AN ARTICULATED SPECIMEN OF THE BASAL TITANOSAURIAN (DINOSAURIA: SAUROPODA) *EPACHTHOSAURUS SCIUTTOI* FROM THE EARLY LATE CRETACEOUS BAJO BARREAL FORMATION OF CHUBUT PROVINCE, ARGENTINA

RUBÉN D. MARTÍNEZ[1], OLGA GIMÉNEZ[1], JORGE RODRÍGUEZ[1], MARCELO LUNA[1], and MATTHEW C. LAMANNA[2]

[1]Laboratorio de Paleontologia de Vertebrados, Universidad Nacional de la Patagonia "San Juan Bosco", C. C. 360,
(9.000) Comodoro Rivadavia, Argentina, rdfmartinez@yahoo.com;
[2]Department of Earth and Environmental Science, University of Pennsylvania, 240 South 33rd Street,
Philadelphia, Pennsylvania 19104–6316, USA

ABSTRACT—We describe an articulated specimen of the titanosaurian sauropod *Epachthosaurus sciuttoi* from the early Late Cretaceous Bajo Barreal Formation of Chubut Province, central Patagonia, Argentina. The skeleton was found in tuffaceous sandstone, with its hindlimbs flexed and its forelimbs widely extended. It is slightly deformed on its left side. The skull, neck, four or five cranial dorsal vertebrae, and several distal caudals are missing.

Epachthosaurus is diagnosed by the following autapomorphies: middle and caudal dorsal vertebrae with accessory articular processes extending ventrolaterally from the hyposphene, a strongly developed intraprezygapophyseal lamina, and aliform processes projecting laterally from the dorsal portion of the spinodiapophyseal lamina; hyposphene-hypantrum articulations in caudals 1–14; and a pedal phalangeal formula of 2-2-3-2-0. The genus shares the following apomorphies with various titanosaurians: caudal dorsal vertebrae with ventrally expanded posterior centrodiapophyseal laminae; six sacral vertebrae; an ossified ligament or tendon dorsal to the sacral neural spines; procoelous proximal, middle, and distal caudal centra with well-developed distal articular condyles; semilunar sternal plates with cranioventral ridges; humeri with squared proximolateral margins and proximolateral processes; unossified carpals; strongly reduced manual phalanges; craniolaterally expanded, nearly horizontal iliac preacetabular processes; pubes proximodistally longer than ischia; and transversely expanded ischia. *Epachthosaurus* is considered the most basal titanosaurian known with procoelous caudal vertebrae.

RESUMEN.—Se describe un espécimen articulado del saurópodo titanosaurio *Epachthosaurus sciuttoi* de la Formación Bajo Barreal, Cretácico Superior temprano, de la provincia del Chubut, Patagonia central, Argentina. El esqueleto fue hallado en un estrato de arenisca tobácea, con sus miembros posteriores flexionados y sus miembros anteriores ampliamente extendidos; su costado izquierdo está ligeramente deformado. El cráneo, cuello, cuatro o cinco vértebras dorsales anteriores y varias caudales distales han desaparecido.

Epachthosaurus es diagnosticado por las siguientes autapomorfías: vértebras dorsales medias y posteriores con procesos articulares accesorios que se extienden ventrolateralmente desde el hipósfeno, presencia de una lámina interprezigapofiseal fuertemente desarrollada y procesos aliformes que se proyectan lateralmente desde la porción dorsal de la lámina espinodiapofiseal; presencia de articulaciones hipósfeno-hipantro en las caudales 1–14 y una fórmula falangeal pedal de 2-2-3-2-0. El género comparte las siguientes apomorfías con otros titanosaurios: vértebras dorsales posteriores con láminas centrodiapofisiales posteriores ventralmente expandidas; seis vértebras sacras; un ligamento osificado o tendón dorsal a las espinas neurales sacras; centros caudales proximales, medios y distales procélicos con conos articulares bien desarrollados; planchas esternales semilunares con crestas ánteroventrales; húmeros con márgenes próximolaterales cuadrados y procesos próximolaterales; carpales no osificados; falanges de la mano fuertemente reducidas; procesos preacetabulares ilíacos casi horizontales; pubis próximodistalmente más largos que los isquiones e isquiones transversalmente expandidos. *Epachthosaurus* es considerado el titanosaurio más basal conocido con vértebras caudales procélicas.

INTRODUCTION

Titanosaurian sauropods were among the most abundant and geographically widespread of Cretaceous herbivorous dinosaurs. The clade was especially diverse in Europe and landmasses derived from the supercontinent of Gondwana, particularly in South America (Bonaparte, 1986). South American titanosaurians described to date include *Aeolosaurus* (Powell, 1986, 1987a; Salgado and Coria, 1993a), *Andesaurus* (Calvo and Bonaparte, 1991), *Antarctosaurus* (Huene, 1929; Bonaparte and Bossi, 1967; Chiappe et al., 2001), *Argentinosaurus* (Bonaparte and Coria, 1993), *Argyrosaurus* (Lydekker, 1893; Powell, 1986), *Epachthosaurus* (Powell, 1990), *Gondwanatitan* (Kellner and Azevedo, 1999), *Laplatasaurus* (Huene, 1929), *Neuquensaurus* (Lydekker, 1893; Powell, 1986), *Pellegrinisaurus* (Salgado, 1996), *Rocasaurus* (Salgado and Azpilicueta, 2000), *Saltasaurus* (Bonaparte and Powell, 1980; Powell,

1992), possibly *Agustinia* (Bonaparte, 1999a), and several undescribed Brazilian and Patagonian taxa (e.g., Powell, 1987b; Calvo et al., 1997, 2001; Martínez, 1998; Campos and Kellner, 1999; González-Riga and Calvo, 1999, 2001; Chiappe et al., 2001; Giménez and Apesteguia, 2001; Santucci and Bertini, 2001; Casal et al., in press). Despite this exceptional diversity, many representatives of Titanosauria are based upon fragmentary, incomplete material. Consequently, evolutionary relationships within the clade remain largely unresolved.

During field research conducted as a part of the project "Los vertebrados de la Formación Bajo Barreal, Provincia de Chubut, Patagonia, Argentina," personnel from the Laboratorio de Paleontologia de Vertebrados of the Universidad Nacional de la Patagonia "San Juan Bosco" recovered a well preserved, articulated skeleton of a medium-sized sauropod. Martínez et al. (1988, 1989) briefly described several characters of this specimen that indicate that it pertains to Titanosauria, including six

sacral vertebrae, a procoelous first caudal vertebra, and an ossified ligament or tendon over the sacral neural spines. They referred the specimen, one of the most complete titanosaurian skeletons known, to the genus *Epachthosaurus*. The goal of the present work is to preliminarily describe this specimen and identify the relationships of *Epachthosaurus* within Titanosauria. One of us (Giménez) is preparing a monograph on the anatomy and phylogenetic position of *Epachthosaurus*.

Institutional Abbreviations—MACN-CH, Museo Argentino de Ciencias Naturales -Colección Chubut, Buenos Aires; **MCT**, Museu de Ciências da Terra, Departamento Nacional de Producão Mineral, Rio de Janeiro; **MLP**, Museo de La Plata, La Plata, Argentina; **PVL**, Fundacíon-Instituto Miguel Lillo, Tucumán, Argentina; **SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas; **UNPSJB-PV**, Universidad Nacional de la Patagonia ''San Juan Bosco''- Paleovertebrados, Comodoro Rivadavia, Argentina.

Anatomical Abbreviations—aart, accessory articular process; **acpl**, anterior centroparapophyseal lamina; **al**, accessory lamina; **alp**, aliform process; **cc**, cnemial crest; **cd**, condyle; **cpol**, centropostzygapophyseal lamina; **ct**, cotyle; **di**, diapophysis; **dpc**, deltopectoral crest; **fhd**, femoral head; **fic**, fibular condyle; **ft**, fourth trochanter; **hpa**, hypantrum; **hpo**, hyposphene; **ilped**, iliac peduncle; **lt**, lateral trochanter; **mt**, metatarsal; **ns**, neural spine; **ol**, olecranon; **ot**, ossified tendon; **pa**, parapophysis; **pc**, pleurocoel; **pcdl**, posterior centrodiapophyseal lamina; **plb**, proximolateral buttress; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **poz**, postzygapophysis; **prap**, preacetabular process; **prsl**, prespinal lamina; **prz**, prezygapophysis; **r**, rib; **rac**, radial condyle; **spc**, proximolateral process; **spdl**, spinodiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina; **tic**, tibial condyle; **tp**, transverse process; **tprl**, intraprezygapophyseal lamina; **up**, ungual phalanx; **I-V**, metapodials I-V; **C**, caudal; **D**, dorsal; **S**, sacral. (We follow Wilson's [1999a] nomenclature for vertebral laminae.)

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA von Huene, 1932
SAUROPODA Marsh, 1878
TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997
TITANOSAURIA Bonaparte and Coria, 1993
EPACHTHOSAURUS Powell, 1990
EPACHTHOSAURUS SCIUTTOI Powell, 1990

Holotype—MACN-CH 1317, an incomplete caudal dorsal vertebra.

Paratype—MACN-CH 18689, a cast, exposed in left lateral and ventral views, of six articulated caudal dorsal vertebrae, the partial sacrum, and a fragment of the pubic peduncle of the right ilium. Due to its occurrence in extremely resistant matrix, the original fossil has not yet been recovered.

Referred Specimen—UNPSJB-PV 920, an articulated skeleton lacking the skull, neck, four or five cranial dorsal and extreme distal caudal vertebrae.

Locality—Estancia ''Ocho Hermanos,'' Sierra de San Bernardo, west of Lago Musters, south-central Chubut Province, central Patagonia, Argentina (Fig. 1).

Horizon and Age—Upper portion of the Lower Member of the Bajo Barreal Formation (Upper Cretaceous: late Cenomanian-early Turonian [Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002]) (Fig. 1). The ''Ocho Hermanos'' tetrapod assemblage, which includes the basal chelid turtles *Bonapartemys* and *Prochelidella* (Broin and Fuente, 2001), the ceratosauroid theropod *Xenotarsosaurus* (Martínez et al., 1986), a carnotaurine abelisaurid (Martínez et al., 1993; Lamanna et al., 2002), the basal titanosaurian *Epachthosaurus* (Powell,
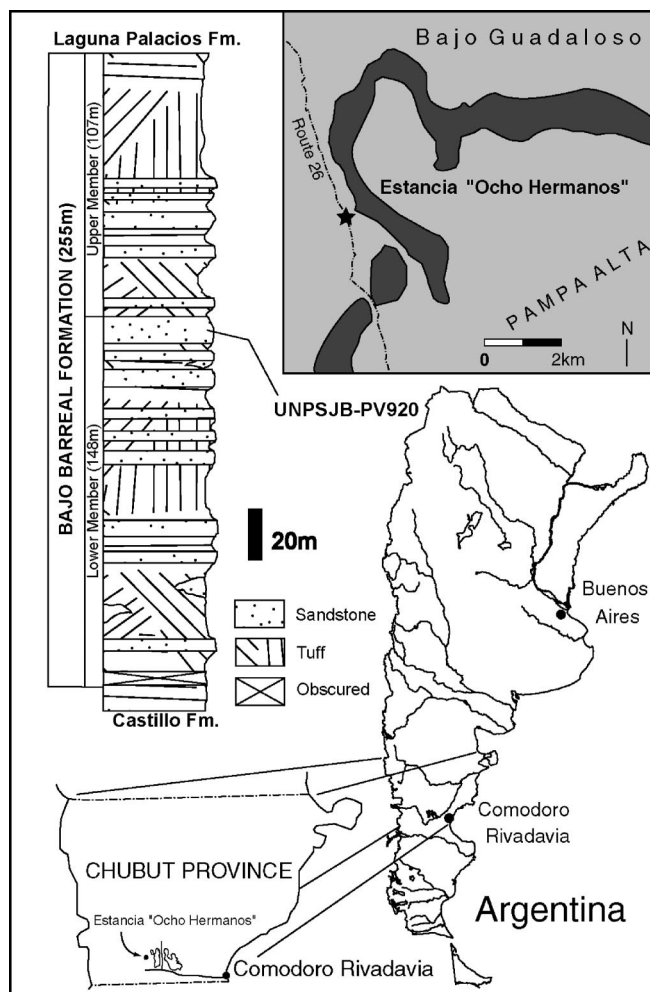

FIGURE 1. Geographic location and geologic context of the new specimen of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). The specimen was obtained from the Lower Member of the early Late Cretaceous (middle Cenomanian–?Coniacian) Bajo Barreal Formation, west of Lago Musters, Estancia ''Ocho Hermanos,'' Chubut Province, Argentina.

1990; this paper), possibly other titanosaurs, and sauropods of unresolved affinity (Powell et al., 1989), provides further evidence in support of an early Late Cretaceous age for outcrops of the Bajo Barreal Formation on the Estancia ''Ocho Hermanos.''

Taphonomy—Based on the sedimentology and taphonomic characteristics of the Bajo Barreal Formation as exposed at the Estancia ''Ocho Hermanos,'' Rodríguez (1993) postulated episodic deposition of large quantities of sediment, resulting in the rapid burial of animal remains. The degree of articulation and body position of UNPSJB-PV 920 are consistent with this hypothesis (Fig. 2). When buried, the sauropod carcass was resting on its ventral surface, with the forelimbs widely extended, both hindlimbs flexed, and the tail extended distally and curved toward the right (Fig. 2A). It is possible that the skull and cervical series were preserved, but have since been destroyed by erosion, as several dorsal vertebrae and the pectoral girdle were damaged by weathering. UNPSJB-PV 920 was probably not transported prior to burial (Rodríguez, 1993).

Diagnosis—Medium-sized titanosaurian sauropod diagnosed by the following autapomorphies: middle and caudal dorsal vertebrae possessing accessory articular processes extending ven-
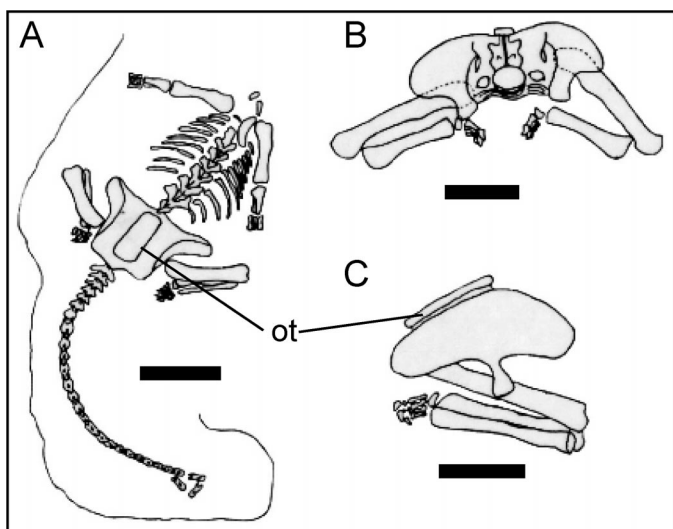
FIGURE 2. Skeletal disposition of *Epachthosaurus sciuttoi* (UNPSJB-PV920). **A**, dorsal view. **B**, cranial view of pelvis and hindlimbs. **C**, lateral view of right ilium and hindlimb. Abbreviations listed in text. Scale bar equals 1 m in A; 50 cm in B and C.

trolaterally from the hyposphene, a strongly developed intra-prezygapophyseal lamina, and aliform processes projecting laterally from the dorsal portion of the spinodiapophyseal lamina; hyposphene-hypantrum articulations in caudals 1–14; and a pedal phalangeal formula of 2-2-3-2-0.

Comments—Powell (1990) diagnosed the genus *Epachthosaurus* on the basis of several characters possessed by the holotype caudal dorsal vertebra (MACN-CH 1317); however, all were subsequently shown to be ambiguous or plesiomorphic (Salgado and Martinez, 1993; Salgado, 1996; Sanz et al., 1999). Powell (1990) also described the occurrence of an "interprezygapophyseal shelf" in the holotype caudal dorsal of *Epachthosaurus* (Salgado, 1996). Salgado (1996) maintained the validity of *Epachthosaurus* on the basis of this character, which he regarded as an autapomorphy of the taxon.

Powell (1990) designated MACN-CH 18689 as the "paraplastotype" of *Epachthosaurus*, based upon its possession of the characters listed in his diagnosis of the genus. However, because none of these features are considered diagnostic (see above), and MACN-CH 18689 does not appear to possess an "interprezygapophyseal shelf" in its caudal dorsal vertebrae, Salgado (1996) concluded that its inclusion within *Epachthosaurus* was not justified. Bonaparte and Coria (1993) and Salgado (1996) further questioned the systematic position of MACN-CH 18689, citing the occurrence of accessory articular

processes extending ventrolaterally from the hyposphene on the caudal dorsal vertebrae of the specimen that are not present in the holotype of *Epachthosaurus*. Based upon this character, they argued that MACN-CH 18689 pertains to a distinct genus with affinity to the giant titanosaur *Argentinosaurus*, which also possesses dorsal vertebrae with accessory articulations. However, Salgado and Martínez (1993) and Sanz et al. (1999) disputed the occurrence of the hyposphene in *Argentinosaurus*, identifying the accessory intervertebral articulations present in the taxon as modified centropostzygapophyseal laminae. Hence, the accessory articulations of *Argentinosaurus* and MACN-CH 18689 are probably not homologous, and the affinities of the latter remain in doubt.

The articulated skeleton described here (UNPSJB-PV 920) resolves several taxonomic issues concerning *Epachthosaurus*. Based upon its possession of a previously determined autapomorphy of the genus, a strongly developed intraprezygapophyseal lamina (="interprezygapophyseal shelf") on its middle and caudal dorsal vertebrae, we refer UNPSJB-PV 920 to *Epachthosaurus*. Furthermore, UNPSJB-PV 920 possesses accessory articular processes extending ventrolaterally from the hyposphene on its caudal dorsals, as in MACN-CH 18689. This character constitutes a synapomorphy of MACN-CH 18689 and UNPSJB-PV 920, and therefore justifies the original assessment of the former as the "paraplastotype" of *Epachthosaurus* (Powell, 1990). In summary, three titanosaurian specimens from the Lower Member of the Bajo Barreal Formation exposed on the Estancia "Ocho Hermanos" pertain to *Epachthosaurus*, and by monotypy, *E. sciuttoi* (MACN-CH 1317 and 18689, and UNPSJB-PV 920). We redesignate the "paraplastotype" MACN-CH 18689 as the paratype of the species, following the International Code of Zoological Nomenclature (Fourth Edition, Recommendation 73D).

DESCRIPTION

Axial Skeleton (Table 1)

Dorsal Vertebrae—All known dorsal vertebrae in *Epachthosaurus* are opisthocoelous. For positional assignments, we assume the presence of ten dorsals in *Epachthosaurus*, as hypothesized by Huene (1929) and shown in an articulated specimen of an unnamed Brazilian titanosaurian (MCT 1488-R; Powell, 1986, 1987b; Campos and Kellner, 1999). We recognize, however, that our assignments may be slightly inaccurate, as Borsuk-Bialynicka (1977) and Curry Rogers and Forster (2001) described eleven dorsals in the titanosaurians *Opisthocoelicaudia* and *Rapetosaurus*.

The fifth dorsal vertebra (Fig. 3A) is the cranialmost preserved. Although damaged by erosion, a large portion of the centrum is present. The cranial region and portions of the neural arch are missing. The centrum is dorsoventrally compressed with well-developed pleurocoels extending medially nearly to

TABLE 1. Vertebral centrum lengths (mm) of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*); * = element incomplete; †, vertebra without distal articular condyle.

|								
Dorsal vertebrae	5	6	7	8	9	10		
Centrum length	300	*	*	*	240	180		
Sacral vertebrae	1	2	3	4	5	6		
Centrum length	150	140	*	115	125	165		
Caudal vertebrae	1	2	3	4	5	6	7	8
Centrum length	130†	115	125	110	*	107†	172	177
Caudal vertebrae	9	10	11	12	13	14	15	16
Centrum length	178	162	115†	117†	270	175	130	177
Caudal vertebrae	17	18	19	20	21	22	23	24
Centrum length	181	175	180	*	135†	160	144	117†
Caudal vertebrae	25	26	27	28	29			
Centrum length	126†	138	130	132	130			
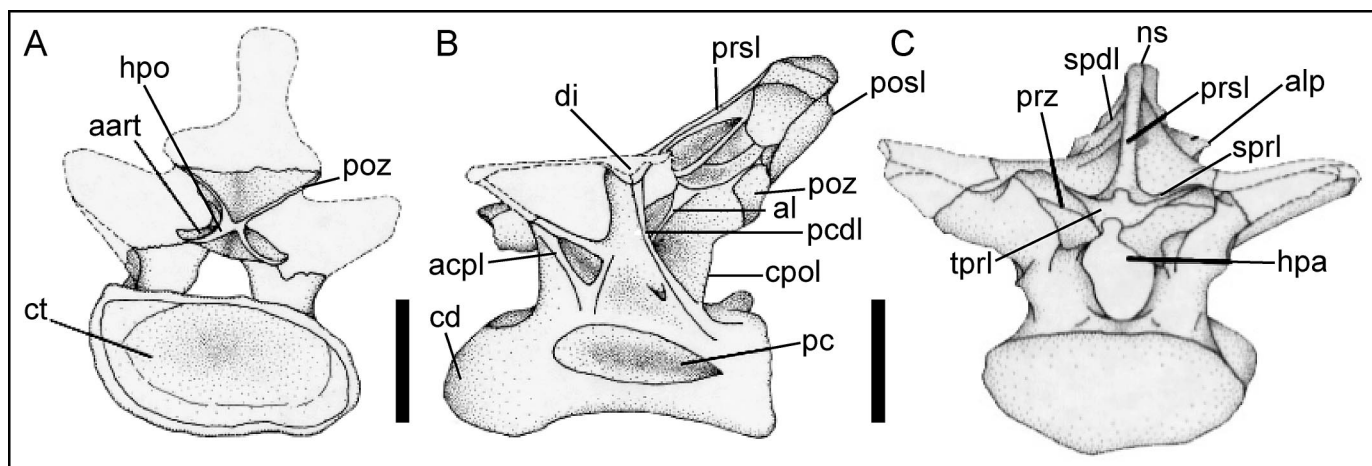
FIGURE 3.   Middle dorsal vertebrae of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, fifth dorsal, caudal view; **B**, sixth dorsal, left lateral view; **C**, sixth dorsal, cranial view. Abbreviations listed in text. Scale bars equal 10 cm.

the sagittal midline of the vertebra. The centrum displays a deeply concave caudal cotyle. On the neural arch, ventral to the postzygapophyses, laminae extend laterally and slightly ventrally from the hyposphene, producing accessory intervertebral articular surfaces.

The sixth dorsal (Fig. 3B, C) is one of the most complete, and has a dorsoventrally compressed, strongly opisthocoelous centrum resembling that of the fifth dorsal. The caudally acuminate pleurocoels deepen towards the cranial margin of the centrum. A weak right parapophysis and well-developed diapophyses are preserved. Laterally, an anterior centroparapophyseal lamina and two laminae of uncertain homology delimit a subtriangular cavity on the ventral portion of the neural arch, caudoventral to the parapophysis. A strong, slightly ventrally widened posterior centrodiapophyseal lamina is present. An accessory, caudodorsally-oriented lamina arises from the approximate midpoint of the posterior centrodiapophyseal lamina and widens dorsally before terminating between the postzygapophysis and diapophysis. This lamina is distinct from the centropostzygapophyseal lamina, which is also present (Wilson, 1999a).

Wilson (1999a) discussed the occurrence of an intraprezygapophyseal lamina in sauropod cervicals and cranial dorsals, but considered it absent caudal to dorsals 4–5. Nevertheless, a strongly developed horizontal lamina joins the prezygapophyses of the sixth dorsal in UNPSJB-PV 920. Curry Rogers and Forster (2001) listed a possibly equivalent character, a ''median interprezygapophyseal lamina'' on the dorsal vertebrae, as an autapomorphy of the Malagasy Late Cretaceous titanosaurian *Rapetosaurus*. Similarly, González-Riga and Calvo (2001) mentioned a prezygapophyseal ''platform'' on the middle caudals of an unnamed Upper Cretaceous titanosaurian from Neuquén Province in northern Patagonia. However, we maintain the distinction of these characters from that present in *Epachthosaurus*, pending further description of the Malagasy and northern Patagonian genera. We regard a strongly developed intraprezygapophyseal lamina (an ''interprezygapophyseal shelf'') on the caudal dorsal vertebrae as an autapomorphy of *Epachthosaurus* (Powell, 1990; Salgado, 1996).

Accessory hyposphenal processes on the sixth dorsal are similar to those on the fifth. The neural spine consists of prespinal, postspinal, and spinodiapophyseal laminae and is inclined caudodorsally. The well-developed prespinal lamina bifurcates ventrally into spinoprezygapophyseal laminae. On the right side, at midlength, the prespinal lamina intersects a small, robust lamina that extends approximately 50 mm ventrolaterally and delimits a pronounced cavity cranially. Subtriangular flattened expansions related to the postzygapophyses, here termed aliform processes, project laterally from the dorsal portions of the spinodiapophyseal laminae. These structures differ from the ''triangular processes'' identified by Upchurch (1995, 1998) on the dorsal neural spines of several macronarians, and represent another autapomorphy of *Epachthosaurus*. The postspinal lamina is weakly developed.

The centrum of the seventh dorsal is crushed and fractured, revealing cancellous internal tissue. The neural spine is more vertically inclined and craniocaudally thicker than in the fifth and sixth dorsals. The prespinal lamina is well-developed, and the cavity ventrolateral to it is deeper than in the previous vertebra and further delimited by a secondary ramus of the spinodiapophyseal lamina.

The eighth dorsal is heavily damaged by erosion. The neural spine is completely vertical and the prespinal lamina is more robust than in more cranial vertebrae.

The ninth dorsal (Fig. 4A, B, and C) is firmly articulated with the tenth. The centrum is slightly dorsoventrally compressed and its shape is nearly cylindrical. The neural spine is poorly preserved. Although the prespinal lamina is missing, a wide basal bifurcation is present, forming spinoprezygapophyseal laminae. A depression occurs between these laminae and the nearly vertical spinodiapophyseal lamina.

Because the centrum of the tenth dorsal (Fig. 4) is affixed to the ninth, many details of the cranial surface cannot be observed. However, the caudal articular surface is perfectly preserved. The hyposphene and accessory articular processes are well-developed. The neural arch possesses a weakly-developed postspinal lamina and robust spinopostzygapophyseal laminae that are separated by a wide depression. The distal end of the neural spine is not preserved.

Dorsal Ribs—Ten pairs of dorsal ribs were found, fractured, eroded, and displaced. The cranialmost ribs are triangular in cross-section proximally, becoming flat and wide distally. The caudal dorsal ribs are cylindrical in cross-section. Internally, they seem to be composed of a thin layer of spongy tissue. Generally, the ribs seem more slender than those of most other sauropods.

Sacrum—The sacrum (Figs. 5, 11A) includes six vertebrae. The cranial (of the 1st sacral) and caudal (of the 6th) articular condyles are convex; however, the latter is less so than the former. A subrectangular ossified ligament or tendon approxi-
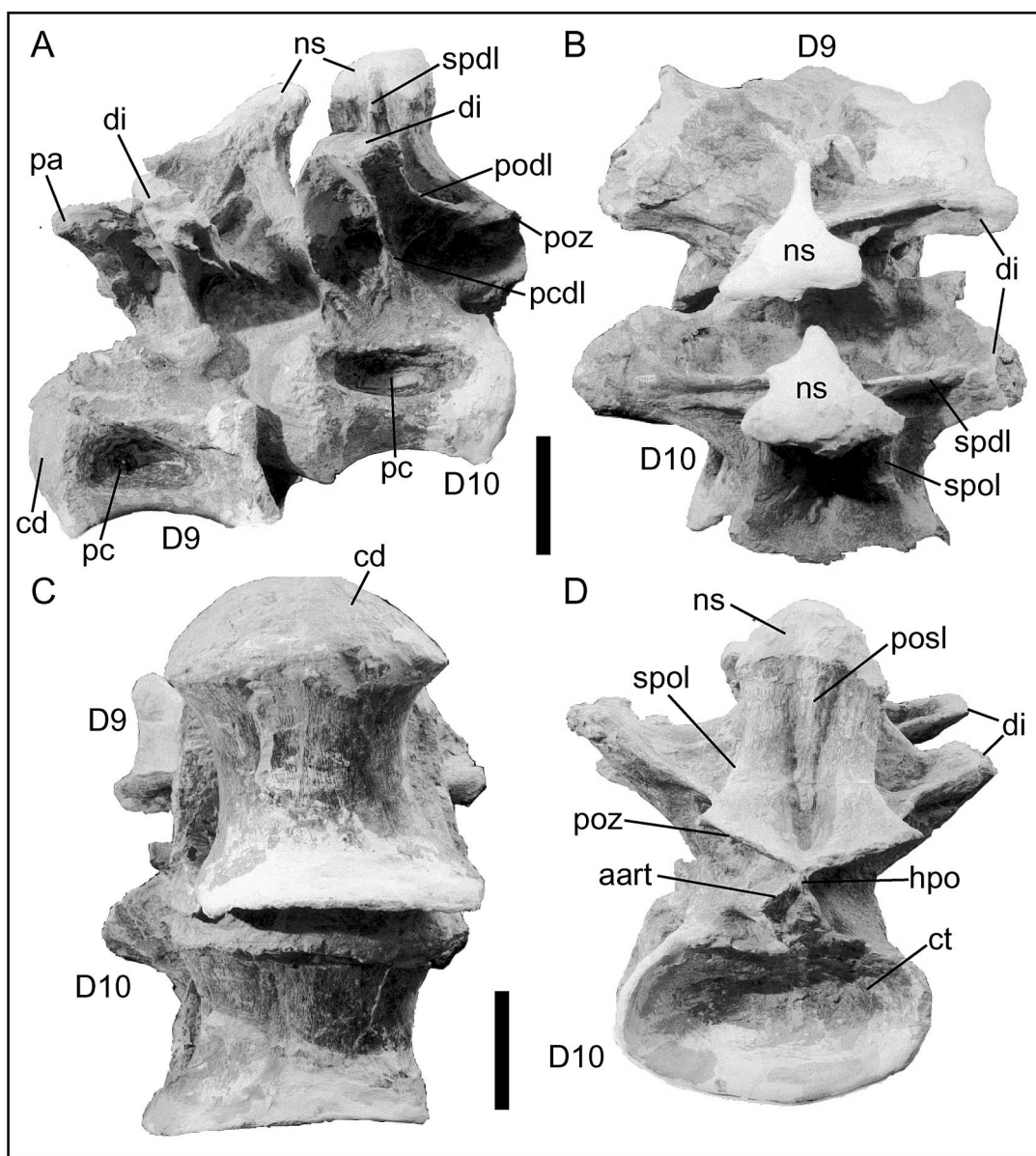
FIGURE 4. Ninth and tenth dorsal vertebrae of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, left lateral view; **B**, dorsal view; **C**, ventral view; **D**, caudal view. Abbreviations listed in text. Scale bars equal 10 cm.

mately 200 mm in transverse width, 800 mm in craniocaudal length, and 50 mm in dorsoventral depth connects the dorsal surfaces of all sacral neural spines. Longitudinal striations are present along the structure. A similar feature was reported in the specimen that the paratype of *Epachthosaurus* (MACN-CH 18689) was based upon (Powell, 1990; Bonaparte, 1996), and in a titanosaurian from Peirópolis, Brazil (MCT 1489-R, Powell, 1987b; Campos and Kellner, 1999). Although this structure is only preserved dorsal to sacrals 2–4 in the latter, it presumably connected all six (Powell, 1987b; Campos and Kellner, 1999).

The first sacral vertebra is similar in morphology to the caudal dorsals. The centrum is dorsoventrally compressed, but not as much as in the dorsal centra. In contrast with some titanosaurians (e.g., *Gondwanatitan*, Kellner and Campos, 1999; *Opisthocoelicaudia*, Borsuk-Bialynicka, 1977; "*Titanosaurus*" *colberti*, Jain and Bandyopadhyay, 1997), well-developed pleurocoels are present on the first sacral. Cranially, the hypantrum

is strongly developed. The damaged parapophyses are located directly ventral to the incomplete diapophyses. A section of the basally bifurcate prespinal lamina is preserved. The diapophyses are fused with the laterally expanded sacral ribs. Ventrally, the sutures between the remaining sacral centra are well-defined, as in MACN-CH 18689. Together with the ilium, the caudalmost four sacral ribs contribute to the formation of the acetabulum.

Caudal Vertebrae—The 29 preserved caudal vertebrae of UNPSJB-PV 920 are all procoelous. Hyposphene-hypantrum articulations occur in the first fourteen. These structures are morphologically distinct from the "hyposphenal ridges" reported in the caudal vertebrae of multiple sauropods by Upchurch (1998). Nevertheless, caudal hyposphene-hypantrum articulations are not unique to *Epachthosaurus*, as similar articulations occur in proximal and middle caudal vertebrae of an unnamed non-titanosaurian titanosauriform from the Early Cretaceous Paluxy Formation of Texas (SMU 61732; Langston,
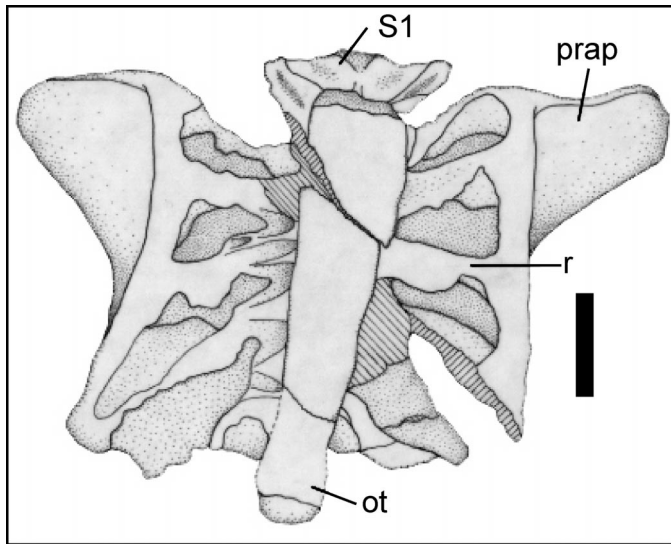
FIGURE 5. Sacrum and ilia of *Epachthosaurus sciuttoi* (UNPSJB-PV 920) in dorsal view. Abbreviations listed in text. Scale bar equals 20 cm.

1974; Gomani et al., 1999; Tidwell et al., 1999; Wedel et al., 2000). Caudal hyposphene-hypantrum articulations may thus be plesiomorphic for *Epachthosaurus*. However, such articulations are not reported in the titanosaurian *Andesaurus* (Calvo and Bonaparte, 1991), which probably occupies a more basal position than *Epachthosaurus* (Salgado and Martínez, 1993; Salgado et al., 1997). Consequently, we consider caudal hyposphene-hypantrum articulations as an autapomorphy of the latter.

We restrict our description to three general regions of the tail that illustrate the morphological changes that occur through the series. The somewhat deformed first caudal (Fig. 6) has a robust centrum with a gently concave and subcircular proximal cotyle. The centrum is also concave ventrally and laterally. The transverse processes emerge from the dorsal portion of the centrum at approximate right angles. Planar expansions on the distal surfaces of the transverse processes may articulate with the transverse processes of the second caudal, but this is impossible to determine due to damage to the latter. The neural arch is situated over the proximal half of the centrum. The neural spine is robust and distally inclined at an angle of 50° from the horizontal. The prespinal lamina is stout. The prezygapophyses arise from a pair of spinoprezygapophyseal laminae that originate at the base of the neural spine. The diameter of the neural canal is very small. The distal margin of the postspinal lamina is poorly developed and is flanked by two strong spinopostzygapophyseal laminae. The postzygapophyses are slender with distolaterally oriented articular faces.

The centrum of the second caudal (Fig. 6A, C) remains articulated with, and is similar to, that of the first. The articular condyle protrudes distally nearly as far as the remainder of the centrum is long. The transverse processes are not preserved. The neural spine is shorter and more distally inclined than that of the first caudal. The third caudal vertebra, damaged by erosion and missing the neural arch, has a deep, concave proximal cotyle.

The seventh caudal (Fig. 7) has a procoelous centrum with a strongly convex distal articular condyle. The apex of the condyle occurs in the dorsal half of the centrum. The stout transverse processes are deflected distally. The prezygapophyses are powerfully developed and extend far past the proximal margin of the centrum. Hyposphene-hypantrum articular facets are
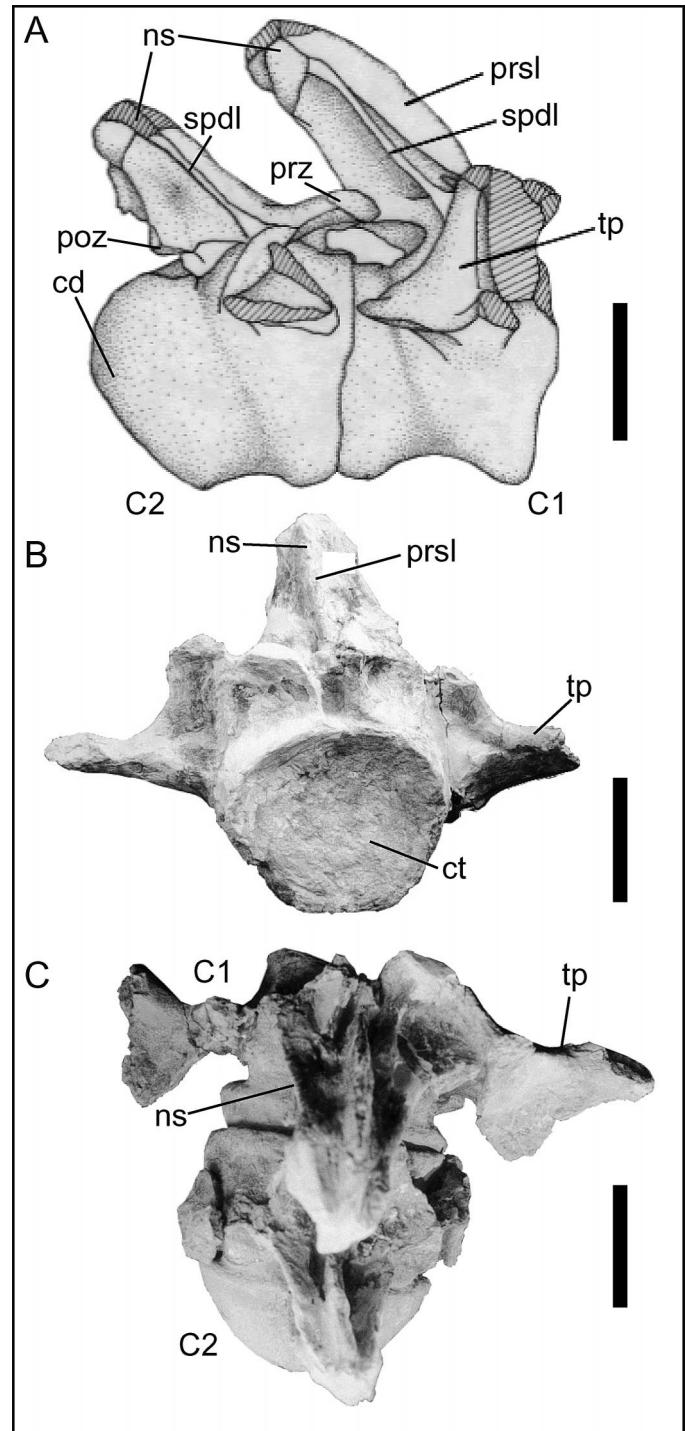

FIGURE 6. First and second caudal vertebrae of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, right lateral view; **B**, proximal view; **C**, dorsal view. Abbreviations listed in text. Scale bars equal 10 cm.

clearly present. The neural spine is proximodistally elongate and generally transversely compressed. Nevertheless, it is slightly transversely expanded dorsally.

Compared with the proximal caudal vertebrae, the tenth (Fig. 8A) and eleventh caudals have proportionally poorly developed distal articular condyles. The centra are proximally concave and possess a well-delineated longitudinal groove ventrally. The neural arches are based within the proximal halves of the centra,
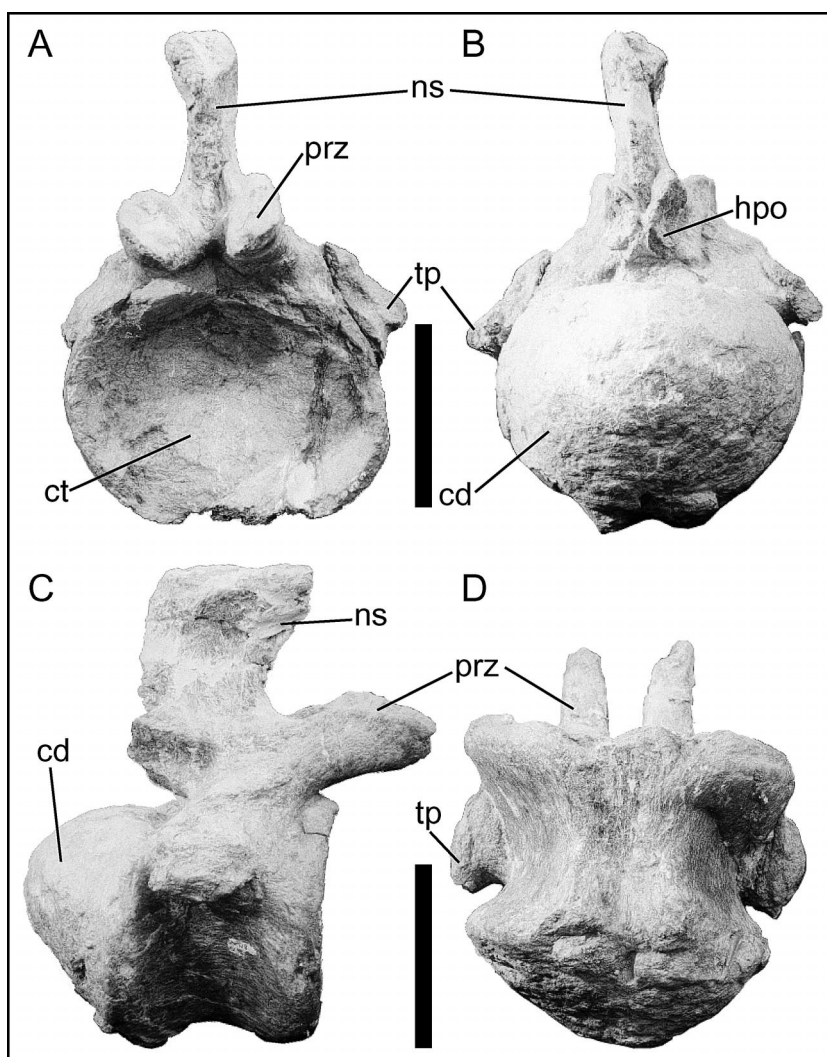
FIGURE 7.   Seventh caudal vertebra of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, proximal view; **B**, distal view; **C**, right lateral view; **D**, ventral view. Scale bars equal 10 cm.

but do not reach their margins, and bear short, horizontal prezygapophyses with medially facing articular surfaces. The vertical, plate-like neural spines are proximodistally elongate. The transverse processes are reduced to ridges located on the dorsal portions of the centra. The postzygapophyses are weak.

The most distal caudal vertebrae, the 27th, 28th (Fig. 8B), and 29th, are approximately the same length as the proximal caudals. The centra are cylindrical and retain traces of longitudinal ventral sulci. The neural arches are placed on the proximal halves of the centra, slightly distal to their margins. The postzygapophyses are fused ventral to vestigial neural spines.

Haemal Arches—19 articulated haemal arches are preserved. The haemal canal is open dorsally and the oval articular surfaces are directed distally and slightly medially. Haemapophysis two has a transversely widened, laminar spine with a thick, round distal border and a sharp proximal margin. Haemal arch 13 has an enlarged haemal canal and a spine less expanded ventrally. Haemapophysis 16 has a wide canal with a reduced spine.

Appendicular Skeleton

Pectoral Girdle—The scapulae and coracoids are poorly preserved. However, the sternal plates, although damaged, ex-

hibit the semilunar contour typical of titanosaurians. The sternal plates have thick, rounded, and concave lateral margins. Ventral crests that articulate with the coracoids are present craniolaterally.

Forelimb (Table 2)—The humerus (Fig. 9A) is of typical sauropod structure with a flat, craniocaudally compressed shaft. The epiphyses are transversely expanded. The proximal and lateral margins of the humerus meet at an approximate right angle. As in several titanosaurs, a process is present proximolaterally that possibly marks the insertion of the supracoracoideus muscle (Borsuk-Bialynicka, 1977; Giménez, 1992; Upchurch, 1998). The deltopectoral crest is strongly developed, and occupies much of the proximal half of the humeral craniolateral margin. In lateral view, the crest is convex, and its distal portion is directed craniomedially. The edge of the crest is rugose, marking the insertion of the pectoral muscle. The humeral head is round, craniocaudally convex, and inclined caudally. The medial projection is subtriangular and not clearly separated from the head. The radial condyle is more strongly developed and rounded than the ulnar.

The ulna (Fig. 9B, C) is more robust than the radius. Its proximal end is triradiate with a prominent olecranon process, and has three well-defined crests delimiting concave surfaces
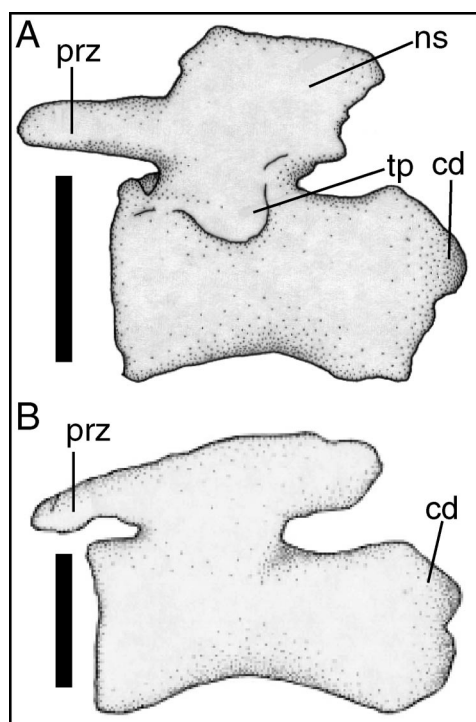
FIGURE 8. Middle and distal caudal vertebrae of *Epachthosaurus sciuttoi* (UNPSJB-PV 920) in left lateral view. **A**, tenth; **B**, 28th. Abbreviations listed in text. Scale bar equals 10 cm in A; 5 cm in B.

that extend the length of the element. The radial articular surface is wide, well defined throughout its proximal third, and projects cranially toward its distal end. The flat distal articular surface is semicircular in outline.

The radius (Fig. 9D) is slightly sigmoid. The proximal region bears a pointed tuberosity. The distal portion of the ulnar articular surface possesses a smooth longitudinal depression, delimited by two ridges. The distal ridge is the more prominent of the two and contacts the medial protuberance of the cranial face of the ulna. The distal articular surface is elliptical with the long axis of the ellipse oriented mediolaterally.

The carpals are not preserved in either forelimb of UNPSJB-PV 920, and were probably unossified. There are five metacarpals (Fig. 10) in each manus. All were found articulated and in excellent condition, especially those of the right manus. When articulated, they intersect at their distal ends, forming a vertically oriented cylinder. This configuration allowed them to efficiently support the great weight they carried.

The proximal articular surfaces of the metacarpals (Table 3) are rugose. They are subtriangular in cross-section, with the bases of the triangles directed externally. The metacarpals become subrectangular in cross-section distally. Metacarpal I is the most robust of the series, and has a straight shaft. Metacarpal II is the same length as the first, but has a slightly sigmoid shaft. The third, fourth, and fifth metacarpals show a progres-

sive decrease in length. The shaft of the fourth metacarpal is compressed at both ends, while metacarpal V is nearly straight.

With the exception of a vestigial element fused to the distal surface of metacarpal IV, no phalanges are present. A nearly identical condition is present in the Mongolian titanosaurian *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). This corroborates the hypothesis that the manual phalanges of titanosaurian sauropods were strongly reduced, unossified, or absent (Giménez, 1992; Salgado et al., 1997).

Pelvic Girdle (Table 4)—The pelvic elements were found slightly displaced, but articulated. The ilium (Figs. 2, 5, 11A) is low, elongate, and internally composed of cancellous tissue. The preacetabular process is damaged, relatively craniocaudally short, and expanded craniolaterally. The pubic peduncle is cranially inclined and transversely elongate. The ischiadic peduncle is only slightly developed, demarked by a smooth convexity ventral to the postacetabular process.

The pubis (Fig. 11B) is heavily damaged caudally, but appears to be a long, flattened element with expanded proximal and distal ends. The lateral margin of the pubis is concave ventrally. On the lateral surface, at the approximate proximodistal midpoint of the element, there is a process for muscular insertion. In both pubes, the middle region of the shaft and the medial process that articulates with the corresponding pubis are deformed. The pubes are strongly thickened distally.

The ischium (Fig. 11C), although badly damaged, appears flattened and shorter than the pubis. It is expanded proximally at the iliac peduncle. The left ischium preserves the pubic and iliac articular surfaces. In dorsomedial view, the ischium displays a pronounced lateral thickness that thins distally and medially.

Hindlimb (Table 5)—The left femur is deformed proximally. For this reason, our description is based principally on the right (Fig. 12A). The right femur is a long and straight bone, damaged in the region of the femoral head. The femoral head extends further dorsally than the greater trochanter and does not project strongly medially. A proximolateral buttress is present, as in most titanosauriforms. Caudomedially, the fourth trochanter emerges as a well-developed ridge approximately halfway down the shaft. Distally, the fibular condyle is divided into medial and lateral portions by a marked subvertical sulcus, and separated from the strongly developed tibial condyle by a poorly defined depression. The tibial condyle articulates with a median concavity on the proximal surface of the tibia.

The tibia (Fig. 12B) is slender and more expanded proximally than distally. The most elevated region of the tibia is laterally positioned and articulates with the intercondylar depression of the femur, between the tibial and fibular condyles. The transversely narrow, proximodistally lengthened, and craniocaudally deep cnemial crest is craniolaterally directed and delineated laterally by a cavity. The proximal tibial surface is rugose but relatively flat, whereas the distal surface possesses a strong, ventrally directed process for articulation with the astragalus.

The fibula (Fig. 12C) is slender with a slightly craniocaudally expanded proximal end. It is ovoid in cross-section distally. The lateral surface of the fibula is convex while its medial surface is flat. Its most notable character is the presence of a prominent

TABLE 2. Measurements (mm) of humerus, ulna, and radius of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*).

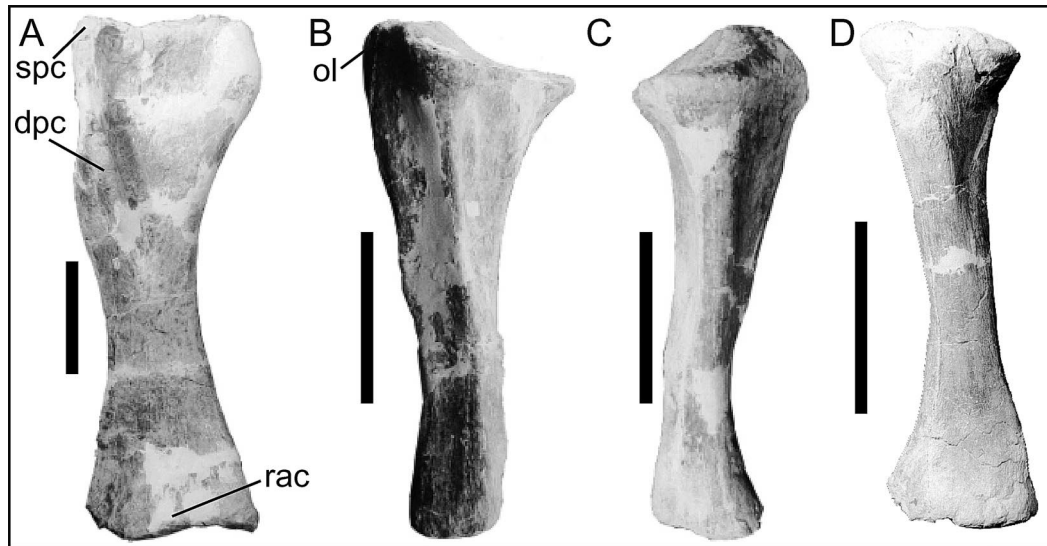|	Right humerus	Left humerus	Right ulna	Left ulna	Right radius	Left radius
Proximodistal length	885	935	597	613	530	550
Proximal transverse width	300	320	255	250	165	165
Distal transverse width	290	290	140	145	190	160
Transverse width, shaft	165	160	105	105	80	80
Shaft circumference	420	425	340	335	240	240

FIGURE 9.   Right forelimb elements of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, humerus, cranial view; **B**, ulna, cranial view; **C**, ulna, lateral view; **D**, radius, craniolateral view. Abbreviations listed in text. Scale bars equal 20 cm.
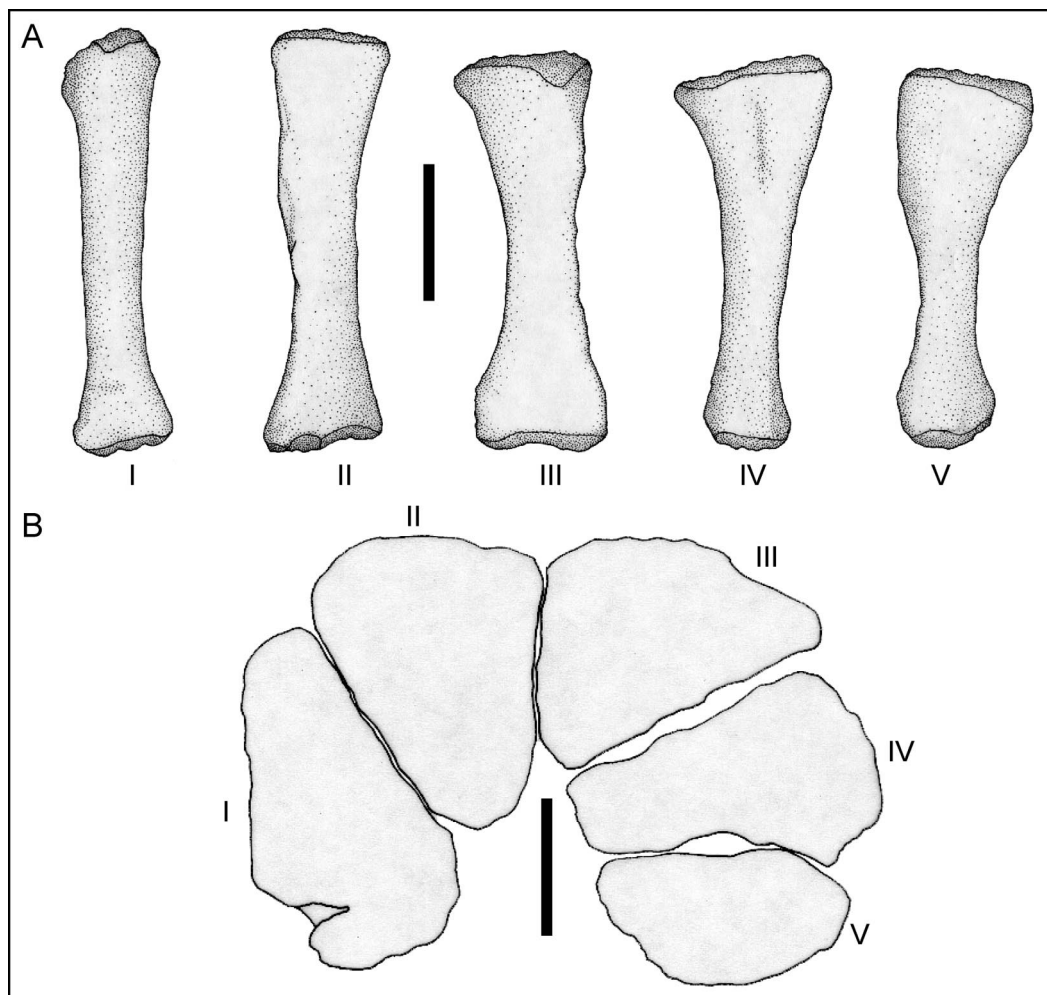

FIGURE 10.   Right metacarpus of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, cranial view; **B**, proximal view. Scale bar equals 10 cm in A; 5 cm in B.

TABLE 3. Proximodistal lengths (mm) of metacarpals of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*).

Right	I	II	III	IV	V
Length	305	303	295	275	268
Left	I	II	III	IV	V
Length	288	297	297	284	270

TABLE 4. Lengths (mm) of right ilium, pubis, and ischium of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*); * = element incomplete.

	Ilium	Pubis	Ischium
Length	770	670	440*

dual tuberosity at midshaft on its lateral surface. This structure, the lateral trochanter, is slightly obliquely directed with respect to the long axis of the shaft.

Articulated astragali (Fig. 12D) were recovered for both hindlimbs. Each is subtriangular, robust, and has a proximodistally elevated and thick lateral portion that gradually decreases in height and thickness medially. The ascending process articulates with a depression in the craniodistal portion of the tibia. The proximal portion of the ascending process is wide and possesses a facet that articulates with the distomedial margin of the fibula. The craniodistal face is elliptical and slightly medio-laterally convex. This grades into a rounded surface that articulates with the proximal ends of metatarsals I, II, and III. The entire astragalar surface displays rugosities typical of cartilaginous insertion. There is no ossified calcaneum in *Epachthosaurus*.

The pedes are complete and articulated in both hindlimbs of UNPSJB-PV920 (Table 6; Fig. 13). *Epachthosaurus* is thus the first South American titanosaurian for which pedal morphology is completely known. The foot is of graviportal structure and retains five radially arranged digits. The foot is wide, with short metatarsals with expanded proximal ends. The metatarsophalangeal articular surfaces are well-developed, and suggest considerable mobility at the majority of the joints. Proximally, the five metatarsals are closely abutted, forming a wide articular surface for the astragalus. The first metatarsal is the most robust. Metatarsals I–IV gradually increase in length sequentially, but metatarsal V is slightly shorter than metatarsal IV.

A possible autapomorphy of *Epachthosaurus* is the reduction of its pedal phalangeal formula to 2-2-3-2-0. The first three digits possess claws. Those of digits I and II are nearly identical, but that of digit III is smaller. The articular surfaces of the ungual phalanges are inclined, suggesting mobility in horizontal and vertical planes, as in an unnamed titanosauriform from the Early Cretaceous of Texas (Gallup, 1989). A keratinous sheath probably covered the claws in life.

Dermal Skeleton—No osteoderms were recovered with UNPSJB-PV 920, and we consequently assume that *Epachthosaurus* was unarmored.

Weight of *Epachthosaurus*—T. Galarza and J. Gallegos (pers. comm., 1998) attempted to determine the live weight of UNPSJB-PV 920. They made a scale model of this individual of *Epachthosaurus* and followed the method outlined by Alexander (1989), obtaining a weight estimate of 11,290 kg.

COMPARISONS

We compared UNPSJB-PV 920 to several Cretaceous South American titanosaurian genera, including the plesiomorphic *Andesaurus* and the more derived *Argentinosaurus*, *Argyrosaurus*, and *Saltasaurus*. *Epachthosaurus* was also compared to the Late Cretaceous Mongolian sauropod *Opisthocoelicaudia*, which has been recently recognized as a titanosaurian (Giménez, 1992; Salgado and Coria, 1993b; Upchurch, 1995, 1998; Salgado et al., 1997; Calvo et al., 1998; Wilson, 1999b).

***Andesaurus delgadoi* (Calvo and Bonaparte, 1991)**—The caudal dorsal centra of *Andesaurus* are weakly opisthocoelous and their neural arches and spines are more dorsally elevated than in *Epachthosaurus*. *Andesaurus* has hyposphene-hypantrum articulations in its caudal dorsal vertebrae, as in *Epachthosaurus*, but the hyposphene of the latter is apomorphically developed, with accessory articular processes extending ventrolaterally. The taxa share several titanosaurian plesiomorphies such as dorsal neural spines with well-developed prespinal laminae that bifurcate ventrally into spinoprezygapophyseal laminae, and reduced postspinal laminae. Unlike *Epachthosaurus*, *Andesaurus* has amphiplatyan caudal vertebrae. The retention of this plesiomorphic character, among others, relegates *Andesaurus* to a basal position within Titanosauria (Salgado and Martínez, 1993; Salgado et al., 1997; Upchurch, 1998).

***Argentinosaurus huinculensis* (Bonaparte and Coria, 1993)**—Although the extremely large titanosaurian *Argentinosaurus* possesses accessory intervertebral articulations in its dorsal column, they are anatomically distinct from those of *Epachthosaurus* (Salgado and Martínez, 1993; Sanz et al., 1999). Moreover, *Argentinosaurus* possesses reduced, non-bifurcate prespinal laminae, implying that this taxon may be more highly derived than *Epachthosaurus* (Salgado et al., 1997). Contrary to the condition in *Epachthosaurus*, sutures between the fused sacral vertebrae of *Argentinosaurus* are indistinct in ventral view (Powell, 1990; Bonaparte and Coria, 1993), although this could be of ontogenetic rather than phylogenetic significance. The fibula of *Argentinosaurus*, originally considered a tibia, (Wilson and Sereno, 1998, contra Bonaparte and Coria, 1993) differs from that of *Epachthosaurus* because it lacks a dual tuberosity in its proximal half.

***Argyrosaurus superbus* (Lydekker, 1893; Bonaparte and Gasparini, 1979; Powell, 1986)**—*Argyrosaurus* is a large titanosaurian originally based upon a left forelimb, MLP 77-V-
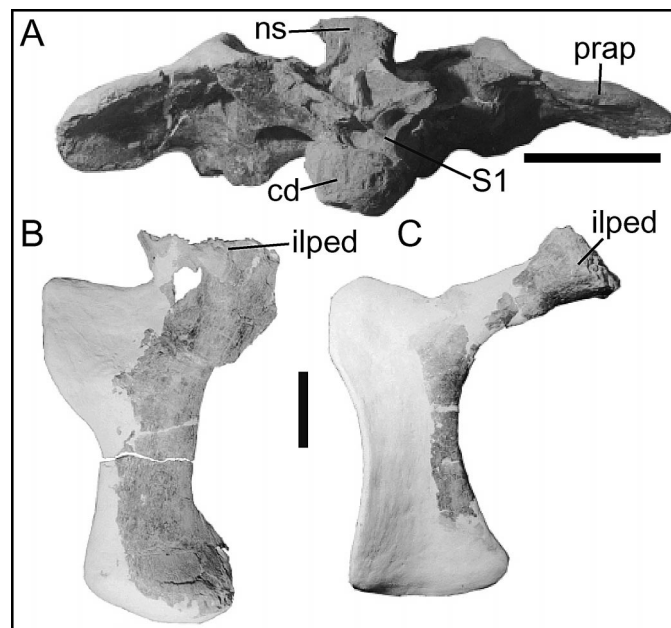

FIGURE 11. Pelvis and reconstructed right pubis and ischium of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, sacrum and ilia, cranial view; **B**, pubis, dorsal view; **C**, ischium, ventral view. Scale bars equal 20 cm.

TABLE 5.   Measurements (mm) of femur, tibia, and fibula of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*); * = element incomplete.

	Right femur	Right tibia	Left tibia*	Right fibula	Left fibula
Proximodistal length	1095	700	662	730	725
Proximal transverse width	340	210	—	150	155
Distal transverse width	310	185	—	110	110
Shaft transverse width	230	130	—	80	80
Shaft circumference	550	335	—	220	215

29-1, possibly from the Bajo Barreal Formation (Lydekker, 1893; Huene, 1929; Bonaparte, 1996). PVL 4628, a titanosaurian partial skeleton, also probably from the Bajo Barreal Formation, has been tentatively referred to *Argyrosaurus* (Powell, 1986; Bonaparte, 1996). As in *Epachthosaurus*, the middle dorsal vertebra of PVL 4628 possesses a lamina that arises from the ventral region of the posterior centrodiapophyseal lamina and terminates between the postzygapophysis and diapophysis (Bonaparte, 1999b). Nevertheless, the dorsal pleurocoels of PVL 4628 are less extensive than in *Epachthosaurus*, and its neural arches and spines are dorsally elevated. Moreover, the preserved caudal dorsal of PVL 4628 is only weakly opisthocoelous. Appendicular elements of MLP 77-V-29-1 and PVL 4628 are similar to those of *Epachthosaurus*. Further study of MLP 77-V-29-1 and PVL 4628 is needed to clarify the status of the genus *Argyrosaurus*, and its possible affinity to *Epachthosaurus*.

***Saltasaurus loricatus* (Bonaparte and Powell, 1980; Powell, 1992)**—The dorsal neural arches of *Saltasaurus* are dorsally elevated, transversely narrow, and have dorsally deflected diapophyses, characters absent in *Epachthosaurus*. The dorsal vertebrae of *Saltasaurus* also differ from those of *Epachthosaurus* in their possession of reduced, undivided prespinal laminae and weakly developed pleurocoels, and their lack of hyposphene-hypantrum articulations. The caudal vertebrae of *Saltasaurus* have proximally-placed neural arches, similar to the condition in *Epachthosaurus*. Appendicular elements of *Saltasaurus* are similar to those of UNPSJB-PV 920.

***Opisthocoelicaudia skarzynskii* (Borsuk-Bialynika, 1977)**—The Mongolian titanosaur *Opisthocoelicaudia* shares many anatomical characters with *Epachthosaurus*, including opisthocoelous dorsal vertebrae with caudally acuminate pleurocoels, low neural arches, and centroparapophyseal laminae; six sacral vertebrae; laterally concave sternal plates; metacarpals with nearly flat articular surfaces; metacarpals I and II subequal in length with symmetrical distal ends; one rudimentary manual phalanx; and a reduced pedal phalangeal formula. All of these characters appear to be synapomorphies of Titanosauria or more inclusive sauropod clades and probably are not reflective of particularly close relationships between *Opisthocoelicaudia* and *Epachthosaurus* within Titanosauria (Giménez, 1992; Salgado et al., 1997). Differences between *Opisthocoelicaudia* and *Epachthosaurus* include bifurcate neural spines in the cranial dorsal vertebrae and opisthocoelous proximal caudal vertebrae in the former.

DISCUSSION

Titanosauria, a term first proposed by Bonaparte and Coria (1993), includes all somphospondylian sauropod dinosaurs more closely related to *Saltasaurus* than to *Euhelopus* (Sereno, 1998). Titanosaurians were initially known principally from fragmentary remains; however, several relatively complete specimens have been identified in recent years (e.g., Powell, 1992; Jain and Bandyopadhyay, 1997; Curry Rogers and Forster, 2001). *Epachthosaurus sciuttoi* is clearly titanosaurian, as it possesses multiple proposed synapomorphies of the clade and subclades nested within it, including caudal dorsal vertebrae with ventrally expanded posterior centrodiapophyseal laminae; six sacral vertebrae; procoelous proximal, middle, and distal caudal centra with well-developed distal articular condyles; semilunar sternal plates with cranioventral ridges; humeri with squared proximolateral margins and proximolateral processes; unossified carpals; strongly reduced manual phalanges; craniolaterally expanded, nearly horizontal iliac preacetabular processes; pubes longer than ischia; and transversely expanded ischia (Giménez, 1992; Salgado and Coria, 1993b; Salgado et al., 1997; Upchurch, 1995, 1998; Wilson and Sereno, 1998; Sanz et al., 1999; Wilson, 1999b; Curry Rogers and Forster, 2001). *Epachthosaurus* is the probably the most basal titanosaurian known that possesses the derived character of procoelous cau-
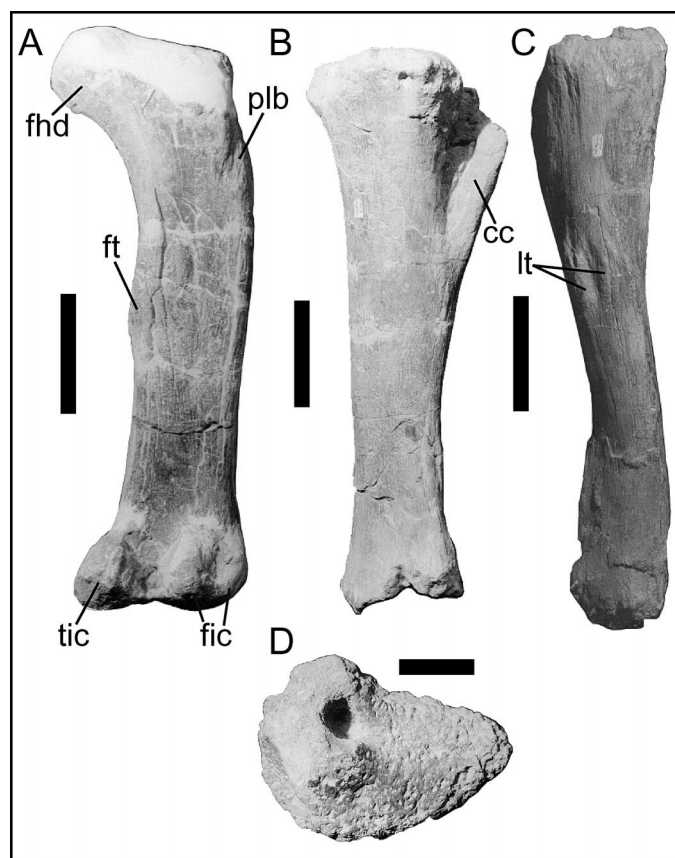

FIGURE 12.   Right hindlimb elements of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, femur, caudal view; **B**, tibia, craniolateral view; **C**, fibula, lateral view; **D**, astragalus, cranial view. Scale bar equals 20 cm in A-C; 5 cm in D.

TABLE 6.   Proximodistal lengths (mm) of right metatarsals of UNPSJB-PV 920 (*Epachthosaurus sciuttoi*).

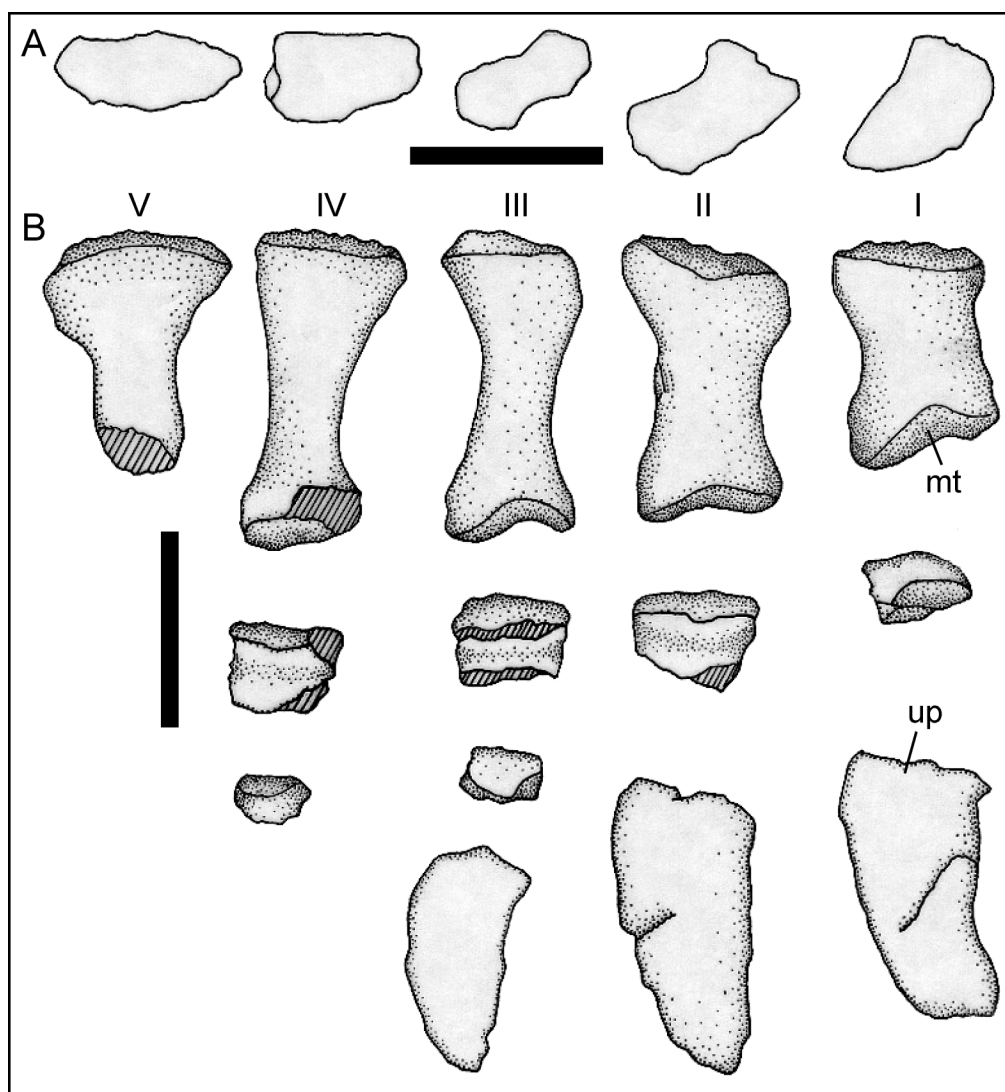|	I	II	III	IV	V
Length	125	153	177	185	153

FIGURE 13.   Right pes of *Epachthosaurus sciuttoi* (UNPSJB-PV 920). **A**, proximal view; **B**, cranial view. Scale bar equals 10 cm.

dal vertebrae. It is intermediate in phylogenetic position between *Andesaurus*, in which all known caudals are amphiplatyan, and most remaining titanosaurians. A forthcoming titanosaurian cladistic analysis that includes *Epachthosaurus* promises to more accurately determine its phylogenetic position (Giménez, unpubl. data).

Epachthosaurus is now among the most completely known titanosaurian genera, and provides insight into several issues concerning the anatomy and evolutionary history of the clade. The sacral vertebrae in *Epachthosaurus* are dorsally united by an ossified ligament or tendon, otherwise described only in an unnamed titanosaurian from the Late Cretaceous of Brazil (Powell, 1987b; Campos and Kellner, 1999). This character may reflect close affinity between these taxa; alternately, it may eventually be found to be synapomorphic of a more inclusive subclade within Titanosauria. Additionally, ossified ligaments or tendons probably developed in several regions of the titanosaurian skeleton, as they were reported associated with the cervical vertebrae of a probable new titanosauriform from the Bajo Barreal Formation (Martínez, 1998), the caudal dorsal neural spines of the specimen upon which the paratype of *Epachthosaurus* (MACH-CH 18689) is based (Powell, 1990; Bonaparte, 1996), and the iliac preacetabular processes of the

titanosaurian ''*Titanosaurus*'' *colberti* (Jain and Bandyopadhyay, 1997). Sanz et al. (1999) hypothesized that similar structures were connected to the planar dorsal surfaces of the caudal dorsal diapophyses in several titanosaurians, including *Lirainosaurus*, *Saltasaurus*, and an unnamed genus from Peirópolis, Brazil.

Epachthosaurus possesses apomorphically developed hyposphene-hypantrum articulations in its dorsal, sacral, and proximal to middle caudal vertebrae. This contrasts with the condition in *Andesaurus*, in which hyposphene-hypantrum articulations are limited to the dorsal vertebrae, and most remaining titanosaurians, in which these structures are absent. Accessory intervertebral articulations, along with ossified ligaments or tendons associated with the caudal dorsal and sacral vertebrae, probably would have greatly increased the rigidity of the axial skeleton in *Epachthosaurus* relative to other sauropods. The functional significance of this situation requires further research.

Several titanosaurians, including *Aeolosaurus* (Salgado and Coria, 1993a), *Ampelosaurus* (Le Loeuff et al., 1994; Le Loeuff, 1995), *Laplatasaurus* (Huene, 1929; Powell, 1980), *Lirainosaurus* (Sanz et al., 1999), *Malawisaurus* (Jacobs et al., 1993; Gomani, 1999), *Neuquensaurus* (Huene, 1929; Powell,

1980), and *Saltasaurus* (Bonaparte and Powell, 1980; Powell, 1980, 1992), and the possible titanosaurian *Agustinia* (Bonaparte, 1999a) are reported to possess osteoderms. Moreover, reports of isolated osteoderms associated with or attributed to titanosaurians are numerous and geographically widespread (e.g., Depéret, 1896; Sanz and Buscalioni, 1987; Chatterjee and Rudra, 1996; Azevedo and Kellner, 1998; Dodson et al., 1998; Csiki, 1999). Nevertheless, UNPSJB-PV 920, a largely complete, articulated skeleton, lacks a dermal skeleton; thus, armor was probably absent in *Epachthosaurus*. Whether this character represents the retention of a plesiomorphic state or constitutes a reversal is unresolved. Interestingly, the extreme development of hyposphene-hypantrum articulations and absence of dermal elements in *Epachthosaurus* is consistent with Le Loeuff et al.'s (1994) hypothesis that osteoderms may have served to limit dorsal mobility in titanosaurians, most of which lack these articulations.

ACKNOWLEDGMENTS

LITERATURE CITED

Alexander, R. M. 1989. Dynamics of Dinosaurs and Other Extinct Giants. Columbia Press, New York, 167 pp.

Archangelsky, S., E. S. Bellosi, G. A. Jalfin, and C. Perrot. 1994. Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. Cretaceous Research 15:127–142.

Azevedo, S. A. K., and A. W. A. Kellner. 1998. A titanosaurid (Dinosauria, Sauropoda) osteoderm from the Upper Cretaceous of Minas Gerais, Brazil. Boletim do Museu Nacional, Nova Serie 44:1–6.

Bonaparte, J. F. 1986. History of the terrestrial Cretaceous vertebrates of Gondwana; pp. 63–95 in J. F. Bonaparte (ed.), Evolucion de los Vertebrados Mesozoicos, IV Congreso Argentino de Paleontologia y Biostratigrafia Mendoza.

Bonaparte, J. F. 1996. Cretaceous tetrapods of Argentina. Munchner Geowissenschaftliche Abhandlungen A 30:73–130.

Bonaparte, J. F. 1999a. An armoured sauropod from the Aptian of northern Patagonia, Argentina; pp. 1–12 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwana Dinosaur Symposium, National Science Museum Monographs 15. National Science Museum of Tokyo, Tokyo.

Bonaparte, J. F. 1999b. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana 36:115–187.

Bonaparte, J. F., and G. Bossi. 1967. Sobre la presencia de dinosaurios en la Formación Pirgua del Grupo Salta y su significado cronológico. Acta Geologica Lilloana 9:25–44.

Bonaparte, J. F., and R. A. Coria. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formacíon Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. Ameghiniana 30:271–282.

Bonaparte, J. F., and Z. B. de Gasparini. 1979. Los saurópodos de los grupos Neuquén y Chubut y sus relaciones cronológicas. Actas V Congreso Geológico Argentino, Neuquén 2:393–406.

Bonaparte, J. F., and J. E. Powell. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). Mémoire de la Société Géologique de France, N.S. 139:19–28.

Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. Acta Palaeontologica Polonica 37:1–64.

Bridge, J. S., G. A. Jalfin, and S. M. Georgieff. 2000. Geometry, lithofacies, and spatial distribution of Cretaceous fluvial sandstone bodies, San Jorge Basin, Argentina: outcrop analog for the hydrocarbon-bearing Chubut Group. Journal of Sedimentary Research 70:341–359.

Broin, F. de Lapparent de, and M. S. de la Fuente. 2001. Oldest world Chelidae (Chelonii, Pleurodira), from the Cretaceous of Patagonia, Argentina. Comptes Rendus de l'Académie des Sciences-Serie IIA-Sciences de la Terre et des Planètes 333:463–470.

Calvo, J. O., and J. F. Bonaparte. 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. Ameghiniana 28:303–310.

Calvo, J. O., R. A. Coria, and L. Salgado. 1997. Uno de los mas completos Titanosauridae (Dinosauria—Sauropoda) registrados en el mundo. Ameghiniana 34:534.

Calvo, J. O., J. Porfiri, C. Veralli, and F. Poblete. 2001. One of the largest titanosaurid sauropods ever found, Upper Cretaceous, Neuquén, Patagonia, Argentina. Journal of Vertebrate Paleontology 21(3, Supplement):37A.

Calvo, J. O., , L. Salgado, and R. A. Coria. 1998. Consideraciones sobre las relaciones filogeneticas de *Nemegtosaurus mongoliensis* (Sauropoda) del Cretacico superior de Mongolia. Acta Geologica Lilloana 18:156.

Campos, D. de A., and A. W. A. Kellner. 1999. On some sauropod (Titanosauridae) pelves from the continental Cretaceous of Brazil; pp. 143–166 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwana Dinosaur Symposium, National Science Museum Monographs 15. National Science Museum of Tokyo, Tokyo.

Casal, G., M. Luna, L. Ibiricu, E. Ivany, R. Martínez, M. Lamanna, and A. Koprowski. In press. Hallazgo de una serie caudal articulada de Sauropoda (Dinosauria) de la Formación Bajo Barreal, Cretácico Superior del sur de Chubut. Ameghinana.

Chatterjee, S., and D. K. Rudra. 1996. KT events in India: impact, rifting, volcanism and dinosaur extinction. Memoirs of the Queensland Museum 39:489–532.

Chiappe, L. M., L. Salgado, and R. A. Coria. 2001. Embryonic skulls of titanosaur sauropod dinosaurs. Science 293:2444–2446.

Csiki, Z. 1999. New evidence of armoured titanosaurids in the Late Cretaceous—*Magyarosaurus dacus* from the Hateg Basin (Romania). Oryctos 2:93–99.

Curry Rogers, K. C., and C. A. Forster. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. Nature 412:530–534.

Depéret, C. 1896. Note sur les dinosauriens sauropodes et théropodes du Crétacé supérieur de Madagascar. Bulletin de la Société Géologique de France, 3e Série 24:176–194.

Dodson, P., D. W. Krause, C. A. Forster, S. D. Sampson, and F. Ravoavy. 1998. Titanosaurid (Sauropoda) osteoderms from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 18:563–568.

Gallup, M. R. 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. Geological Society of America Special Paper 238:71–74.

Giménez, O. 1992. Estudio preliminar del miembro anterior de los sauropodos titanosauridos. Ameghiniana 30:154.

Giménez, O., and S. Apesteguia. 2001. The Late Jurassic-Early Cretaceous worldwide record of basal titanosauriforms and the origin of titanosaurians (Sauropoda): new evidence from the Aptian (Lower Cretaceous) of Chubut Province, Argentina. Journal of Vertebrate Paleontology 21(3, Supplement):54A.

Gomani, E. M. 1999. Dinosaurs of the Cretaceous sedimentary rocks of northern Malawi, Africa. Unpublished Ph.D. dissertation, Southern Methodist University, Dallas, 257 pp.

Gomani, E. M., L. L. Jacobs, and D. A. Winkler. 1999. Comparison of the African titanosaurian, *Malawisaurus*, with a North American Early Cretaceous sauropod; pp. 223–233 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwana Dinosaur Symposium, National Science Museum Monographs 15. National Science Museum of Tokyo, Tokyo.

González-Riga, B. J., and J. O. Calvo. 1999. Unusual caudal series of Titanosauridae of the Late Cretaceous in the Río Colorado Formation, border between the Neuquén and Mendoza Provinces, Argentina. VII International Symposium on Mesozoic Terrestrial Ecosystems Abstracts: 29–30.

González-Riga, B. J., and J. O. Calvo. 2001. A new genus and species of titanosaurid sauropod from the Upper Cretaceous of Rincón de

los Sauces, Neuquén, Argentina. Journal of Vertebrate Paleontology 21(3, Supplement):55A–56A.

Huene, F. von. 1929. Los Saurisquios y Ornitisquios del Cretáceo Argentino. Anales del Museo de La Plata 3:1–196.

Huene, F. von. 1932. Die fossile reptil-ordnung Saurischia, ihre entwicklung und geschichte Teil I und II. Monographien zur Geologie und Palaeontologie 1:1–361.

International Commission on Zoological Nomenclature. 2000. International Code of Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature, London, 306 pp.

Jacobs, L. L., D. A. Winkler, W. R. Downs, and E. M. Gomani. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. Palaeontology 36:523–534.

Jain, S. L., and S. Bandyopadhyay. 1997. A new titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. Journal of Vertebrate Paleontology 17:114–136.

Kellner, A. W. A., and S. A. K. d. Azevedo. 1999. A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil; pp. 111–142 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwana Dinosaur Symposium, National Science Museum Monographs 15. National Science Museum of Tokyo, Tokyo.

Lamanna, M. C., R. D. Martínez, and J. B. Smith. 2002. A definitive abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. Journal of Vertebrate Paleontology 22:58–69.

Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. Geoscience and Man 8:77–102.

Le Loeuff, J. 1995. *Ampelosaurus atacis* (nov. gen., nov. sp.), un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé supérieur de la Haute Vallée de l'Aude (France). Comptes Rendus de l'Academie des Sciences Paris, Série IIA 321:693–699.

Le Loeuff, J., E. Buffetaut, L. Cavin, M. Martin, V. Martin, and H. Tong. 1994. An armoured titanosaurid sauropod from the Late Cretaceous of southern France and the occurrence of osteoderms in the Titanosauridae; pp. 153–159 in M. G. Lockley, V. F. d. Santos, C. A. Meyer, and A. Hunt (eds.), Aspects of Sauropod Paleobiology, Gaia 10. Universidade de Lisboa, Lisbon.

Lydekker, R. 1893. The dinosaurs of Patagonia. Anales del Museo de la Plata, Seccion de Paleontologia 2:1–14.

Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Part II. American Journal of Science (Third Series) 21:411–416.

Martínez, R. 1998. An articulated skull and neck of Sauropoda (Dinosauria: Saurischia) from the Upper Cretaceous of central Patagonia, Argentina. Journal of Vertebrate Paleontology 18(3, Supplement):61A.

Martínez, R., O. Giménez, J. Rodríguez, and G. Bochatey. 1986. *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae) un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina. Simposio de Evolucion de los vertebrados Mesozoicos: IV Congreso Argentino de Paleontología y Bioestratigrafía: 23–31.

Martínez, R., O. Giménez, J. Rodríguez, , and M. Luna. 1988. A Patagonian discovery. Archosaurian Articulations 3:23–24.

Martínez, R., O. Giménez, J. Rodríguez, , and M. Luna. 1989. Un titanosaurio articulado del genero *Epachthosaurus*, de la Formación Bajo Barreal, Cretacico del Chubut. Ameghinana 26:246.

Martínez, R., A. Maure, M. Oliva, and M. Luna. 1993. Un maxilar de Theropoda (Abelisauria) de la Formación Bajo Barreal, Cretácico Tardio, Chubut, Argentina. Ameghiniana 30:109–110.

Powell, J. E. 1980. Sobre la presencia de una armadura dermica en algunos dinosaurios titanosauridos. Acta Geologica Lilloana 15:41–47.

Powell, J. E. 1986. Revision de los Titanosauridos de America del Sur. Doctoral dissertation, Universidad Nacional de Tucumán, Tucumán, 340 pp.

Powell, J. E. 1987a. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina, part VI—the titanosaurids. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 3:147–153.

Powell, J. E. 1987b. Morfologia del esqueleto axial de los dinosaurios titanosauridos (Saurischia, Sauropoda) del Estado de Minas Gerais, Brasil. Anais do X Congresso Brasileiro de Paleontologia 155–159.

Powell, J. E. 1990. *Epachthosaurus sciuttoi* (gen. et sp. nov.) un dinosaurio sauropodo del Cretácico de Patagonia (Provincia de Chubut, Argentina). V Congreso Argentino de Paleontologia y Bioestratigrafia, Tucumán, Actas 1:123–128.

Powell, J. E. 1992. Osteologia de *Saltasaurus loricatus* (Sauropoda—Titanosauridae) del Cretácico Superior del noroeste Argentino; pp.

165–230 in J. L. Sanz, and A. D. Buscalioni (eds.), Los Dinosaurios y Su Entorno Biotico, Actas del Segundo Curso de Paleontologia in Cuenca Institutio 'Juan de Valdes', Cuenca.

Powell, J. E., O. Giménez, R. Martínez, and J. Rodríguez. 1989. Hallazgo de saurópodos en la Formacíon Bajo Barreal de Ocho Hermanos, Sierra de San Bernardo, Provincia de Chubut (Argentina) y su significado cronológico. Anais do XI Congresso Brasileiro de Paleontologia, Curitiba 165–176.

Rodríguez, J. F. R. 1993. La depositacion de las areniscas verdes (Formación Bajo Barreal—Cretacico Tardio) y sus implicancias tafonomicas. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos Actas 1:194–199.

Salgado, L. 1996. *Pellegrinisaurus powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, northwestern Patagonia, Argentina. Ameghiniana 33:355–365.

Salgado, L., and C. Azpilicueta. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. Ameghiniana 37:259–264.

Salgado, L., and R. A. Coria. 1993a. El genero *Aeolosaurus* (Sauropoda, Titanosauridae) en la Formación Allen (Campaniano-Maastrichtiano) de la Provincia de Río Negro, Argentina. Ameghinana 30:119–128.

Salgado, L., and R. A. Coria. 1993b. Consideraciones sobre las relaciones filogeneticas de *Opisthocoelicaudia skarynskii* (Sauropoda) del Cretácico superior de Mongolia. Ameghinana 30:339.

Salgado, L., R. A. Coria, and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. Ameghiniana 34:3–32.

Salgado, L., and R. Martínez. 1993. Relaciones filogeneticas de los titanosauridos basales *Andesaurus delgadoi* y *Epachthosaurus* sp. Ameghiniana 30:339–340.

Santucci, R. M., and R. J. Bertini. 2001. New titanosaurids from the Bauru Group, continental Upper Cretaceous of southeastern Brazil. Journal of Vertebrate Paleontology 21(3, Supplement):96A.

Sanz, J. L., and A. D. Buscalioni. 1987. New evidence of armored titanosaurs in the Upper Cretaceous of Spain; pp. 197–202 in P. J. Currie and E. H. Koster (eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers, Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Sanz, J. L., J. E. Powell, J. Le Loeuff, R. Martínez, and X. Pereda-Suberbiola. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships; pp. 235–255 in H. Astibia, J. C. Corral, X. Murelaga, X. Orue-Etxebarria, and X. Pereda-Suberbiola (eds.), Geology and Palaeontology of the Upper Cretaceous Vertebrate-bearing Beds of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula), Estudios del Museo de Ciencias Naturales de Alava 14, Número Especial 1. Museo de Ciencias Naturales de Alava, Alava.

Seeley, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. Proceedings of the Royal Society of London 43:165–171.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 210:41–83.

Tidwell, V., K. Carpenter, and W. Brooks. 1999. New sauropod from the Lower Cretaceous of Utah, USA. Oryctos 2:21–37.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. Philosophical Transactions of the Royal Society of London B 349:365–390.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society 124:43–103.

Wedel, M. J., R. L. Cifelli, and R. K. Sanders. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. Acta Palaeontologica Polonica 45:343–388.

Wilson, J. A. 1999a. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19:639–653.

Wilson, J. A. 1999b. The evolution and phylogeny of sauropod dinosaurs. Unpublished Ph.D. dissertation, University of Chicago, Chicago, 384 pp.

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir 5:1–68.