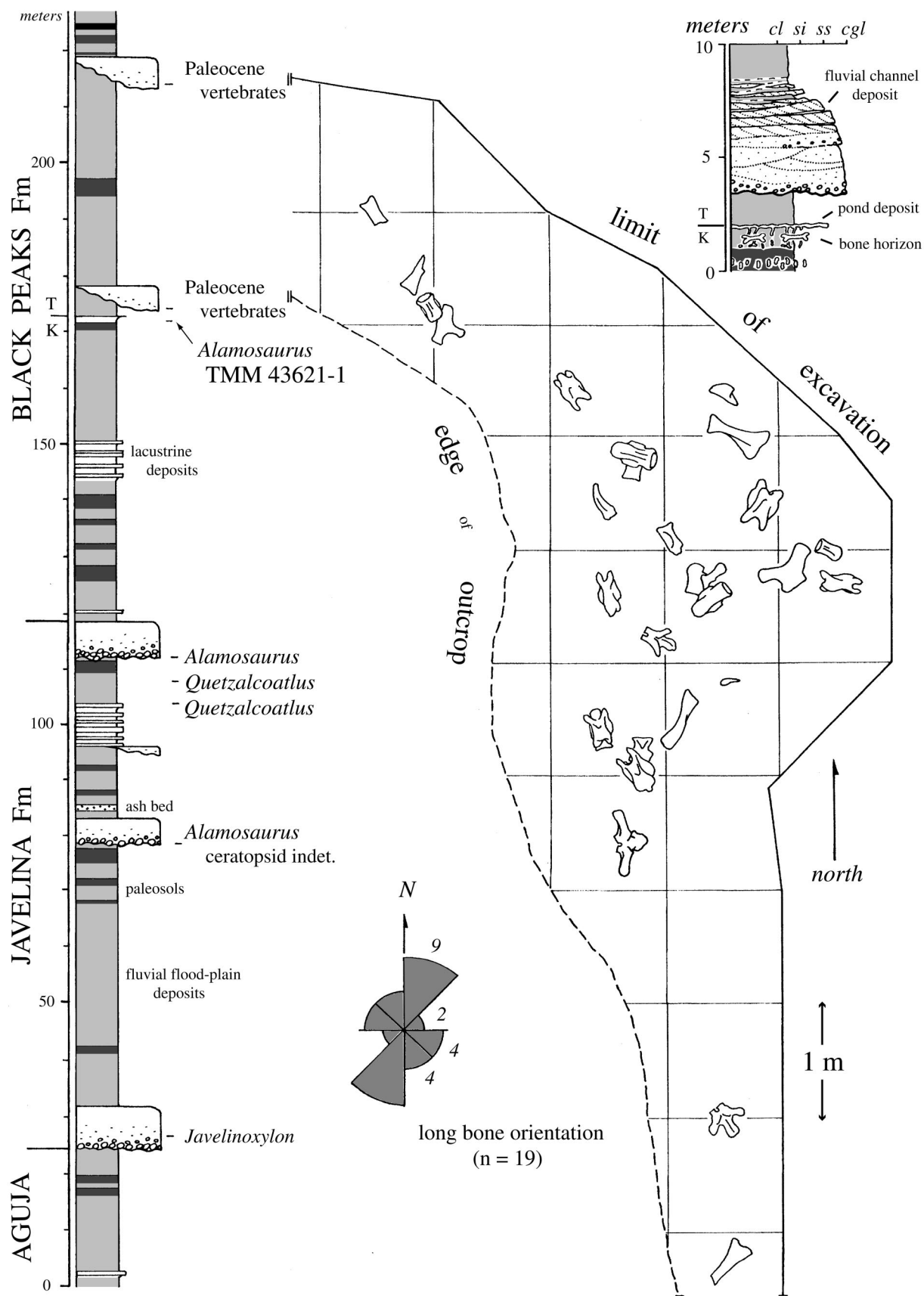
The purpose of this paper is to describe a juvenile specimen of *Alamosaurus sanjuanensis* (TMM 43621-1). This specimen was recovered from the Black Peaks Formation, immediately above the contact with the underlying Javelina Formation in Big Bend National Park of southwestern Texas. The collection site is just below the Cretaceous/Tertiary boundary horizon, and is stratigraphically the highest dinosaur-bearing locality yet known in this region (Fig. 1). TMM 43621-1 includes skeletal elements that have not been previously described for *A. sanjuanensis*, and thus provides significant new osteological information. The new material further supports the validity of *A. sanjuanensis*, and allows for improved comparison with other titanosaurid sauropods, as well as an opportunity to provide a full skeletal reconstruction for this species.

TAPHONOMY

Strata of the Javelina and Black Peaks Formations consist primarily of fluvial channel and overbank flood-plain facies (Lehman, 1989; Straight, 1996; Coulson, 1998). The sauropod remains were preserved in deposits of a flood-plain pond or shallow lake; an interpretation based on the presence of a thin pellicular limestone breccia layer with remains of freshwater organisms (including amiid and lepisosteid fishes, charophyte algae, and gastropods) just above the bone-bearing horizon. The bones occur in a dark olive-gray calcareous mudstone layer several decimeters below the thin limestone bed. Large cylindrical smooth-walled burrows, filled with pellicular microcrystalline calcite, descend from the limestone layer and penetrate through the underlying mudstone, surrounding the bones and ramifying beneath the bone-bearing horizon (Fig. 1).

The specimen described herein (TMM 43621-1) comprises part

FIGURE 1—Stratigraphic section (modified from Straight, 1996) showing position of juvenile *Alamosaurus sanjuanensis* site (TMM 43621-1), north of Grapevine Hills in Big Bend National Park, Texas; detailed section at the site showing bone-bearing level relative to the Cretaceous/Tertiary (K/T) boundary; quarry diagram showing primary bone concentration (excavated area continues to north and south of area shown); orientation of long axes of bones collected in place.



of a juvenile skeleton of *Alamosaurus* that had completely disarticulated prior to burial (Fig. 1). Although none of the skeletal elements were preserved in articulation, they were recovered from a single stratigraphic horizon within 20 m of each other, and are compatible in size with no duplicated elements, and with no associated bones of other dinosaurs. Hence, it is likely that these are the remains of a single individual. All of the preserved paired skeletal elements are from the left side of the body except for parts of the right tibia and right fibula, which were found 5 m south of the main bone accumulation. The bones had been subjected to a varied degree of pre-burial weathering. Some elements had been exposed at the surface for an extended time prior to burial, resulting in fragmentation and loss of the external cortical bone; other bones had been buried quickly, and so have delicate bone laminae preserved. There is no direct evidence, such as bite marks or shed carnivore teeth, to indicate that the skeleton had been dismembered by a predator or scavenger, but this seems likely nonetheless. Following burial, most of the bones were distorted by compaction of the sediment matrix, and some were broken into pieces along smooth fractures, with the parts remaining near their original position and orientation. The remains were entombed in fine-grained mudstone, indicating that burial occurred near the place of death. The preservation of the delicate neural arch laminae in cervical and dorsal vertebrae further indicates that the bones underwent little transport. However, the completely disarticulated nature of the skeleton necessitates that some form of pre-burial dispersal occurred.

The orientation of long bones in situ suggests that a weak current may have affected the remains prior to burial. The axes of long bones exhibit a crude bimodal orientation, with the two directions roughly perpendicular to each other (Fig. 1). Partially submerged bones easily affected by a weak current tend to have their long axes oriented parallel to flow, while bones just rolled by the current may have their long axes oriented perpendicular to flow (e.g., Voorhies, 1969). The lack of small, easily transported elements in the collection also suggests current activity, as such elements may be quickly winnowed out of a bone assemblage. The cervical neural arches were all found with their dorsal side facing up, and the dorsal neural arches were all found with their anterior side facing up. These positions may represent the most stable current orientation for these elements.

Most of the bones are covered in a thin layer of concretionary microcrystalline calcite, and in part the bones are pseudomorphically replaced by calcite. Burrows, filled with similar pelloidal microcrystalline calcite, also surround and invade the bones. The pustular and pelletal texture of this calcite suggests that it represents an algal or microbial precipitate, deposited while the bones lay in the lake water or shortly after they were buried. Calcareous charophyte algal gyrogonites are found throughout the clay matrix surrounding the bones, and in the overlying limestone layer. However, many of the bones are further surrounded by an additional layer of radial-fibrous calcite, and this appears to represent a later diagenetic precipitate.

This young animal probably died in a shallow nearshore lake environment, with its body mired on its left side in mud, and either partially submerged or just onshore. The skeleton disarticulated, and most of the right side of the skeleton was removed or destroyed. Weak currents affected the remaining bones, winnowing out the easily transported elements and reorienting those that remained. Those bones not completely buried were exposed on the surface for a period of time, resulting in deterioration of the outer surfaces of the bone. It is likely that the lake waters were ephemeral, in accordance with the calcareous flood-plain paleosols in the surrounding strata that indicate semi-arid climatic conditions in the Big Bend region during Late Cretaceous time (Lehman, 1989, 1990).

Institutional abbreviations.—The following institutional abbreviations are used herein: DGM, Divisao de Geologia y Minerologia, Direccion Nacional of Producao Minerologia, Rio de Janeiro, Brazil; MCT, Earth Science Museum, Direccion Nacional of Producao Minerologia, Rio de Janeiro, Brazil; PMU, Paleontological Institute, Uppsala University, Sweden; TMM, Texas Memorial Museum, Austin, Texas; TTU, Texas Tech University Museum, Lubbock; UNM, University of New Mexico, Albuquerque; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UTEP, Centennial Museum of the University of Texas at El Paso.

SYSTEMATIC PALEONTOLOGY

Family TITANOSAURIDAE Lydekker, 1885

Genus ALAMOSAURUS Gilmore, 1922

ALAMOSAURUS SANJUANENSIS Gilmore, 1922

Figures 2–11

Emended diagnosis.—Cervical vertebrae elongate with weak pleurocoels, short pedicels, non-bifid neural spines deflected posteriorly, strong spinozygapophyseal laminae, deep postspinal fossae, and postzygapophyses attached directly to the posterior base of the neural spine; anterior and middle dorsal vertebrae with short pedicels, transversely expanded spatulate neural spines inclined posteriorly, with prominent prespinal laminae but no postspinal laminae, and lacking hyposphene-hypantrum articulations; the first caudal centrum is biconvex, caudal vertebrae with procoelous centra throughout, prominent acromion process of scapula; ischium with dorsoventrally extended puboischial contact and short distal process.

Types.—The holotype of *Alamosaurus sanjuanensis* consists of a left scapula (USNM 10486). A right ischium (USNM 10487) collected at the same time at the same locality was designated a paratype, because it was uncertain whether it pertained to the same individual as the scapula (Gilmore, 1922). Later workers designated additional fragmentary sauropod bones as topotypes that had been collected in the vicinity of the type locality (Kues et al., 1980; Mateer, 1976, 1981; Lucas et al., 1987). These include parts of a right ilium and sacral vertebrae (PMU.R.280 and 281), a caudal vertebra (USNM 15658), part of a right femur (UNM FKK-033), and several teeth (UNM FKK-029 and 034).

Other material examined.—TMM 43621-1, a partial skeleton of a juvenile individual. Comparable skeletal elements are less than half the size of those associated with the type specimens, and others assigned to *Alamosaurus* from the same region (e.g., humerus length = 605 mm, versus 1360 mm for the humerus of USNM 15560, and 1503 mm for TMM 41541-1). Apart from its small size, the lack of coossification between the neural arches and their corresponding centra, and the free sacral ribs indicates that these are the remains of an immature animal. The morphology of its skeletal elements may therefore reflect in part the juvenile condition of the specimen, and may not necessarily be diagnostic of characters expressed in adult individuals.

Concretionary calcite that coats the bones of TMM 43621-1 is difficult to remove, and complete preparation of the specimen will require years of additional effort. Nevertheless, the skeletal morphology is readily apparent. Measurements of the bones, however, in some cases may exceed the actual dimensions by several millimeters. The illustrations given here show only those features that are anatomically important; adhering masses of concretionary calcite are not shown. Measurements of the specimen are given in Appendix I.

Additional referred specimens examined include: TMM 40597, 41060, 41063, 41398, 41450, 41541, 42495, 42595, 43598, 43599, 43600; TTU 542, 546; UTEP P25.

Occurrence.—TMM 43621-1 was recovered from the lower

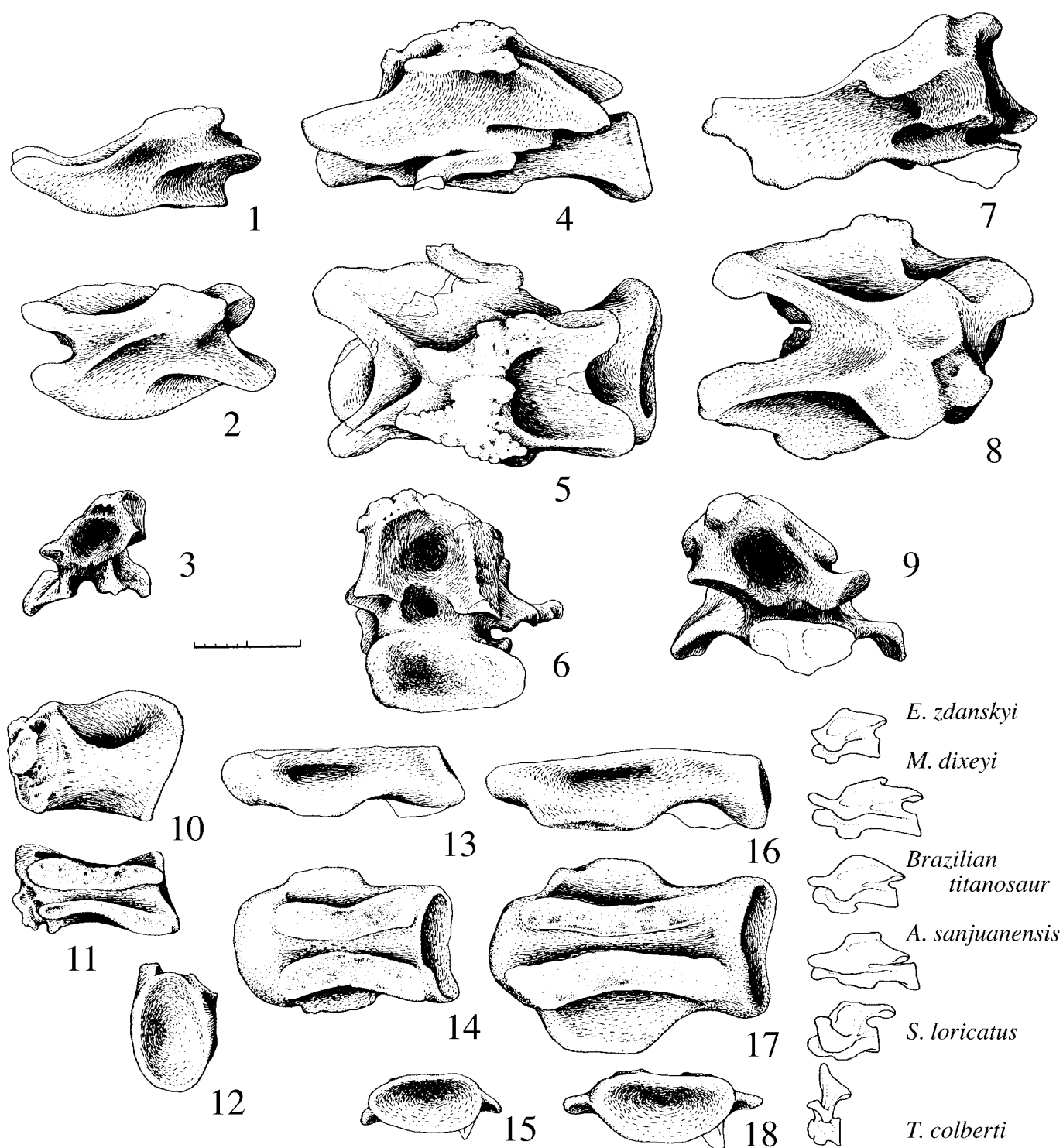


FIGURE 2—*Alamosaurus sanjuanensis* (TMM 43621-1), cervical vertebrae. Neural arch of anterior cervical vertebra in 1, lateral; 2, dorsal; and 3, posterior view. Mid cervical vertebra in 4, lateral (image reversed); 5, dorsal; and 6, posterior view. Posterior cervical vertebra in 7, lateral; 8, dorsal; and 9, posterior view. Centrum of axis vertebra in 10, lateral; 11, dorsal; and 12, posterior view. Centrum of mid cervical vertebra in 13, lateral; 14, dorsal; and 15, posterior view. Centrum of posterior cervical vertebra in 16, lateral; 17, dorsal; and 18, posterior view. Scale bar is 10 cm. Inset compares mid cervical vertebrae in lateral view (not to scale) of *Euhelopus zdanskyi*, *Malawisaurus dixeyi*, an unnamed titanosaur from Peiropolis, Brazil, *Alamosaurus sanjuanensis*, *Saltasaurus loricatus*, and *Titanosaurus colberti*; see Figure 8 for citations.

part of the Black Peaks Formation, approximately 50 m above the contact with the Javelina Formation, north of Grapevine Hills in Big Bend National Park, Texas (field number "NGH 10-12," location map and section given by Straight, 1996). Exact locality information is available at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, Austin, Texas. The Cretaceous/Tertiary boundary is no more than 2 m above the *Alamosaurus* bone horizon, based on the presence of Paleocene vertebrates recovered higher in the section (Fig. 1). This site is stratigraphically the highest dinosaur-bearing locality thus far known in the Big Bend region.

DESCRIPTION

Skull.—No cranial elements are preserved with this specimen, and none have yet been described for *Alamosaurus*. A few isolated teeth have been referred to *A. sanjuanensis* (Kues et al., 1980), and several similar rod shaped tooth fragments, 6 to 8 mm in diameter, were recovered with the present specimen.

Cervical vertebrae.—Parts of at least seven or eight cervical vertebrae are preserved; one is nearly complete, six centra and five neural arches were found separated (Fig. 2). The disarticulated neural arches cannot be confidently paired with their corresponding centra. Because they were not preserved in articulation, the cervical vertebrae are arranged for purpose of description from the axis (second cervical) through the eighth, interpreting their position by gradual increase in length (see Appendix). The presumed seventh vertebra is preserved with the neural arch attached.

The cervical centra are composed throughout of open, coarsely cancellous spongy bone, with only a very thin and discontinuous external layer of finished lamellar bone. The centra are strongly opisthocelous and dorsoventrally compressed. The dorsoventral flattening is at least in part a result of post-burial compression because two of the centra are laterally compressed instead (Fig. 2). On most centra, the ventral lip of the posterior cup-like articulation extends farther posteriorly than the dorsal lip. This is in accordance with habitual dorsal curvature of the neck in life, but may also have resulted in part from post-burial compression of the centra. The sutural surfaces for the neural arch pedicels are long, constricted medially, and very low; hence, the walls of the neural canal are formed almost entirely by the neural arch. The parapophyses are broad, elongate, wing-like projections that protrude ventrolaterally from the anteromedial margin of each centrum. Parapophyses are poorly differentiated on the shortest, presumed anteriormost of the cervical centra, but are more distinct, elongate, and extend farther laterally in the longer, presumed middle cervical centra. Two of the centra have accessory flanges along one side of their posteroventral surface, although these may be pathological or even an artifact of poor preservation (Fig. 2.13, 2.16). The centra have shallow, poorly developed pleurocoels along their lateral margins, a characteristic considered synapomorphic for titanosaurs (Wilson and Sereno, 1998). The pleurocoels do not invade the parapophyses and they lack septal partitions. The axis possesses an ovate odontoid process for articulation with the preceding atlas. The ventral surfaces of the centra are slightly concave.

The neural arches of sauropod vertebrae are comprised of thin laminae of bone connecting the zygapophyses, diapophyses, and neural spine. The descriptive terminology for these laminae was developed by Osborn (1899) and Janensch (1929), and reviewed by McIntosh (1990) and Wilson and Sereno (1998). The convention used herein is that recently summarized by Wilson (1999). In the present specimen, the neural arches of the cervical vertebrae are low and comparatively simple, lacking deep excavations between the laminae, although this may also be in part due to its juvenile condition. In most of the preserved neural arches, the

neural spines are distorted from their normal central position so that they are inclined laterally to some degree. The neural spines are single (non-bifid), though they are widened transversely with protruding lateral flanges. The neural spines are deflected posteriorly to overlie the postzygapophyses, and their tips are drawn out posteriorly to form a short posteriorly directed knob, except in the longest (?seventh) cervical vertebra, in which the neural spine is more centrally positioned (Fig. 2.4). This change in orientation of the neural spine is observed in the cervical series of many sauropods beginning at the seventh to ninth cervical position. The neural spine orientation, combined with the length of this vertebra relative to the other cervical neural arches, supports placement of this specimen posterior to the sixth cervical vertebra. In all of the preserved cervical vertebrae, spinoprezygapophyseal and spinopostzygapophyseal laminae are very well developed, with those arising from the postzygapophyses enclosing a deep fossa on the posterior face of the neural spine. The prezygapophyses project anteriorly beyond the base of the neural arch and are connected transversely by a well developed intraprezygapophyseal lamina. The zygapophyses are not highly elevated above the base of the neural arch, as they are in some sauropods (e.g., *Apatosaurus excelsus*; see Ostrom and McIntosh, 1966, pl. 14); hence, the centroprezygapophyseal and centropostzygapophyseal laminae are poorly developed.

The diapophyses are broad, low, and not set apart from their connecting laminae. Together with the wide prezygodiapophyseal laminae and posterior centrodiapophyseal laminae, the diapophyses form expanded, ventrally deflected sheets of bone. Postzygodiapophyseal laminae are weakly developed. In the seventh vertebra, part of the tuberculum of the right cervical rib is attached to the right diapophysis (Fig. 2.5). Otherwise, only detached fragments of cervical ribs were found.

Dorsal vertebrae.—Parts of at least six or seven dorsal vertebrae are preserved (Figs. 3-5). These consist of one vertebral centrum and four neural arches, along with parts of neural spines and transverse processes belonging to at least two other vertebrae.

The single dorsal centrum is not well preserved, but is short and dorsoventrally compressed, probably due largely to post-burial deformation (Fig. 4.4). The centrum has well defined pleurocoels that are not, however, deeply invaginated and do not excavate the entire body of the centrum as they do in some sauropods (e.g., *Camarasaurus grandis*; see Ostrom and McIntosh, 1966, pl. 23). As in the cervical vertebrae, sutural surfaces for the neural arch pedicels are barely elevated above the dorsal surface of the centrum, and so the floor of the neural canal is only shallowly impressed. The ventral surface of the centrum is mildly concave. In contrast to the cervical vertebral centra, the dorsal centrum is shorter and more mildly opisthocelous.

The four preserved neural arches of dorsal vertebrae exhibit significant variation in their morphology, indicating that they come from different regions of the back. A presumed anterior dorsal vertebra is larger than the others, with a broad neural spine and very elongate, laterally directed diapophyses, and with no parapophyses on the neural arch (Fig. 3). Such vertebrae are typical for the first and second dorsal vertebrae in many sauropods (e.g., *Atlantosaurus immanus*; see Ostrom and McIntosh, 1966, pl. 16). Unlike the middle and posterior dorsal vertebrae, this one has prezygapophyses that extend markedly forward from the base of the neural arch, well developed prezygodiapophyseal and postzygodiapophyseal laminae, and only a weak prespinal lamina. In these ways this vertebra resembles the posterior cervical vertebrae described above. An anterior dorsal vertebra (TMM 41398-1) from an adult specimen referred to *Alamosaurus*, recovered from a nearby locality, is similar in having a weak prespinal lamina and forwardly extended prezygapophyses, but differs in having a more transversely expanded neural spine with protruding lateral flanges.

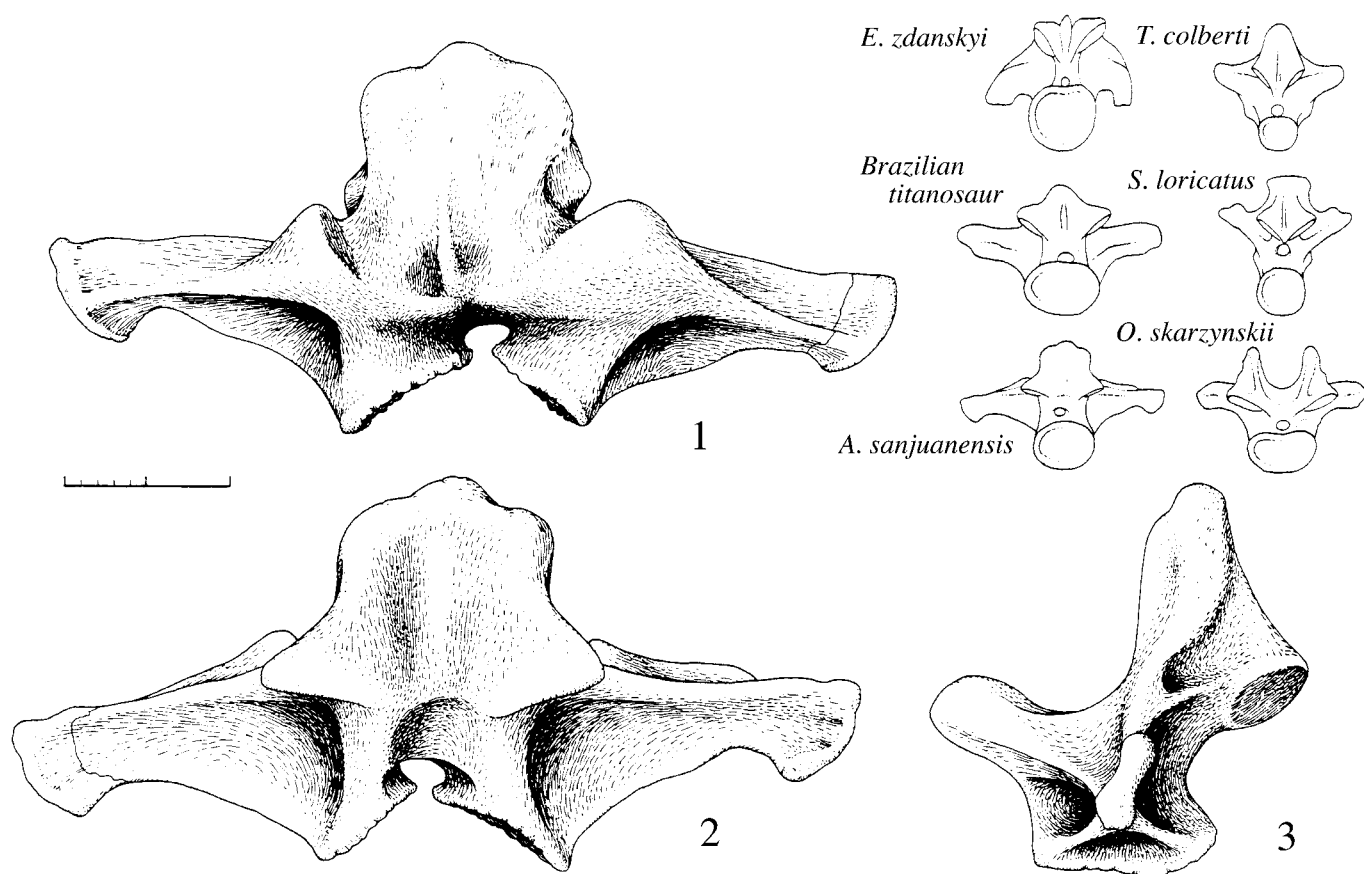


FIGURE 3—*Alamosaurus sanjuanensis* (TMM 43621-1), neural arch of anterior dorsal vertebra in 1, anterior; 2, posterior; and 3, left lateral view. Scale bar is 10 cm. Inset compares anterior dorsal vertebrae in posterior view (not to scale) of *Euhelopus zdanskyi*, an unnamed titanosaur from Peiropolis, Brazil, *Alamosaurus sanjuanensis*, *Opisthocoelicaudia skarzynskii*, *Saltasaurus loricatus*, and *Titanosaurus colberti*; see Figure 8 for citations.

Two presumed middle dorsal vertebrae have transverse processes directed posterolaterally with distinct diapophyses and parapophyses lying in an anteriorly inclined plane, and posteriorly deflected neural spines (Fig. 4). The tips of the neural spines in these vertebrae extend posteriorly beyond the limits of the postzygapophyses. The neural arches of the two preserved middle dorsal vertebrae are nearly identical in form, and they were probably adjacent to one another in the dorsal series. Part of a third neural arch resembles these, but has a more elevated transverse process. Such vertebrae are typical of the third through eighth dorsal vertebrae in other titanosaurid sauropods. They are similar to the middle dorsal vertebrae in an adult specimen (TMM 41541-1) referred to *Alamosaurus*, where; however, the neural spines are more pyramidal in form, with protruding lateral flanges.

One presumed posterior dorsal vertebra has transverse processes directed dorsolaterally, with distinct diapophyses and parapophyses lying in a vertical plane, and an erect neural spine (Fig. 5). In this vertebra, the tip of the neural spine lies directly over the base of the neural arch. A preserved fragment of another neural arch is similar to this one; however, with the parapophyses slightly more elevated. Such vertebrae are typical of the ninth and tenth dorsal vertebrae in other titanosaurid sauropods (e.g., Powell, 1986, 1987).

In all of the dorsal vertebrae, the neural arches are comparatively simple, and lack deep or partitioned excavations between the zygapophyseal and diapophyseal laminae. The neural canal is

almost entirely surrounded by the neural arch, unlike the condition in some sauropods (e.g., *Camarasaurus grandis*; see Ostrom and McIntosh, 1966, pl. 23) where the sutural pedicels arising from the centra nearly or entirely enclose the neural canal. The base of the neural arch is also relatively short, with the zygapophyses positioned just above the neural canal, unlike in some sauropods where the pedicels of the neural arch are dorsoventrally elongated (e.g., *Camarasaurus grandis*; see Ostrom and McIntosh, 1966, pl. 23). Except in the presumed anterior dorsal vertebra, the zygapophyses do not project far beyond the base of the neural arch. Spinopostzygapophyseal laminae are well developed, and enclose a fossa that deepens ventrally on the posterior face of the neural spine. Distinct hyposphene/hypantrum articulations are absent; however, a vertical lamina of bone descending between the postzygapophyses and a corresponding notch between the prezygapophyses may represent the rudimentary (or vestigial) form of these features in the middle and posterior dorsal vertebrae (Fig. 5.1, 5.2).

The neural spine is single (non-bifid), broad transversely, and spatulate in anterior and middle dorsal vertebrae with protruding lateral flanges as in the cervical vertebrae. The neural spines in posterior dorsal vertebrae lack distinct lateral projections. The prespinal lamina is very well developed in middle and posterior dorsal vertebrae, but the postspinal lamina is absent or nearly so. Strong spinodiapophyseal laminae extend from the posterolateral faces of the neural spine to the diapophyses.

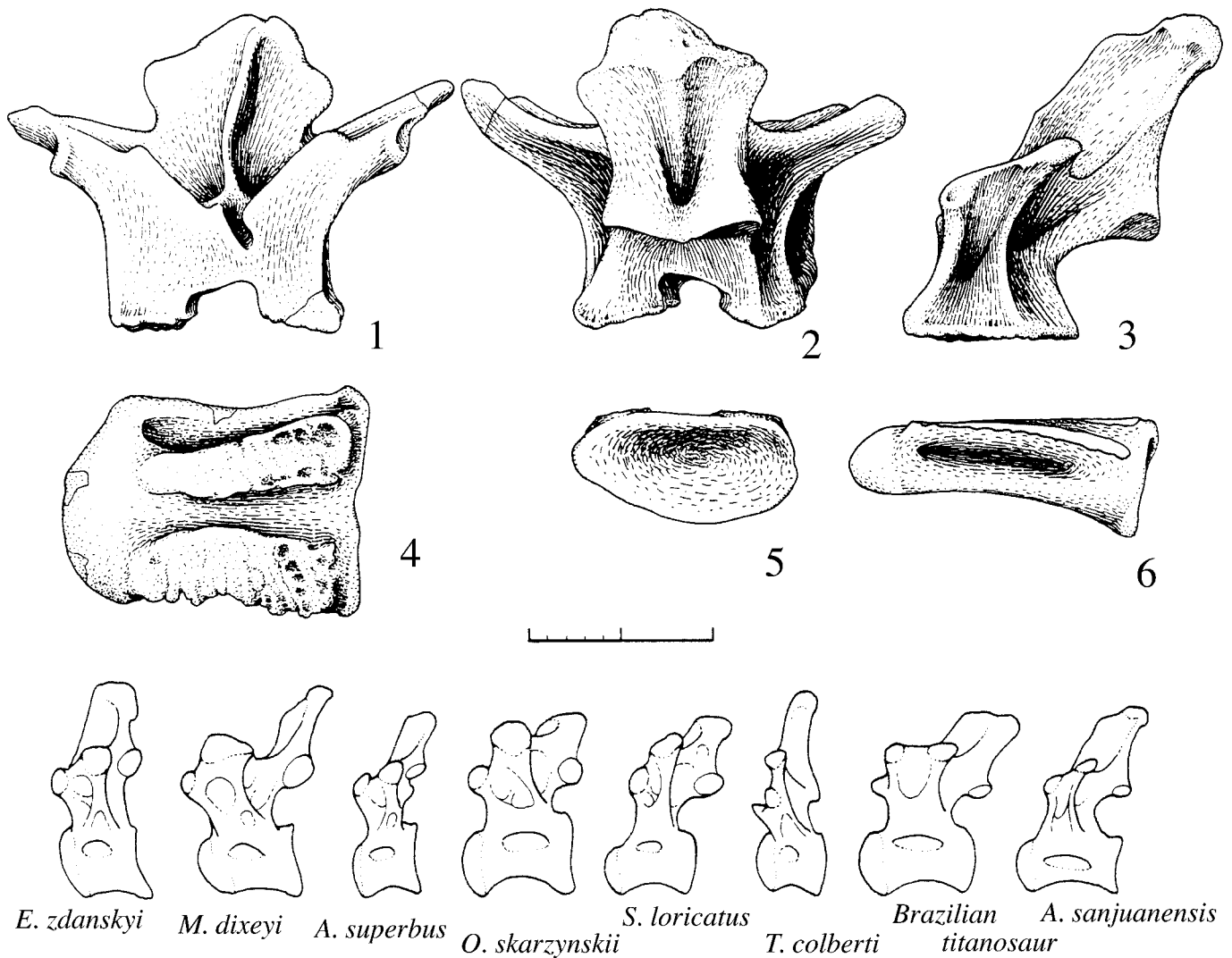


FIGURE 4—*Alamosaurus sanjuanensis* (TMM 43621-1), neural arch of mid dorsal vertebra in 1, anterior; 2, posterior; and 3, left lateral view. Centrum of dorsal vertebra in 4, dorsal; 5, posterior; and 6, left lateral view. Scale bar is 10 cm. Inset compares mid dorsal vertebrae in left lateral view (not to scale) of *Euhelopus zdanskyi*, *Malawisaurus dixeyi*, *Argyrosaurus superbis*, *Opisthocoelecaudia skarzynskii*, *Saltasaurus loricatus*, *Titanosaurus colberti*, an unnamed titanosaur from Peiropolis, Brazil, and *Alamosaurus sanjuanensis*; see Figure 8 for citations.

The anterior centrodiapophyseal and posterior centrodiapophyseal laminae are well developed on all preserved dorsal vertebrae, and they enclose fossae on the lateral surfaces of the pedicels. These laminae do not widen markedly or bifurcate at their base, as they do in some other titanosaur (*Malawisaurus dixeyi*, *Argyrosaurus superbis*, *Argentinosaurus huinculensis*, and *Euhelopus zdanskyi*; Salgado et al., 1995). In the middle dorsal vertebrae, centropostzygapophyseal laminae are also well developed, but neither centropostzygapophyseal or centroprezygapophyseal laminae are found in the posterior dorsal vertebra. The prezygodiapophyseal and postzygodiapophyseal laminae are well marked only in the anterior dorsal vertebra.

Only a few fragments of dorsal ribs are preserved in this specimen; however, a number of complete examples have been collected with adult specimens (e.g., Lawson, 1972; TMM 41061, 41541). The middle and posterior dorsal ribs are massively built and have remarkably straight shafts with much of their curvature only at the proximal and distal ends. The rib shafts are triangular in cross section proximally, but become elliptical and flattened

distally. The anterior and posterior faces of the rib head have depressed fossae between the tuberculum and capitulum, but they lack pneumatic foramina.

Sacrum and caudal vertebrae.—Apart from a free sacral rib and centrum of a sacral vertebra, the sacrum and tail are not preserved in the present specimen. Sacra belonging to adult individuals have been collected from nearby localities (e.g., TMM 41541-1), and appear to be comprised of as many as six vertebrae, but these have yet to be completely prepared for study. A nearly complete articulated series of caudal vertebrae, also belonging to an adult individual of *A. sanjuanensis*, was illustrated and described in detail by Gilmore (1946). The first caudal vertebra is biconvex, and the centra are strongly procoelous throughout, with neural arches positioned anteriorly, and with strong prespinal but weak postspinal laminae. Although no caudal vertebrae are preserved with the present specimen, isolated vertebrae from throughout the caudal series (e.g., TTU 546, TMM 41398-2, 41450-1, 43598-1, 43599-1, 43600-1) have been collected from

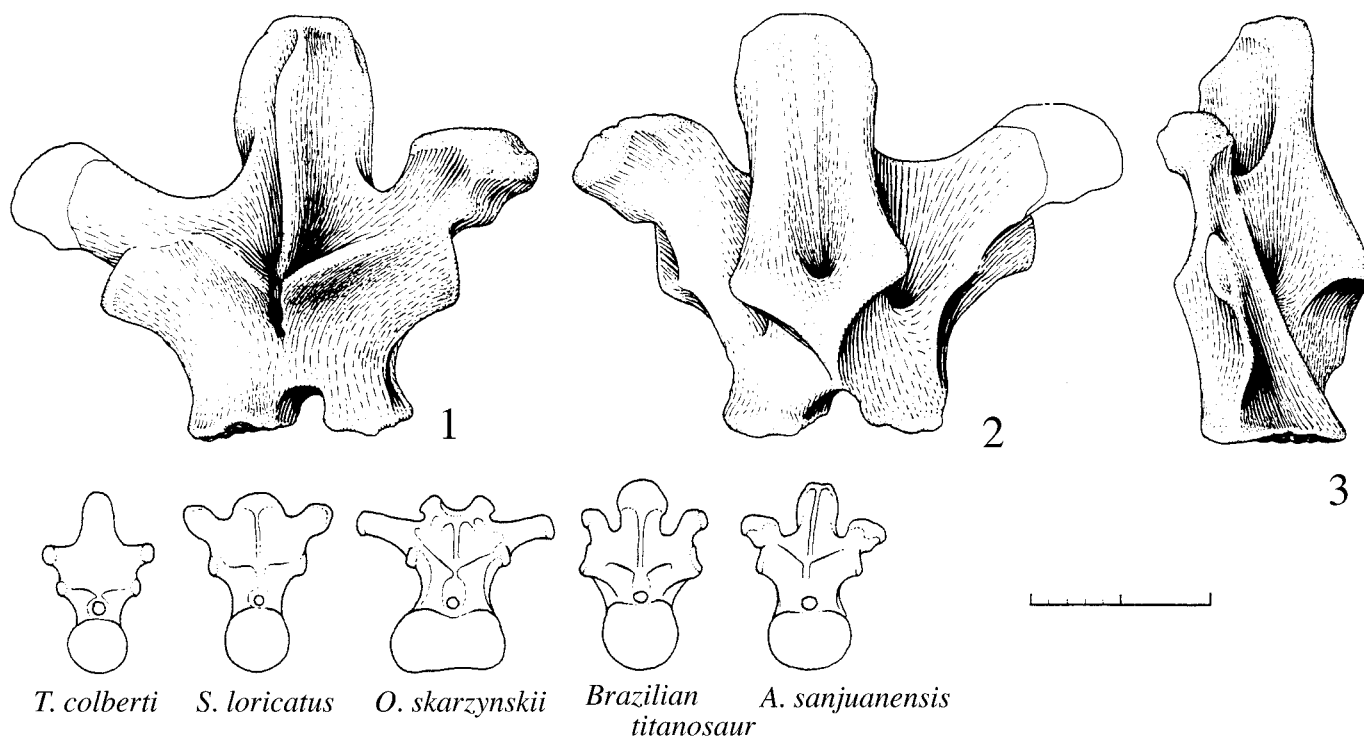


FIGURE 5—*Alamosaurus sanjuanensis* (TMM 43621-1), posterior dorsal vertebra in 1, anterior; 2, posterior; and 3, left lateral view. Scale bar is 10 cm. Inset compares posterior dorsal vertebrae in anterior view (not to scale) of *Titanosaurus colberti*, *Saltasaurus loricatus*, *Opisthocoelecaudia skarzynskii*, an unnamed titanosaur from Peiropolis, Brazil, and *Alamosaurus sanjuanensis*; see Figure 8 for citations.

nearby localities, and these are indistinguishable from those described by Gilmore (1946). Some of these specimens (e.g., TMM 43598-1) reveal that, unlike some other titanosaurs (e.g., *Saltasaurus*; Sanz et al., 1999), the open coarsely cancellous bone tissue characteristic of the presacral vertebral centra does not extend into the anterior caudal vertebral centra of *Alamosaurus*.

Shoulder girdle and forelimb.—No scapulae are preserved with this specimen; however, a partial scapula from a nearby site (TMM 43599-1) is similar to the type and referred specimens (USNM 10486, 15560) which have been thoroughly described and illustrated. The left coracoid is, however, well preserved in the present specimen (Fig. 6). It is quadrangular in outline, with a markedly convex lateral surface perforated by the coracoid foramen. The foramen is closer to the scapular border than in USNM 15560, and passes posterodorsally through the bone, opening near the dorsal margin of the concave medial surface. The sutural surface for the scapula is also relatively straight, lacking the marked sigmoidal curvature present in USNM 15560. The glenoid surface of the coracoid faces slightly laterally. On the posteroventral corner of the coracoid, just below the glenoid, is a beveled articulation surface for the sternal bone. The large semilunar sternal bones of USNM 15560 were described by Gilmore (1946).

The left humerus is complete except for a small part of the proximolateral corner, though the shaft is mildly crushed (Fig. 7). It is very slender, and lacks the strong proximal and distal expansion found in referred adult specimens (USNM 15560, TMM 41398-2, 41541-1, 42495-6). The proximal anterior face of the bone is deeply concave. The humeral head is positioned medially relative to the shaft, and does not expand markedly onto the posterior surface. The lateral edge is straight, a condition exaggerated by the highly elevated proximolateral corner. The shaft is circular in cross section at mid length, and curves anteriorly. The radial

and ulnar condyles also project anteriorly, imparting a forward inclination to the distal end of the bone. The condyles are well differentiated and separated by a deep olecranon fossa posteriorly, though this is in part a result of postmortem compression. The deltopectoral crest is relatively low, positioned high on the shaft, with a short medial projection. In adult specimens, the condyles are not as well defined and the deltopectoral crest is more massive, expanded transversely, and overhangs the center of the shaft. Such differences likely reflect the juvenile condition of the present specimen. The adult specimens are otherwise similar in having an elevated proximolateral corner, straight lateral border, and curved medial border.

The left ulna is complete and well preserved (Fig. 7). The proximal end is expanded to such an extent that it is remarkable it could belong to the same individual as the humerus described above. The olecranon process is well developed with its summit projecting above the level of the sigmoid notch to form a rugose head. The proximolateral face of the ulna is concave where it would cradle the head of the radius. The articular surface for the trochlear condyle of the humerus projects far anteromedially, and the distal end of the bone twists medially, resulting in a markedly concave anteromedial border. The posteromedial border is relatively straight, with a prominent ridge extending from the olecranon along the length of the shaft to the distal end. The shaft is slender and triangular in cross section at mid length. The distal end is expanded and semicircular in outline, with a flat anteromedial surface for articulation with the radius. The articulation surface for the carpus is mildly concave. The ulna is generally similar to that in adult individuals (USNM 15560, TMM 41450-2, 42595-2) but has relatively more expanded proximal and distal ends. The ratio of ulna length to humerus length is 0.77 in the present specimen, compared to 0.65 in USNM 15560. This may also reflect the juvenile condition of the present specimen. The

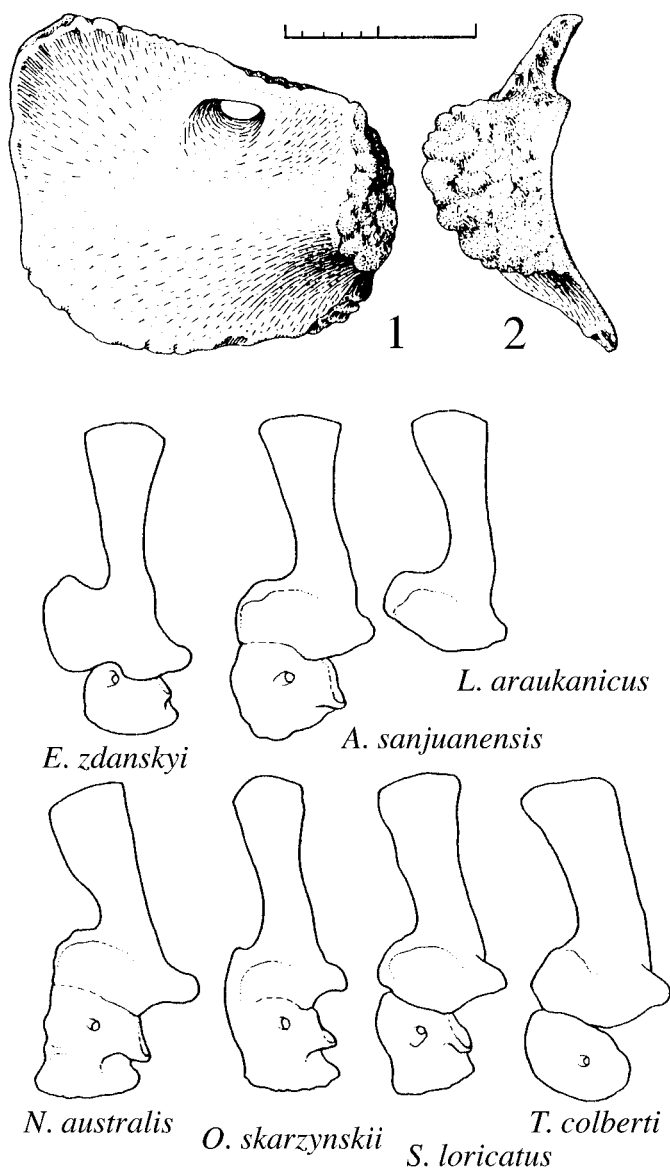


FIGURE 6—*Alamosaurus sanjuanensis* (TMM 43621-1), left coracoid in 1, lateral; and 2, posterior view. Scale bar is 10 cm. Compared below are scapula and coracoid (not to scale) of *Euhelopus zdanskyi*, *Alamosaurus sanjuanensis*, *Laplatasaurus* (? *Titanosaurus*) *araukanicus*, *Neuquensaurus australis*, *Opisthocoelicaudia skarzynskii*, *Saltasaurus loricatus*, and *Titanosaurus colberti*; see Figure 8 for citations.

radius, carpus, and manus are not preserved in this specimen, but have been described for USNM 15560 (Gilmore, 1946).

Pelvic girdle and hindlimb.—Only parts of the acetabular border of the ilium and pubis are preserved in this specimen; however, Lawson (1972) described these bones based on more complete specimens collected nearby (Fig. 8). The ilium has an anterodorsally expanded preacetabular process that is strongly deflected laterally, just anterior to the first sacroiliac facet (Lawson, 1972; TMM 41060). There are only four obvious sacroiliac facets, but it is likely that ribs of an additional dorsosacral vertebra braced the preacetabular process, which diverges at nearly a right angle from the medial surface. A sacrocaudal vertebra braced the postacetabular process (Mateer, 1976). The pubic peduncle is very

slender and elongate. The thickened postacetabular process extends ventrally to the same level as the short ischial peduncle.

The left ischium is well preserved in the present specimen (Fig. 9). It is nearly identical in form to the paratype (USNM 10487; Gilmore, 1922) and referred specimen (USNM 15560; Gilmore, 1946), although this is from a much smaller individual. It differs in lacking the thin ossified inner acetabular wall, but this is in keeping with its immature condition. The puboischial contact is very deep dorsoventrally, a condition common to titanosaurs, but reaching an extreme development in *Alamosaurus*. There is a shallow fossa on the lateral surface just posterior to the articulation for the pubis. The ischial shaft is a short but broad, flattened plate, comparable in length to the iliac peduncle. The sutural surface for the adjacent ischium is narrow, such that when in articulation, the distal ends of the ischial shafts are coplanar and joined along their entire length (e.g., see Gilmore, 1946). Although only part of the pubis is preserved in this specimen, several are preserved with adult specimens (TMM 41063, 40597-5, 41541-1), and these indicate that the pubic shaft is relatively much greater in length than that of the ischium. The pubis is elongate and mildly curved anteriorly, with a slightly expanded distal end and a thin medial edge. The obturator foramen appears to be completely enclosed, although the puboischial border is not well preserved in any of the specimens.

The femur is not preserved in the present specimen; however, several femora from adult individuals have been collected at nearby sites (TMM 41541-1, UTEP P25, TTU 542). These have a marked lateral bulge along the proximal third of the shaft, characteristic of titanosaurs (Fig. 10). The femoral shaft is slightly curved posteriorly, compressed anteroposteriorly, and elliptical in cross section, attaining its minimum diameter at about one-third of its height. The proximal half of the shaft is mildly concave on both anterior and posterior faces. The distal half of the shaft has a faint longitudinal ridge running along the midline of the anterior face. A rugose fourth trochanter is present along the medial edge of the posterior face just above mid length. The head of the femur is only slightly expanded anteroposteriorly, and is not markedly elevated above the greater trochanter as it is in some sauropods, and particularly in other titanosaurs. The articular surfaces on the distal condyles are well differentiated and expand onto both the anterior and posterior face of the shaft. The tibial condyle extends farther anteroposteriorly than the fibular condyle.

Parts of both tibiae are preserved, although neither is complete (Fig. 10.4, 10.5). Both are broken near mid length, below the cnemial crest. The shaft is roughly circular in cross section at mid length, and the distal end of the tibia is expanded mediolaterally. The articular surface for the ascending process of the astragalus is inset, and inclined anteriorly; the posteroventral process (sensu Wilson and Sereno, 1998) is relatively narrow. A better preserved adult *Alamosaurus* tibia (TMM 42495-4) is similar, with an expanded, laterally deflected cnemial crest arising just above mid length.

The left fibula is nearly complete, lacking the lateral edge of the proximal end (Fig. 10). However, part of the proximal end of the right fibula is also preserved, and so the entire form of the bone is apparent. These compare well with a fibula from an adult *Alamosaurus* specimen (TMM 42495-5) collected from a nearby site. The shaft of the fibula is strongly curved posteriorly, and has a pronounced, though not rugose, lateral tuberosity (or lateral trochanter) at the inflection in curvature near mid length. Along its entire length the medial surface is flattened, and there is no distinct facet for articulation with the tibia, although this area is not well preserved. The shaft is roughly triangular in cross section. The anterior edge of the bone is sharp, with a slight swelling near the proximal end, presumably marking the position of the anterior trochanter (Wilson and Sereno, 1998). The posterior edge is broadly rounded. The proximal end is expanded anteroposteriorly.

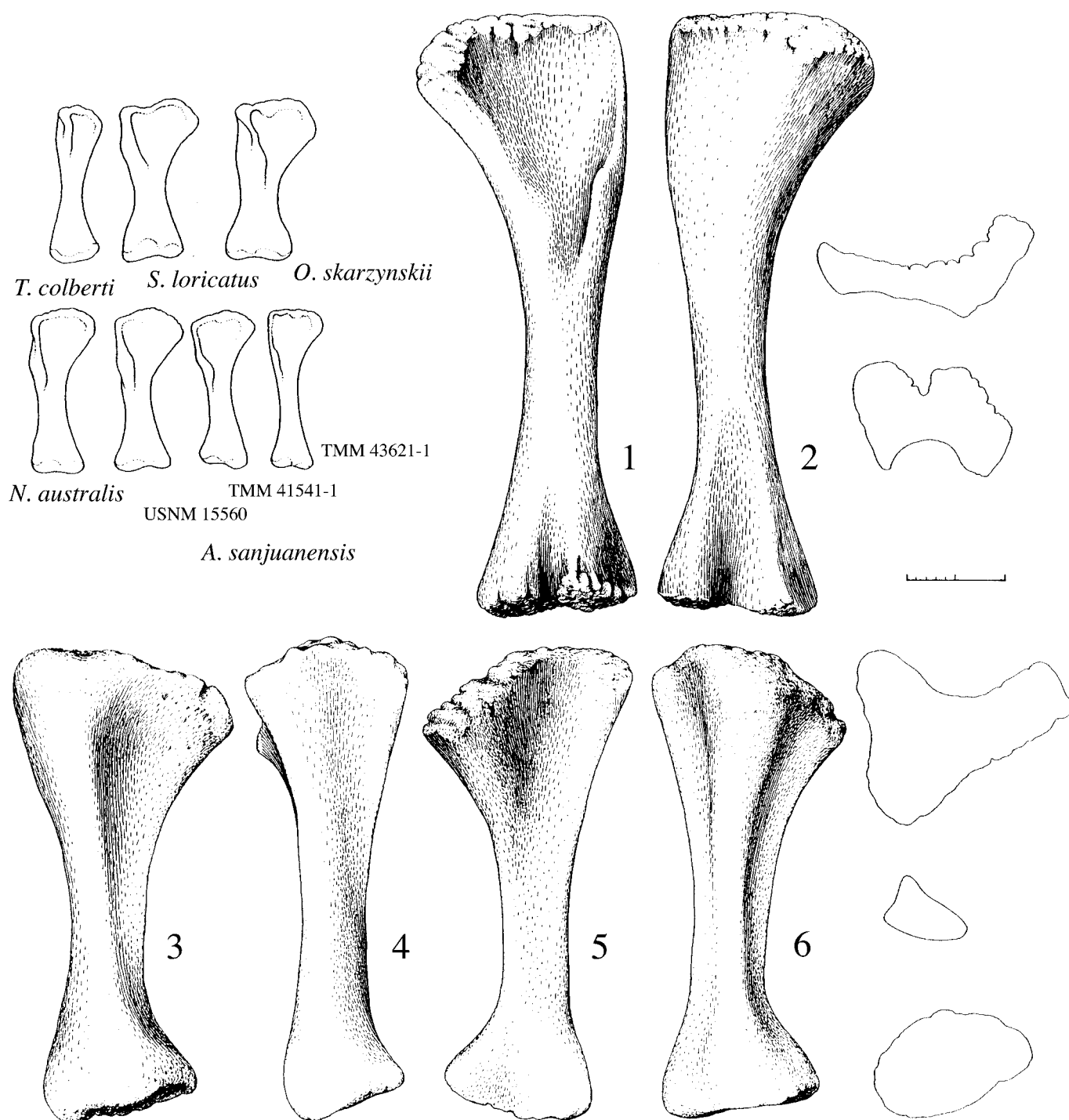


FIGURE 7—*Alamosaurus sanjuanensis* (TMM 43621-1), left humerus in 1, anterior; and 2, posterior view, with outlines of proximal and distal ends. Left ulna in 3, posteromedial; 4, lateral; 5, anterior; and 6, posterior view, with outlines of proximal and distal ends, and cross section of shaft at mid length. Scale bar is 10 cm. Inset compares right humerus in anterior view (not to scale) of *Titanosaurus colberti*, *Saltasaurus loricatus*, *Opisthocoelicaudia skarzynskii*, *Neuquensaurus australis*, and three specimens of *Alamosaurus sanjuanensis*; see Figure 8 for citations.

Apart from a fragmentary metatarsal, the tarsus and pes are not preserved in this specimen. An astagalus and single metatarsal were collected with an adult specimen (TMM 42495-1, 42495-2) but the hind foot remains poorly known in *Alamosaurus sanjuanensis*.

COMPARISON WITH OTHER SAUROPODS

As many as twenty genera, most of them monospecific, are included in the Titanosauria of Bonaparte and Coria (1993). Most recent authors (e.g., Wilson and Sereno, 1998) include *Aeolosaurus*, *Alamosaurus*, *Ampelosaurus*, *Andesaurus*, *Argentinosaurus*,

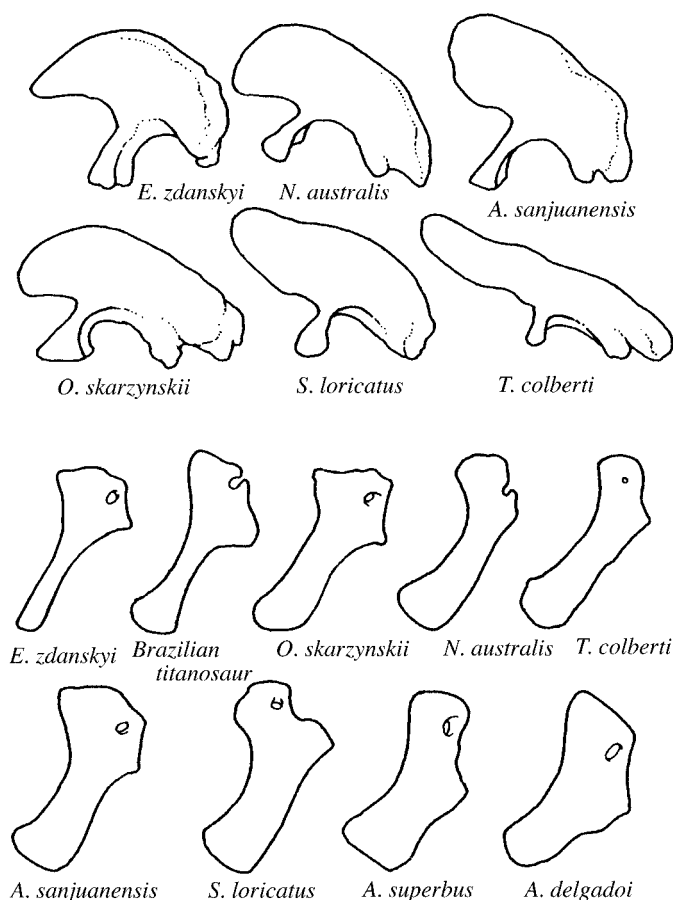


FIGURE 8—Comparison of left ilium (above, in lateral view) of *Euhelopus zdanskyi* (Wiman, 1929), *Neuquensaurus australis* (Huene, 1929; Powell, 1986), *Alamosaurus sanjuanensis* (Gilmore, 1946; Lawson, 1972), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Saltasaurus loricatus* (Powell, 1992), and *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997). Comparison of the left pubis (below, in lateral view) of *Euhelopus zdanskyi*, unnamed titanosaur from Peiropolis, Brazil (Powell, 1986, 1987; McIntosh, 1990), *Opisthocoelicaudia skarzynskii*, *Neuquensaurus australis*, *Titanosaurus colberti*, *Alamosaurus sanjuanensis*, *Saltasaurus loricatus*, *Argyrosaurus superbus* (Calvo and Bonaparte, 1991), and *Andesaurus delgadoi* (Calvo and Bonaparte, 1991); not to scale. Shown in other Figures are elements from *Aeolosaurus rionegrinus* (Powell, 1986), *Malawisaurus dixeyi* (Jacobs et al., 1993, 1996), and *Laplatasaurus araukanicus* (Huene, 1929).

Epachthosaurus, *Gondwanatitan*, *Lirainosaurus*, *Magyarosaurus*, *Malawisaurus*, *Neuquensaurus*, *Opisthocoelicaudia*, *Saltasaurus*, and *Titanosaurus* within the Titanosauria. Lesser known and enigmatic forms *Aegyptosaurus*, *Antarctosaurus*, *Argyrosaurus*, *Laplatasaurus*, *Macrurosaurus*, and *Janenschia* (= *Tornieria*; Wild, 1991), as well as several known only from skulls (*Nemegtosaurus*, *Quaesitosaurus*), are also included by some authors, but these are difficult to compare with other titanosaurs and their affinities are debated (e.g., McIntosh, 1990; Upchurch, 1999). Most titanosaurs are known only from very incomplete specimens, and so they are all difficult to compare with one another. Hence, the relationships among species included within the Titanosauria are mostly unresolved, and so this widespread and diverse clade remains in need of continued study (Upchurch, 1995; Wilson and Sereno, 1998).

The general anatomy of titanosaurs has, however, become better known in recent years as a result of the description of nearly

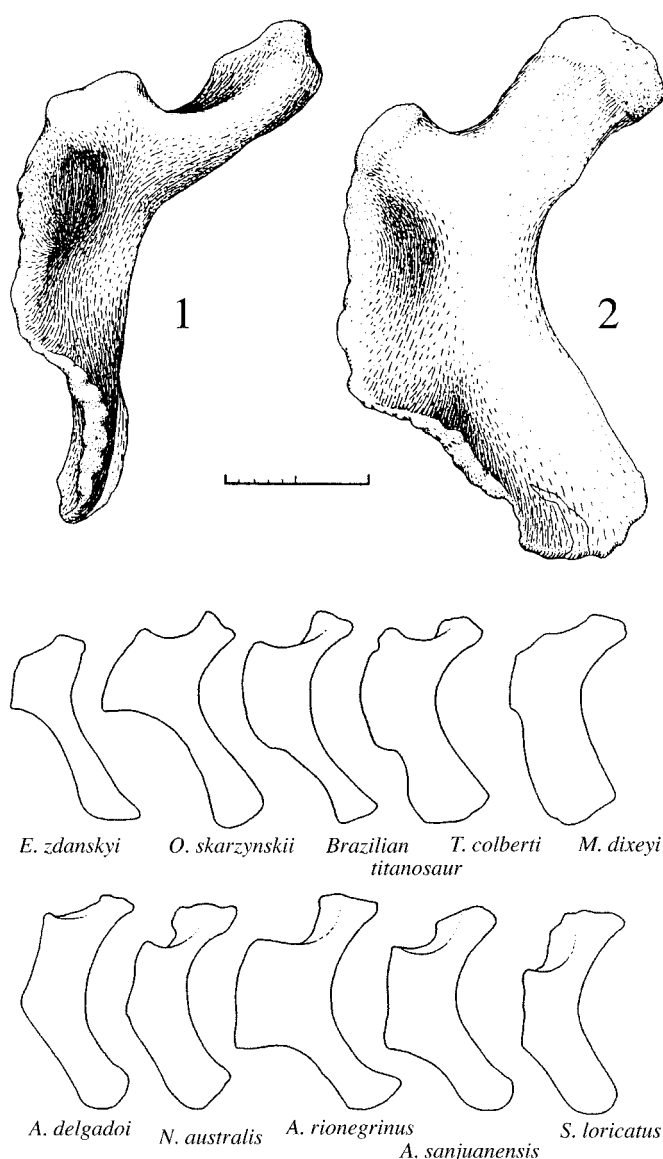


FIGURE 9—*Alamosaurus sanjuanensis* (TMM 43621-1), left ilium in 1, anterior; and 2, ventrolateral view. Scale bar is 10 cm. Below is comparison of left ilium in ventrolateral view (not to scale) of *Euhelopus zdanskyi*, *Opisthocoelicaudia skarzynskii*, unnamed titanosaur from Peiropolis, Brazil, *Titanosaurus colberti*, *Malawisaurus dixeyi*, *Andesaurus delgadoi*, *Neuquensaurus australis*, *Aeolosaurus rionegrinus*, *Alamosaurus sanjuanensis*, and *Saltasaurus loricatus*; see Figure 8 for citations.

complete skeletons of the Argentinian species *Saltasaurus loricatus* (Powell, 1992; Bonaparte and Powell, 1980) and Indian species *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), and the recognition that *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977) from Mongolia is also a member of this clade (Salgado and Coria, 1993). Recent general discussions of titanosaur systematics and skeletal anatomy have been given by McIntosh (1990), Jacobs et al. (1993, 1996), Wilson and Sereno (1998), and Upchurch (1995). Features generally considered synapomorphic for Titanosauria (reviewed by Wilson and Sereno, 1998) include 1) strongly procoelus anterior caudal vertebral centra; 2) prespinal and postspinal laminae on neural spines of anterior through middle caudal vertebrae; 3) large sternal plates with

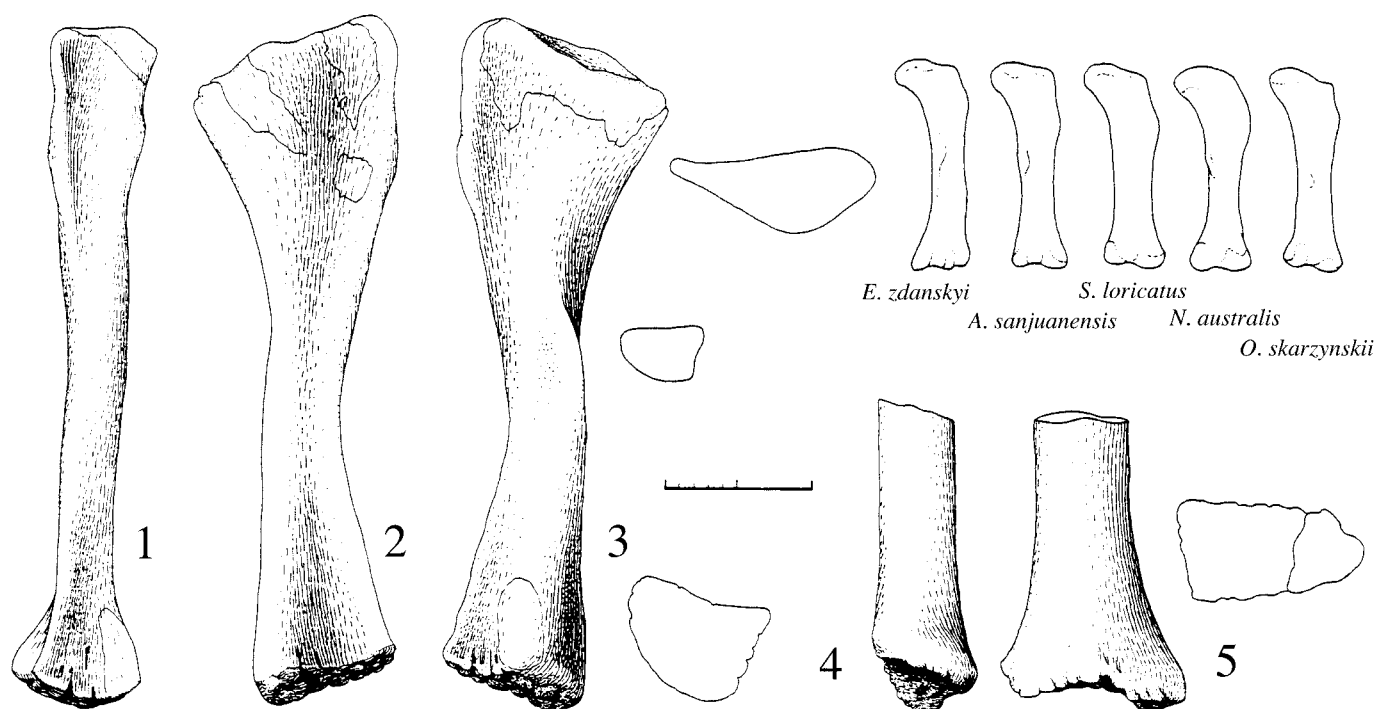


FIGURE 10—*Alamosaurus sanjuanensis* (TMM 43621-1), left fibula in 1, anterior; 2, medial; and 3, lateral view, with outlines of proximal and distal ends, and cross section of shaft at mid length. Distal end of right tibia in 4, lateral, and 5, anterior view, with outline of distal end. Scale bar is 10 cm. Inset compares right femur in posterior view (not to scale) of *Euhelopus zdanskyi*, *Alamosaurus sanjuanensis*, *Saltasaurus loricatus*, *Neuquensaurus australis*, and *Opisthocoelicaudia skarzynskii*; see Figure 8 for citations.

deeply concave lateral margins; 4) prominent olecranon process on the ulna; 5) carpals absent or unossified; and 6) pubis longer than ischium. *Alamosaurus* shares all of these traits, although postspinal laminae are not well developed on the caudal vertebrae.

Additional features listed by Salgado and Coria (1993) and Salgado et al. (1995) may also prove to be synapomorphic for Titanosauria, or for more exclusive groups among titanosaurs. These features include 1) elongate, strongly opisthocoelous dorsal centra; 2) absence (loss) of hyposphene-hypantrum articulations in dorsal vertebrae; 3) prespinal laminae in dorsal vertebrae extend to base of neural spine; 4) posterior centrodiapophyseal laminae thicken and/or bifurcate toward their base and/or extend to the parapophyses; 5) six fused vertebrae in sacrum; 6) neural arches on caudal vertebrae anteriorly placed; 7) preacetabular process of ilium strongly deflected laterally; 8) summit of acetabulum at base of pubic peduncle; 9) coracoid quadrangular; 10) manual phalanges absent; and 11) distal end of tibia expanded transversely. *Alamosaurus* appears to share these traits except the dorsal centra are not particularly elongate, and the posterior centrodiapophyseal laminae do not bifurcate or thicken markedly at their base.

Most Late Cretaceous titanosaurs, including *Alamosaurus*, seem to exemplify the "typical" titanosaur condition, and have been assigned to the family Titanosauridae (Lydekker, 1885). Some Early and Middle Cretaceous titanosaurs (e.g., *Andesaurus*, *Epachthosaurus*, and *Argentinosaurus*) exhibit presumed plesiomorphic features such as retention of hyposphene-hypantrum articulations on their dorsal vertebrae and/or amphiplatyan to mildly amphicoelous middle and posterior caudal vertebrae; and so are thought to comprise a basal titanosaur family Andesauridae (Bonaparte and Coria, 1993; Calvo and Bonaparte, 1991). However, Andesauridae, as variously constituted, is probably a paraphyletic group (Salgado et al., 1997), and many workers prefer instead to refer to those taxa lacking some features typical of Titanosauridae

simply as basal titanosaurs (e.g., Calvo, 1999). *Malawisaurus* and *Janenschia* (= "*Tornieria*") are apparently basal titanosaurs (Jacobs et al., 1993), as is perhaps *Pleurocoelus* (Salgado et al., 1995; but see Goman et al., 1999).

In the following discussion, *Alamosaurus sanjuanensis* will be compared primarily with the basal titanosaur *Malawisaurus dixeyi* (Jacobs et al., 1993, 1996), and derived species *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), *Saltasaurus loricatus* (Powell, 1992), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), and an unnamed titanosaur from Peiropolis, Brazil (DGM "series A" and "series B" of Powell, 1987; MCT 1488-R and 1536-R of Campos and Kellner, 1999). Some have suggested that more than one species is represented among the material assigned to the unnamed Peiropolis titanosaur (e.g., Campos and Kellner, 1999), and some place *O. skarzynskii* as a sister taxon to Titanosauria (e.g., Sanz et al., 1999).

The cervical vertebrae in *Alamosaurus* are comparatively simple in structure, with poorly developed pleurocoels, low undivided neural spines, and rudimentary (or reduced) neural arch laminae, particularly in the anterior and middle cervical vertebrae. This general condition is thought to be shared among titanosaurs and *Euhelopus zdanskyi* (together the Somphospondyli of Wilson and Sereno, 1998). In fact, the cervical vertebrae of *Alamosaurus* are quite similar to those of *Euhelopus* and the basal titanosaur *Malawisaurus dixeyi* (Fig. 2). They share this simple design also with the unnamed titanosaur from Peiropolis, Brazil (DGM "series A" of Powell, 1986, 1987). In *Alamosaurus* the cervical neural spines are more strongly inclined posteriorly and thus enclose a more pronounced postspinal fossa, and have a reduced prespinal fossa, but are otherwise quite similar to these taxa. In contrast, the cervical vertebrae of *Titanosaurus colberti* are relatively much shorter anteroposteriorly, with taller, erect neural spines that are also wider transversely and possess prespinal laminae (Fig. 2). Those

of *Saltasaurus loricatus* have very low, anteriorly placed neural spines, and are unique among titanosaurs in having elongated postzygapophyses that extend well beyond the posterior ends of the centra. They are similar to those of *Alamosaurus*, however, in having a deep postspinal fossa and lateral tuberosities on the neural spines. The cervical vertebrae of *Opisthocoelicaudia skarzynskii* possess bifid neural spines.

The dorsal vertebrae of *Alamosaurus* also exhibit a relatively simple structure with low neural arches, and with the neural spines of anterior and middle dorsal vertebrae posterodorsally inclined (a condition also uniting *Euhelopus zdanskyi* Wiman, 1929, and titanosaurs; Wilson and Sereno, 1998). Upchurch (1995) considered the presence of a strong postspinal lamina on neural spines of the dorsal vertebrae a derived condition uniting titanosaurs and diplodocids; however this lamina is now known to be absent in dorsal vertebrae of *A. sanjuanensis*. In *A. sanjuanensis*, centroprezygapophyseal, centropostzygapophyseal, and postspinal laminae are lacking or poorly developed. Prezygodiapophyseal and postzygodiapophyseal laminae are also very weak. By contrast, in *Malawisaurus*, the centropostzygapophyseal and postspinal laminae are well developed, and the posterior centroprezygapophyseal lamina bifurcates at its base; a similar condition is observed in at least some of the dorsal vertebrae of *Euhelopus*, *Argyrosaurus*, *Argentinosaurus*, and the Peiropolis titanosaur (Fig. 4). Moreover, in *Malawisaurus* complex fossae are present on the posterior face of the diapophysis (within the "infradiapophyseal cavity" of Jain and Bandyopadhyay, 1997). In *Saltasaurus* the neural spines are lower, and the centroprezygapophyseal, centropostzygapophyseal, and postspinal laminae are well developed. Strong postspinal laminae are also present in the dorsal vertebrae of the Peiropolis titanosaur. In *Titanosaurus colberti*, the spinodiapophyseal laminae form broadly expanded sheets and the prespinal laminae are weak. *Opisthocoelicaudia* has low bifurcated neural spines with strong postspinal laminae and fossae within the spinopostzygapophyseal laminae. The dorsal vertebrae of *Alamosaurus* are most similar in general form and neural arch laminae to those of the Peiropolis titanosaur. Their posterior dorsal vertebrae have strikingly similar neural arches (Fig. 5), and both species have particularly elongate, laterally directed, diapophyses on the anterior dorsal vertebrae (Fig. 3). However, *Alamosaurus* dorsal vertebrae lack the bifurcated posterior centroprezygapophyseal laminae, strong postspinal laminae, and accessory spino-diapophyseal laminae found in the Peiropolis titanosaur.

The "accessory spino-diapophyseal" laminae (sensu Salgado and Martinez, 1993; see also Powell, 1990; Calvo and Bonaparte, 1991) found in some of the dorsal vertebrae of *Argentinosaurus*, *Epachthosaurus*, *Opisthocoelicaudia*, and the titanosaur from Peiropolis are not found in any of those preserved in *Alamosaurus*. However, in anteriormost dorsal vertebrae of several adult *Alamosaurus* specimens (e.g., TMM 41541-1) there are vestiges of the spinoprezygapophyseal laminae (very pronounced in the preceding cervical vertebrae), diverging laterally from the incipient prespinal lamina (lacking in cervical vertebrae). It is possible that the "accessory spino-diapophyseal" laminae are similar to, if not the same as these vestigial spinoprezygapophyseal laminae.

The caudal vertebrae of *Alamosaurus* exemplify the derived, strongly procoelous titanosaur condition, and so are similar to those typically referred to indeterminate Titanosauridae, or formerly broadly to "*Titanosaurus*" (e.g., Powell, 1986). Wilson and Sereno (1998) indicated that the presence of prespinal and postspinal laminae on the neural spines of anterior and middle caudal vertebrae is a synapomorphic condition for Titanosauria. However, although *Alamosaurus* caudal vertebrae have strong prespinal laminae, postspinal laminae are absent or very weak. All titanosaurs tend to have the base of the neural arch placed anteriorly on the caudal centra (Salgado and Martinez, 1993), but differ

regarding whether or not the first caudal centrum is biconvex, and in the degree and extent of procoely throughout the caudal series. The caudal vertebrae of *Alamosaurus* are particularly similar to those of *Neuquensaurus australis*, but differ in only subtle ways from those of *Titanosaurus colberti* and *Saltasaurus loricatus*. However, in both latter species the first caudal centrum is not biconvex, as it is in *Alamosaurus* and the Peiropolis specimen referred to *Titanosaurus* sp. (DGM "series C" of Powell, 1987). The caudal vertebrae of *Alamosaurus* are quite unlike those of *Aeolosaurus rionegrinus* and *Gondwanatitan faustoi* (Kellner and Azevedo, 1999) which have highly elongate prezygapophyses and low anteriorly deflected neural spines. They also differ markedly from those of *Argyrosaurus superbus* which have very short centra but tall neural spines, and from those of *Opisthocoelicaudia* which are opisthocoelous and have coossified haemal arches.

Bones of the forelimb and shoulder girdle in *Alamosaurus*, except the ulna, differ substantially from those of *Titanosaurus colberti*. In *T. colberti*, the coracoid is ovoid with a reduced coracoid foramen, the humerus is slender with only slight proximal expansion and poorly differentiated condyles, and with the deltopectoral crest close to the proximal end (Fig. 6). A very slender humerus is also found in *Gondwanatitan faustoi* (Kellner and Azevedo, 1999). In contrast, the humerus and ulna of *Alamosaurus* are very similar to those of *Neuquensaurus australis* (Powell, 1986; Huene, 1929). The scapula of *N. australis* is, however, very distinct with a constricted scapular blade and posteriorly extended glenoid (Fig. 6). The acromion is reduced in some titanosaurs (e.g., *Opisthocoelicaudia*, *Saltasaurus*, *T. colberti*), but remains relatively large and divergent from the scapular blade in *Alamosaurus*, though not forming an acute angle as in *Euhelopus* (Fig. 6). Both *Saltasaurus* and *T. colberti* also have a wide scapular blade compared to other titanosaurs. The suture between the scapula and coracoid is markedly curved in adult individuals of *Alamosaurus*, as it is in *Euhelopus*, but this is not apparent in the juvenile specimen described herein. The dorsal expansion of the coracoid along the anterior margin of the scapula, thought to be a derived character state uniting *Alamosaurus* and *Saltasaurus* by Upchurch (1995), appears to be present in most titanosaurs when compared to *Euhelopus*. As noted by Gilmore (1946), the scapula of *Alamosaurus* is nearly identical to that of *Laplatasaurus araukanicus* (Huene, 1929; = *Titanosaurus araukanicus* of Powell, 1986). The large semilunar sternal plates in *Alamosaurus* are similar to those of other titanosaurs, and distinctive among sauropods, exemplifying the derived condition in Titanosauria (Salgado and Coria, 1993; Wilson and Sereno, 1998).

In *Saltasaurus*, *Argyrosaurus*, and *Opisthocoelicaudia*, the humerus is relatively much stouter than in *Alamosaurus*, with strong proximal and distal expansion (Fig. 7). The humerus in *Alamosaurus* is slender, and similar in form to that of *Neuquensaurus australis*, though with a more ventrally extended ulnar condyle, as in *Lirainosaurus astibiae* (Sanz et al., 1999). The ulna/humerus length ratio is very low in *Titanosaurus colberti* (0.56) and high in *Saltasaurus loricatus* (0.74) and generally varies between 0.65 and 0.77 among titanosaurs for which data are available (McIntosh, 1990). However, the marked contrast in this ratio between adult (0.65) and juvenile (0.77) individuals of *Alamosaurus* suggests that this limb ratio may be subject to substantial ontogenetic variation (Fig. 7). The occurrence of titanosaur individuals with either "robust" or "gracile" forelimbs in the same deposits may perhaps reflect ontogenetic or sexual variation. The ulna is very distinctive in titanosaurs; the prominent olecranon process (Lawson, 1972; Wilson and Sereno, 1998) and expanded concave articular surface for the trochlear condyle of the humerus (Upchurch, 1995) are considered derived states shared among titanosaurs, including *Alamosaurus*. Hence, the ulna is generally similar among titanosaurs, differing mostly in relative robustness.

Considering the variability in the titanosaur shoulder girdle and forelimb, it is remarkable that the hindlimb elements are so similar. For example, in spite of other differences, the femur is nearly identical in most genera (Fig. 10). Pelvic elements vary subtly among titanosaurs. The typical titanosaur ilium has a preacetabular process that is sharply deflected laterally and anterodorsally expanded compared to *Euhelopus*. However, in *Alamosaurus* the preacetabular blade of the ilium is not further everted horizontally as in *Titanosaurus colberti* and *Saltasaurus loricatus* (Fig. 8). The pubic peduncle is relatively more slender and elongate than in *Opisthocoelicaudia*. The ilium in *Alamosaurus* is most similar in form to that in "*Titanosaurus*" *robustus* (Huene, 1929). The pubis is generally similar among titanosaurs; most have a wider shaft and expanded distal end compared to *Euhelopus*. In *Alamosaurus*, the shaft of the pubis is relatively broad and anteriorly curved, resembling that in *Titanosaurus colberti*, *Neuquensaurus australis*, and *Opisthocoelicaudia* (Fig. 8). The pubis is much more slender in the Peiropolis titanosaur, and in contrast relatively shorter and broader in *Andesaurus* and *Argyrosaurus*.

Among titanosaurs, the ischium varies in the depth of the puboischial contact, and the relative length of the ischial shaft, though all have a relatively short and broad ischium compared to other sauropods (Fig. 9). In sauropods generally, the length of the distal process of the ischium is equal to or greater than the length of the pubic articular peduncle and ilial articular peduncle combined, as for example in *Euhelopus*. In *Opisthocoelicaudia* and the Peiropolis titanosaur, the shaft of the ischium remains relatively slender, elongate, less strongly curved posteriorly, and the puboischial contact is not as deep dorsoventrally as in other titanosaurs. In *Neuquensaurus australis*, *Andesaurus*, and *Aelosaurus rionegrinus* the ischium is very short and broad, as in *Alamosaurus*, but the distal process remains longer and broader than the ilial articular peduncle. In *Malawisaurus dixeyi* and *Titanosaurus colberti* the distal process is expanded anteroposteriorly. The ischial shaft is reduced to an even greater extent in *Saltasaurus*, where the distal process is shorter than the ilial articular peduncle.

Given our present level of understanding, it is not possible to convincingly determine the relationships of *Alamosaurus* to other titanosaurs. Sauropod phylogeny in general remains controversial, and significant differences exist among the various phylogenetic analyses of Sauropoda presented to date (e.g., McIntosh, 1990; Upchurch, 1995, 1999; Wilson and Sereno, 1998). Hypotheses of ingroup relationships among titanosaurs also disagree, are weakly supported, and rely excessively on subtle differences in single characters (e.g., Salgado et al., 1997; Sanz et al., 1999; Kellner and Azevedo, 1999). This is in part because the unresolved outgroup relationships make it difficult to assess likely character state polarity and homoplasy among titanosaurs. For example, if *Euhelopus* and Titanosauria together constitute a natural group (Somphospondyli of Wilson and Sereno, 1998), then *Alamosaurus* would appear to have lost some presumed ancestral features, such as bifurcated posterior centrodiapophyseal laminae and accessory spinodiapophyseal laminae in the dorsal vertebrae, while the same features might be regarded as derived homoplastic features were *Euhelopus* not considered the sister taxon to Titanosauria.

Alamosaurus presents a mosaic of features that suggest relationships with different groups of titanosaurs. Analysis of different features specifies different groups. Based on similarities in their axial skeletons, *Alamosaurus* may be most closely related to the unnamed titanosaur(s) from Peiropolis, Brazil (Powell, 1987; Campos and Kellner, 1999). Their presacral vertebral structure is very similar to the presumed ancestral condition in *Euhelopus* and in the basal titanosaur *Malawisaurus*. However, the full extent of

procoely in their caudal vertebral series typifies the derived condition in Titanosauridae. The further hypertrophied prezygapophyses in caudal vertebrae of *Aelosaurus* and *Gondwanatitan* suggests that they may comprise a more exclusive group within Titanosauridae (Kellner and Azevedo, 1999). Similarly, *Titanosaurus colberti* and *Saltasaurus* exhibit quite different vertebral structure compared to *Euhelopus*, and appear to be among the more derived titanosaurids. In contrast, the appendicular skeleton of *Alamosaurus* resembles most closely that in *Neuquensaurus australis* (as well as material referred to "*Titanosaurus*" *robustus* and "*Laplatasaurus*" *araukanicus* from the same deposits in Argentina) where the vertebral column is poorly preserved.

SKELETAL RECONSTRUCTION

The combined skeletal material now available from multiple specimens is sufficient to offer a composite skeletal reconstruction of *Alamosaurus sanjuanensis* (Fig. 11). The restoration given here is based primarily on the articulated tail, shoulder girdle, and forelimb of USNM 15560. The pelvis and hindlimb are based on TMM 41060, 41063, 41541, and 42495 which have some comparable skeletal elements (e.g., humerus) that allow for correct scaling. All of these specimens are very nearly the same size, and they probably represent mature individuals that approached the maximum adult body size prior to their death. Using the method of Anderson et al. (1985) based on the combined circumferences of the humerus and femur (661 mm and 740 mm in TMM 41541), the adult body mass is estimated to have been about 30 metric tonnes. Hence, *Alamosaurus* was among the largest of sauropod dinosaurs.

The presacral vertebral column is restored by doubling the dimensions of TMM 43621-1, which is about 50 percent the size of the other specimens. The total number of cervical vertebrae is estimated to be 13, based on resemblance to the Peiropolis titanosaur (DGM "series A" of Powell, 1987), although only parts of eight are preserved in TMM 43621. The neck in *Alamosaurus* is therefore relatively long compared to some other titanosaurids (e.g., *Saltasaurus loricatus*, *Titanosaurus colberti*). The total number of dorsal and sacral vertebrae are estimated to be ten and six, respectively; also based on similarity with the Peiropolis titanosaur (DGM "series B" of Powell, 1987). Although 30 caudal vertebrae are preserved in USNM 15560, the shape of the last two centra (Gilmore, 1946) suggests that the tail probably had a "whiplash" composed of as many as 20 additional vertebrae, as reconstructed here. Distinct fused ribs ("transverse processes") are present on the first eight caudal vertebrae, with raised knobs on the next three or four. Intervertebral chevron bones articulate with the first through twenty fifth caudal vertebrae, and following that point the zygapophyses are not in contact.

A single manual phalanx is shown on the first digit of the fore foot, although it is possible, or even likely that none of the manual phalanges were ossified (e.g., Wilson and Sereno, 1998). The structure of the hind foot is entirely conjectural, as only a few isolated metatarsals have been found in association with *Alamosaurus* remains. Similarly, although the dentition is known to consist of slender rod shaped teeth, the form of the skull is unknown. A generalized sauropod skull, based on that of *Nemegtosaurus* is shown here. Although some titanosaurs are known to have possessed dermal armor plates (e.g., *Saltasaurus*; Powell, 1987), no osteoderms have been found in association with *Alamosaurus*, nor in the deposits which bear its remains, and it is assumed to have been unarmored.

CONCLUSIONS

TMM 43621-1 is assigned to *Alamosaurus sanjuanensis*, based on the unique morphology of the ischium. Although less than half the size of the type and referred specimens, comparable elements

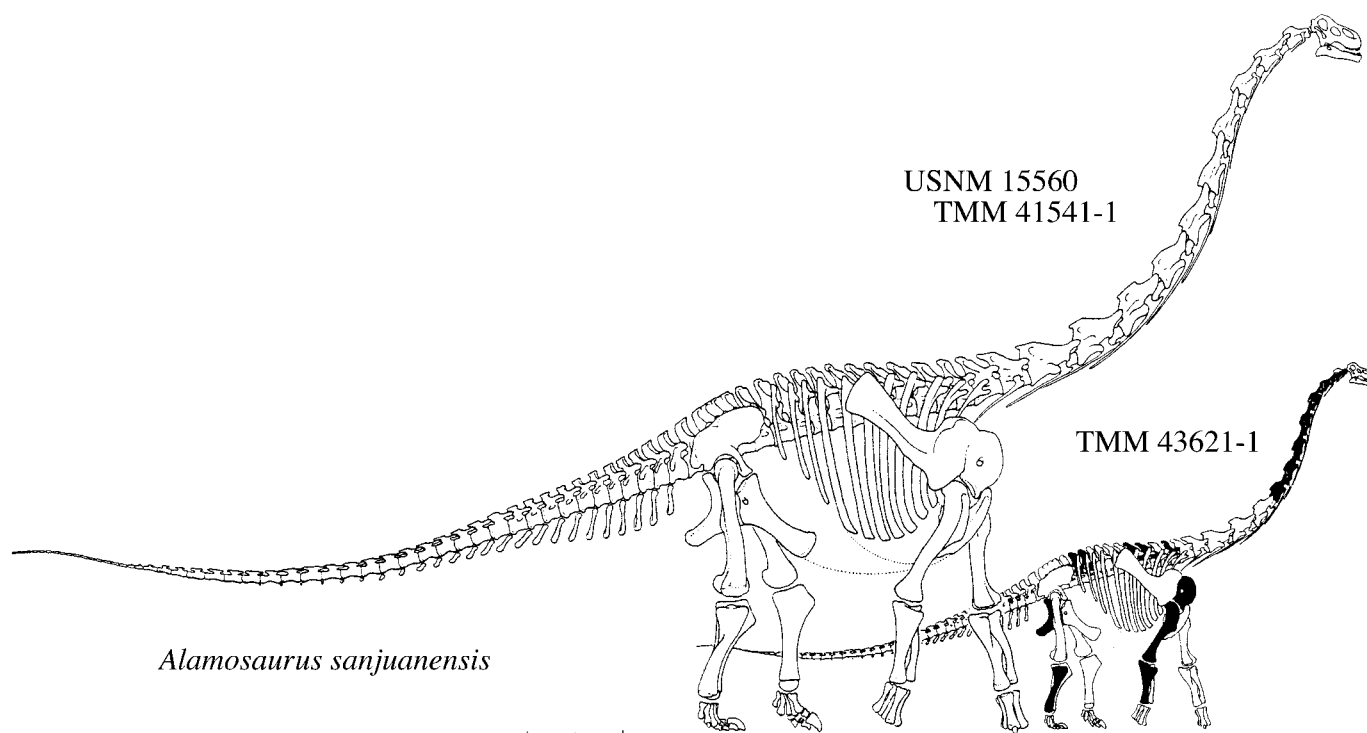


FIGURE 11—*Alamosaurus sanjuanensis*, reconstruction of adult skeleton based primarily on USNM 15560 and TMM 41541-1; juvenile skeleton based on TMM 43621-1 with preserved elements shown in black. Scale bar is 1 m.

are essentially identical. The small size of the skeletal elements in TMM 43621-1 and the lack of fusion between centra and neural arches indicate that this skeleton is that of a juvenile individual. The specimen preserves cervical and dorsal vertebrae and hindlimb elements previously undescribed for this species, and so provides new osteological information for *Alamosaurus*, which remains one of the few titanosaurid taxa based on a reasonable number of unambiguous specimens. As additional material is prepared and studied, *A. sanjuanensis* may ultimately become one of the better known titanosaurs. No other sauropods are yet known from Upper Cretaceous strata in southwestern North America. Comparison with other titanosaurid species based on adequate specimens demonstrates that *Alamosaurus sanjuanensis* is a valid taxon, most similar to the unnamed titanosaur(s) from Peiropolis, Brazil, and *Neuquensaurus australis* from Argentina (Powell, 1986, 1987).

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APPENDIX 1

Measurements of TMM 43621-1, *Alamosaurus sanjuanensis*. All measurements are given in millimeters.

Anterior cervical vertebra (2, axis)	
length of centrum	130
length of pedicel suture	110
maximum diameter of posterior end of centrum	100
Anterior cervical vertebra (?3, centrum)	
length of centrum	223
length of pedicel suture	135
maximum diameter of posterior end of centrum	105
width across parapophyses	132
Anterior cervical vertebra (?3, neural arch)	
length of neural arch (pre- to postzygapophyses)	225
length of pedicel suture	140
transverse width across zygapophyses	95
transverse width across diapophyses	125
height (base of pedicel to tip of neural spine)	100
Anterior cervical vertebra (?4, neural arch)	
length of pedicel suture	140
transverse width across diapophyses	130
height (base of pedicel to tip of neural spine)	105
Anterior cervical vertebra (?5, neural arch)	
length of neural arch (pre- to postzygapophyses)	235
transverse width across zygapophyses	105
transverse width across diapophyses	155
Anterior cervical vertebra (?5, centrum)	
length of centrum	230
length of pedicel suture	170
maximum diameter of posterior end of centrum	110
width across parapophyses	105
Anterior cervical vertebra (?6, centrum)	
length of centrum	575
length of pedicel suture	200
maximum diameter of posterior end of centrum	135
width across parapophyses	194
Middle cervical vertebra (?7)	
length of neural arch (pre- to postzygapophyses)	327
length of pedicel suture	195
transverse width across zygapophyses	145
transverse width across diapophyses	210
height (base of pedicel to tip of neural spine)	110
length of centrum	305
maximum diameter of posterior end of centrum	140
width across parapophyses	145
Posterior cervical vertebra (?9, neural arch)	
length of neural arch (pre- to postzygapophyses)	305
length of pedicel suture	215
transverse width across zygapophyses	155
transverse width across diapophyses	225
height (base of pedicel to tip of neural spine)	130
Posterior cervical vertebra (?10, neural arch)	
length of neural arch (pre- to postzygapophyses)	310
transverse width across zygapophyses	160
transverse width across diapophyses	250
height (base of pedicel to tip of neural spine)	135
Posterior cervical vertebra (?11, centrum)	
length of centrum	180
length of pedicel suture	100
maximum diameter of posterior end of centrum	130
width across parapophyses	150

APPENDIX 1

Continued

Anterior dorsal vertebra (?1)	
length of pedicel suture	125
transverse width across zygapophyses	195
transverse width across diapophyses	500
height (base of pedicel to tip of neural spine)	250
Middle dorsal vertebra (?5)	
length of pedicel suture	90
transverse width across zygapophyses	85
transverse width across diapophyses	230
height (base of pedicel to tip of neural spine)	165
Middle dorsal vertebra (?6)	
length of pedicel suture	75
transverse width across zygapophyses	90
transverse width across diapophyses	250
height (base of pedicel to tip of neural spine)	170
Middle dorsal vertebra (?7)	
length of pedicel suture	100
transverse width across diapophyses	330
Middle dorsal vertebra (?8, centrum)	
length of centrum	167
length of pedicel suture	110
maximum diameter of posterior end of centrum	120
Posterior dorsal vertebra (?9)	
length of pedicel suture	85
transverse width across zygapophyses	93
transverse width across diapophyses	240
height (base of pedicel to tip of neural spine)	235
Posterior dorsal vertebra (?10)	
transverse width across diapophyses	320
Coracoid (left)	
length of scapular border	150
length of glenoid surface	80
maximum length (anteroposterior)	180
maximum length (dorsoventral)	165
Humerus (left)	
length	605
maximum width of proximal end	205
maximum width of distal end	145
minimum width of shaft	65
minimum circumference of shaft	240
Ulna (left)	
length	464
maximum width of proximal end	230
maximum width of distal end	160
minimum width of shaft	43
minimum circumference of shaft	226
Ischium (left)	
length of contact for pubis	210
length of contact for ischium	225
length of ilial peduncle	120
Tibia (right)	
transverse width of distal end	135
minimum width of shaft	50
minimum circumference of shaft	196
Fibula (left)	
length	480
maximum width of proximal end	145
maximum width of distal end	95
minimum width of shaft	35
minimum circumference of shaft	165