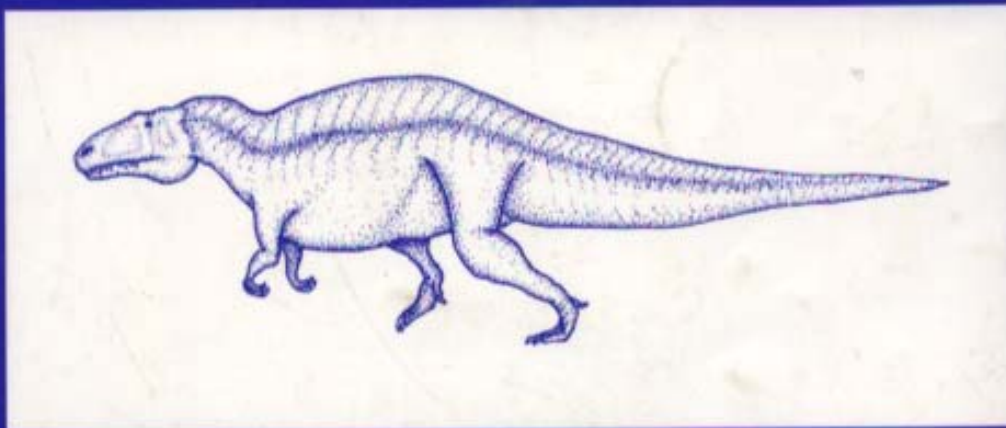Bulletin 13

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A Reanalysis of *Acrocanthosaurus atokensis*, its Phylogenetic Status, and Paleobiogeographic Implications, Based on a New Specimen from Texas

by

Jerald David Harris

ALBUQUERQUE, 1998

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DEDICATION

In memorium, with much love, to

Mary Jane Gerrard-Lee

Jan. 11, 1962 – Dec. 21, 1997

the very best of friends, who was the heart and soul of this work, and who was there to support me

when I needed it most. I can never repay all that you gave me. May your afterlife be as beautiful as

the southern Utah desert you loved, and as filled with dinosaur bones for you to discover.

And to her son,

Edan Spencer Griffin Lee

the brightest of shining stars, whose love of dinosaurs promises to make him

the best of the next generation of paleontologists.

A Reanalysis of *Acrocanthosaurus atokensis*, Its Phylogenetic Status, and Paleobiogeographic Implications, Based on a New Specimen From Texas

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ABSTRACT: A new specimen of the large, Aptian-Albian theropod dinosaur *Acrocanthosaurus atokensis* from northern Texas contains many elements, including the palatine, surangular, articular, prearticular, teeth, cervical, dorsal, sacral, and caudal vertebrae, scapulae, ischia, and femora, that were insufficiently known previously. Diagnostic features of *Acrocanthosaurus* include a reduced divisory ridge in the mandibular glenoid; cervical, dorsal, sacral, and proximal caudal vertebrae with highly elongate neural spines possessing pronounced inter- and supraspinous ligament insertion sites with numerous associated asymmetrical fossae and foramina; cervical vertebral neural spines with triangular cranial processes that insert into caudal overhangs; dorsal vertebrae with fossae on lateral surfaces of neural spine separated by very thin laminae; and arched pre- and postzygapophyseal facets on the mid- and caudal dorsal and sacral vertebrae. *Acrocanthosaurus* displays autapomorphies of the Allosauroidea, including a distally expanded jugal process of the palatine, basioccipital absent from the basal tubera, and surangular twice as deep as the angular. It is most closely related to *Carcharodontosaurus* from the Albian (or Cenomanian) of Africa, sharing with that taxon laterally expanded, reniform caudal articular facets on the cervical vertebrae and rudimentary caudal pleurocoelous fossae; close relationships to the allosauroids *Neovenator* from Europe, *Chilantaisaurus* from Asia, and *Giganotosaurus* from South America are also, albeit less strongly, supported. *Allosaurus* is more distantly related. The relative closeness of *Acrocanthosaurus* to *Carcharodontosaurus* implies that dispersal of their common ancestor probably occurred through South America and into Africa prior to the separation of North and South America sometime in the Early Cretaceous before the Aptian.

INTRODUCTION

Compared to the Late Jurassic and Late Cretaceous dinosaurian faunas of North America, those from the Early Cretaceous are quite poorly known. In the 19th Century, fragmentary dinosaurian remains were recovered from the Arundel Formation of the East Coast (Marsh, 1888) and from the Trinity Group of Texas and Oklahoma (Hill, 1887a). More complete remains have since been discovered in the Cloverly Formation of Wyoming and Montana (Ostrom, 1970), the Cedar Mountain Formation of Utah (Kirkland et al., 1993), and from the Trinity Group (Winkler et al., 1988, 1989, 1997). Almost all of these fossils are ornithischians and sauropodomorph saurischians; with the exception of *Deinonychus* (Ostrom, 1969), theropod material has been fragmentary. The only large theropod from any of these formations based on a substantial portion of the skeleton is *Acrocanthosaurus atokensis* (Stovall and Langston, 1950) from the Trinity Group of Oklahoma.

Here, a skeleton with approximately 70% of the elements represented (SMU 74646; also catalogued as FWMSH 93B-9; see Appendix 1 for abbreviations used in text) of a large theropod dinosaur from Hobson Ranch (Trinity Group, north-central Texas) is compared to the holotype and paratype specimens of *Acrocanthosaurus atokensis* Stovall and Langston (1950) and attributed to the same species. A revised diagnosis of the taxon is presented.

In the original description, *Acrocanthosaurus* was placed within the Allosauridae (Antrodemidae Marsh, *per* Stovall and Langston [1950]), based largely on geographic proximity to the Late Jurassic *Allosaurus fragilis*. Nevertheless, in most subsequent analyses of theropod systematics, it has remained close to *Allosaurus* in the Allosauridae, representing a Cretaceous extension of the lineage of better-known North American Late Jurassic theropods, as opposed to an Early Cretaceous rise of the otherwise Late Cretaceous tyrannosaurid theropods (Walker, 1964; Britt, 1993). However, new theropod discoveries and detailed cladistic analyses in the last decade have, while clarifying some aspects of theropod phylogeny, obfuscated the precise position of *Acrocanthosaurus* (Fig. 1). Most recently, Sereno et al. (1996) proposed a closer relationship of *Acrocanthosaurus* to both *Carcharodontosaurus saharicus* from the Albian (or Cenomanian) of northern Africa and *Giganotosaurus carolinii* (Coria and Salgado, 1995) from the Albian (or Cenomanian) of Argentina than to *Allosaurus*. Sereno et al. (1996) place *Acrocanthosaurus* in the Carcharodontosauridae within a more inclusive Allosauroidea (Currie and Zhao, 1993). If this is correct, then *Acrocanthosaurus* is a representative element of a poorly understood paleobiogeographic distribution of large theropods, instead of simply being a derivative of earlier North American theropods. Analysis of SMU 74646 allows emendation of the formal diagnosis of the genus, thus allowing better understanding of its relationships within the Allosauroidea, clarifying Early Cretaceous theropod global biogeography.

Stovall and Langston (1950)
Theropoda
 Carnosauria
  Antrodemidae (=Allosauridae)
   Allosaurus, **Acrocanthosaurus**
  Megalosauridae
  Deinodontidae (=Tyrannosauridae)
  Spinosauridae
   Spinosaurus

Walker (1964)
Theropoda
 Carnosauria
  Tyrannosauroidea
   Ornithosuchidae
   Tyrannosauridae
    Albertosaurus, Deinodon
    (=*Tyrannosaurus*)
  Spinosauridae
   Acrocanthosaurus,
   Altispinax, Spinosaurus
  Megalosauroidea
   Megalosauridae
    Antrodemus (=*Allosaurus*),
    Bahariasaurus, ?Carcharodontosaurus,
    Eustreptospondylus, Megalosaurus,
    Metriacanthosaurus

Madsen (1976)
Theropoda
 Carnosauria
  Allosauridae
   Allosaurus, **Acrocanthosaurus**

Gauthier (1986)
Theropoda
 Ceratosauria
 Tetanurae
  Carnosauria
   Albertosaurus, Allosaurus,
   Acrocanthosaurus, *Tyrannosaurus*
  Coelurosauria
   Ornithomimidae
   Maniraptora
    Ornitholestes
   Deinonychosauria
   Avialae

Paul (1988)
Theropoda
 Paleotheropoda
  Ceratosauria

Intertheropoda
 Megalosauridae
  Megalosaurinae, Abelisaurinae
 Eustreptospondylidae
  Eustreptospondylinae,
  Metriacanthosaurinae
Avetheropoda
 Compsognathia, Coeluria
 Allosauria
  Allosaurinae
   Allosaurus, **Acrocanthosaurus,**
   Baharisaurus, Carcharodontosaurus,
   Chilantaisaurus
  Tyrannosauridae

Holtz (1994, 1996)
Theropoda
 Tetanurae
  Torvosaurus
  unnamed node
   Megalosaurus
   Avetheropoda
    Allosauridae
     Allosaurus, **Acrocanthosaurus**
    Coelurosauria
     Compsognathus
     Maniraptoriformes
      Ornitholestes
      Arctometatarsalia
       Tyrannosauridae

Sereno (1996)
Theropoda
 Neotheropoda
  Ceratosauria
  Tetanurae
   Torvosauridae
   Spinosauridae
    Spinosaurus
   Neotetanurae
    Allosauroidea
     Sinraptoridae, *Crylophosaurus,*
     Monolophosaurus, Allosaurus
     Carcharodontosauridae
      Acrocanthosaurus,
      Carcharodontosaurus,
      Giganotosaurus
    Coelurosauria
     Ornitholestes
     unnamed node
      Deltadromeus
      Maniraptora
       Tyrannosauridae

Figure 1. Previously hypothesized taxonomic and phylogenetic positions of *Acrocanthosaurus* relative to other theropods, particularly allosauroids and tyrannosaurids.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

SMU 74646 was found at Hobson Ranch, SMU Locality #261. This locality, discovered and owned by Philip R. Hobson and family, is located in Parker County, Texas, west of Fort Worth (exact site information is on file at SMU). Although not reported until 1990, the site was known to the Hobson family prior to that time. The locality is in the Twin Mountains Formation, and occurs in a cross-bedded and concretionary sandstone facies.

Geological Setting

The Twin Mountains Formation, named and defined by Fisher and Rodda (1966), is the lowest member of the Trinity Group in north-central Texas, which is generally accepted as containing, in stratigraphic sequence, the Twin Mountains Formation, the Glen Rose Limestone, and the Paluxy Formation. Although no radiometric ages have been derived from the Trinity Group (Winkler et al., 1989), foraminiferal (Michael, 1972), ammonite (Young, 1986) and vertebrate (Winkler et al., 1989, 1990, 1997; Jacobs et al., 1991) biostratigraphic correla-

tion as well as $\partial^{13}C$ data (Rennison, 1996) support a late Aptian-early Albian age for the group and a late Aptian age for the Twin Mountains Formation in particular. The Aptian-Albian boundary was estimated as 112 ± 1 Ma by Obradovich (1994) and Gradstein et al. (1994, 1995).

Twin Mountains Formation sediments were first recognized by Hill (1887a) as part of the "Dinosaur Sands." Although he did not give a specific age for the sediments, he placed them between recognized Carboniferous and Lower Cretaceous formations. Hill (1887b) later voiced his suspicion that the "Dinosaur Sands" would prove to belong to the Upper Jurassic. Later, Hill (1891) recognized lithostratigraphic divisions within these sediments, defining the "Trinity Sands" and the Glen Rose beds. The stratigraphically lowest Cretaceous sediments (those between the Carboniferous basement and the Glen Rose Limestone) in central and north-central Texas have also been referred to as the Bluffdale or Bluff Dale Sands (Hill, 1901), but Boone (1968) has shown the Bluff Dale Sand to be a geographically restricted facies of the Glen Rose Limestone. Twin Mountains sediments have also been referred to as "Basement" sands (Hill, 1901; Scott, 1930; Scott and Armstrong, 1932; Knopp, 1957).

Hill (1891:505) recognized that the "fine, white, cross-bedded sand" is mostly unconsolidated and calcareous; he acknowledged that the sediments are erosional detritus of the underlying Paleozoic formations. He proposed that their deposition marked the initial, nearshore stages of a marine transgression that eroded a barrier of Paleozoic formations into a terrain of inland lakes, culminating ultimately in the deposition of the overlying marine Glen Rose beds. Although there was not a single transgressive event (Young, 1986), the overall portrait of the Twin Mountains Formation (and correlative facies to the south [Fisher and Rodda, 1966]) as continental, nearshore facies of a marine transgressive sequence (induced by subsidence of the continental mass) remains accurate (Markovic, 1951; Knopp, 1957; Gibson, 1967; Hendricks, 1967; Boone, 1968; Stricklin et al., 1971; Young, 1986). Cross-bedding in the Twin Mountains Formation, at least within the Middle Sand portion, has been interpreted as the result of fluvial deposition (Markovic, 1951).

Sediment comprising the blocks in which SMU 74646 was found consists of calcite-cemented, medium- to fine-grained, well-sorted, quartzose sandstone. The precipitation of calcite around decaying organic matter due to anaerobic bacterial action is relatively well-known (e.g., Brett and Baird [1986] and references cited therein). Fragmentary plant matter (locally abundant immediately surrounding many elements of SMU 74646), coupled with the decay of the specimen, may have contributed to the formation of these nodules.

The Glen Rose Limestone in Parker County, Texas (where SMU Locality 261 occurs) thins, changes lithology from limestone to marly shales, and becomes discontinuous, forming lenses that are difficult to correlate with one another or the main limestone body (Hendricks, 1957; Gibson, 1967). To the north, it disappears altogether (Scott and Armstrong, 1932; Hendricks, 1967), so the Twin Mountains and Paluxy Formations merge to form the Antlers Formation (which, in this region, comprises the Trinity Group in its entirety), as first noted by Hill (1894). In the south (including the southern portion of Parker County), the Glen Rose is a prominent, mappable unit that lies between the Twin Mountains and the Paluxy Formations. SMU Locality 261 occurs roughly 130 m below the nearest outcrop of the Glen Rose Limestone and an undetermined distance from the contact of the Twin Mountains Formation and the Paleozoic basement.

Stovall and Langston (1950) do not provide information about the stratigraphic levels at which the holotype and paratype specimens of *Acrocanthosaurus* were found with respect to the base and top of the Antlers Formation. Rennison (1996) correlates the $\partial^{13}C$ sequence of the lower Antlers Formation of Oklahoma with the mid-portion of the Trinity Group in north-central Texas.

Paleontology of the Twin Mountains Formation

Twin Mountains Formation dinosaurs include the sauropod *Pleurocoelus*, the basal iguanodontian *Tenontosaurus dossi* (Winkler et al., 1997), an unnamed hypsilophodontid (Winkler et al., 1988; Winkler and Murry, 1989), and numerous small theropod teeth, including some similar to the dromaeosaurid *Deinonychus*. Mammals recovered include an indeterminate therian jaw and teeth of the triconodont *Astroconodon* (Slaughter, 1969; Winkler et al., 1989, 1990). Other vertebrates include a turtle referable to *Naomichelys*, plus osteichthyans, chondrichthyans, amphibians, and crocodilians (Winkler et al., 1989, 1990).

Invertebrate fossils from the Twin Mountains Formation include bivalve molluscs and ?annelid tubes (Hendricks, 1967; Winkler et al., 1989). One site (Paluxy Church), was apparently a lagoonal or estuarine setting, including both marine and terrestrial fossils (Winkler et al., 1989).

Although fragmentary plant material is locally abundant in the Twin Mountains Formation, the only identifiable material thus far reported has been a possible cycad or cycadeoid specimen (Böse, 1917), some charophyte gyrogonites (Hendricks, 1967) and some gymnosperm wood from the SMU locality from which material of *Tenontosaurus dossi* was recovered (Jacobs, 1989; Winkler et al., 1989).

TAPHONOMY

All the elements in SMU 74646 possess individual numbers, placed in white paint labels on each bone. The first digit reflects the block from which the bone originated, and the second number (after the hyphen) is the number in the sequence in which bones were removed from that block. In some cases, two or more separately numbered pieces found to fit together are from the same element; these are denoted in this report by presenting both (or at least two, if more than two pieces were involved) specimen numbers, separated by a slash.

Fragile elements of SMU 74646, such as the thin processes of the palatine and ectopterygoid and the laminae on many of the dorsal vertebrae, are relatively complete. Such thin bone

is unlikely to have survived much mechanical transport or other abrasion. The retention of ribs and gastralia in articulation, more easily transportable elements (Voorhies, 1969; Behrensmeyer, 1975), also supports the idea that little mechanical transport occurred prior to burial of the skeletal elements. The preservation of such fragile and lightweight elements as the palatine and gastralia, but the absence of more robust elements, such as the humeri and tibiae, is not expected if simple, pre-burial hydraulic transportation is the sole explanation for missing elements.

The positions of the bones with respect to each other (Figs. 2, 3) indicate that the pre-disarticulation position of the body is still visible. The specimen lay on its right side with the head and neck and tail arched backward, a pose typical of dessicated specimens (Weigelt, 1989). This position implies exposure prior to burial.

All of the bones recovered from the locality preserve excellent surface integrity: they do not display the kind of cracking or flaking induced by continual surface exposure described by Behrensmeyer (1978) and Fiorillo (1988). A few bones were abraded (e.g., some rib and gastralium fragments), but this appears to be a result of modern weathering. Some bones of SMU 74646 retained some connective tissue (weathering stages 0-1 of Fiorillo [1988]), as indicated by the articulation of some elements (e.g., sequences of vertebrae, ribs, and gastralia). In contrast, a large number of elements (e.g., ribs and caudal vertebra 1-19/1-25) appear to have been broken prior to or during burial, and their pieces separated from one another. Most of the shearing of the vertebrae appears to have been done during preparation, as evidenced by the lack of matrix on the sheared surfaces, although the presence of matrix in the interior camellae of the sixth cervical (3-60) implies that at least this one was broken prior to or during burial.

Only one element found, metatarsal II, possesses what may be a spiral fracture. Spiral fractures can be induced in modern bones by carnivores (Hayes, 1980; Shipman, 1981) or trampling (Fiorillo, 1989). Most of the elements occur in planar relation to one another; none of the elements appears to have been trampled (Fiorillo, 1989) or deposited on an irregular terrain (Voorhies, 1969): both processes tend to produce numerous elements oriented at significant angles from the horizontal.

None of the elements shows grooves, punctures, or unhealed tooth marks indicative of scavenging (Fiorillo, 1988, 1989, 1991; Rogers, 1990). However, the presence of two crocodilian teeth and one tooth of an unidentified animal (possibly fish) with the specimen suggests that minor scavenging may have occurred. Scavenging by crocodilians may explain the absence of some of the smaller elements from SMU 74646, but is insufficient to explain the absence of many of the larger elements.

Erosion of the specimen for several decades prior to collection is the most likely explanation for the absence of some bones from SMU 74646, while simultaneously allowing for the presence of fragile elements. This may be particularly true of the distal caudals, since three of the medial caudals

(K1, K2, and K3) were collected in soft, weathered sediment. Exposure of the nodules on the bank of a modern stream allowed for rotation or some slight movement of individual blocks subsequent to reexposure in modern times, explaining some of the slightly out-of-place locations of individual blocks of material (Fig. 3).

Many of the articulated elements in SMU 74646 (e.g., segments of the vertebral column, series of gastralia) are those in which the length:width ratio is < 2:1, which should be moved less easily (Morris et al., 1996), while many of the unarticulated, polarized elements (e.g., scapular blade, ischia, femora, some ribs) are those that appear to have been moved the most. The disarticulated elements are those that were freed first from soft tissue attachment (similar to the sequence of some large mammals described by Hill [1979] and Hill and Behrensmeyer [1984]) and thus could be moved. For example, the femur was isolated prior to any individual dorsal vertebra, so that, as hydraulic equivalents, comparison must be made of the femur to the articulated dorsal vertebral sequence, rather than to an individual dorsal vertebra, that would be moved before the femur (Voorhies, 1969). The vertebrae were, in life, enmeshed in a network of strong ligaments (see sections on the presacral and sacral vertebrae, below), which may have been massive and resistant enough to decay to allow them to retain articulation beyond the point at which many of the other elements, such as the femora and pelvic elements, were freed from soft tissue connections.

Because the position of the *Acrocanthosaurus* carcass prior to partial disaggregation can be readily discerned (Fig. 3), whatever processes produced the disarticulation present in SMU 74646 were neither strong nor persistent enough to apportion the entire skeleton, although they were sufficient to move individual sections with respect to their life positions and each other. These processes occurred prior to total soft tissue decay.

DESCRIPTION

Comparison with Holotype and Paratype

The sole, previously published osteology of *Acrocanthosaurus* is Stovall and Langston (1950; see also Britt, 1993). The formal diagnosis *per* Stovall and Langston (1950:700) is: carnivorous saurischian of gigantic size and heavy proportions with (1) massive and greatly elongated neural processes; (2) proportionately massive skull; (3) moderately heavy arcades (the arches of bone surrounding the temporal openings [W. Langston, personal communication, 1997]); (4) orbits and postorbital fenestra somewhat reduced; (5) jugular foramen (= jugal pneumatic recess, on the maxillary process of the jugal) greatly enlarged; (6) frontals and parietals solidly coossified; (7) quadratosquamosal movement somewhat reduced; (8) cervical centra opisthocoelous and of moderate length; (9) pleurocentral cavities (= pleurocoelous fossae on the cervical and dorsal vertebrae) deep and well marginated; (10) cranial dorsals distinctly opisthocoelous; (11) medial caudals with supplementary neural processes; (12) chevrons closed proximally by transverse bar;
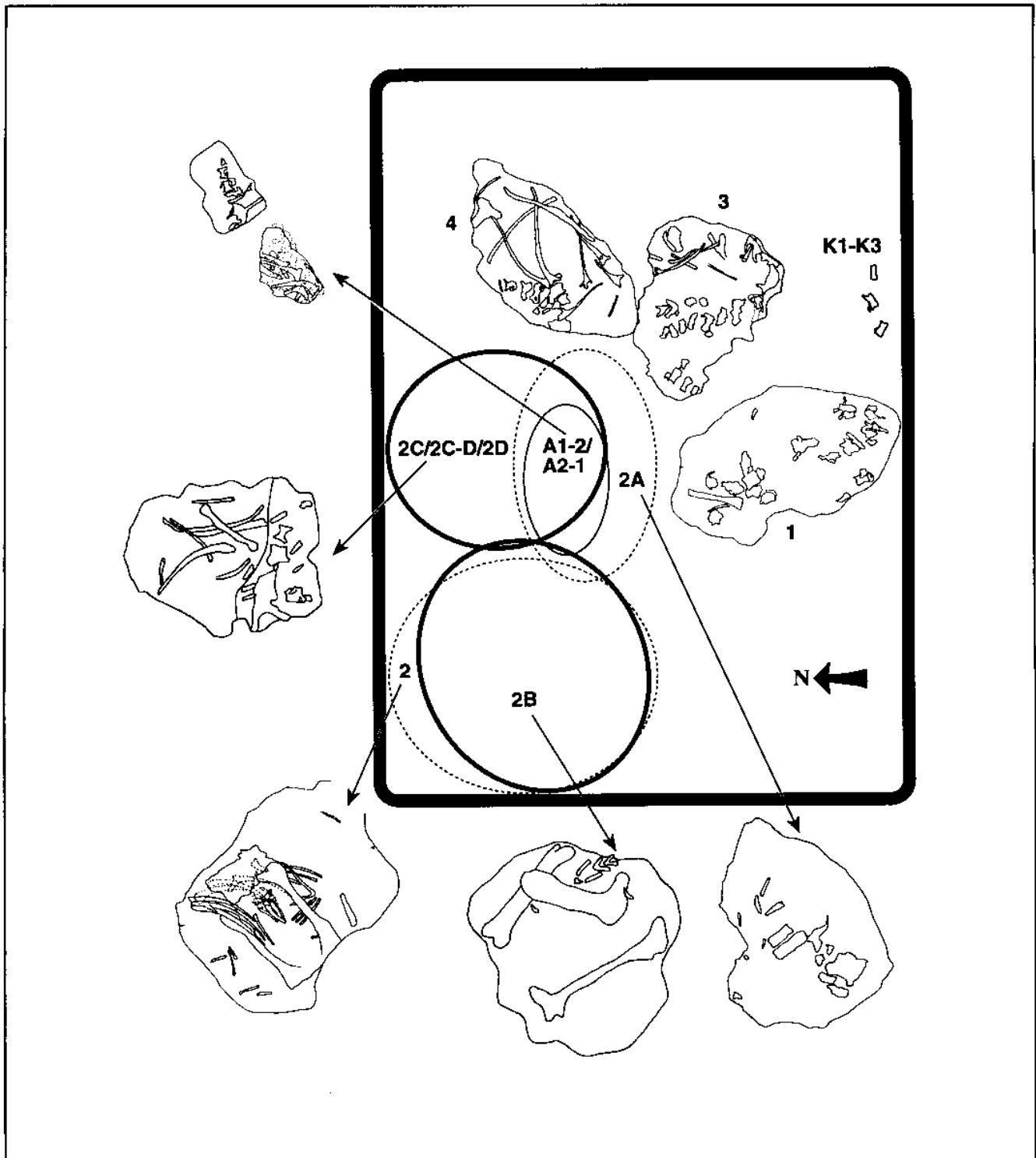
Figure 2. Layout of blocks of SMU 74646 as found in the field (inside heaviest line). Positions of Block 2 and subsidiary blocks indicated by ovals (heavy lines indicate blocks on top, light lines indicate blocks in middle, and dashed lines indicate blocks on bottom).

(13) chevrons exhibiting cranial, upward projecting process on each ramus; (14) pelvic elements not coossified; (15) pubis slender with broadly expanded distal termination; (16) ischium straight, slender, elongate, and somewhat expanded distally; (17) tibia strongly bowed outward; and (18) metatarsal III somewhat constricted proximally by lateral elements.

Of these, characters 4, 5, 6, 7, 17, and 18 cannot be compared with SMU 74646 because comparable material is not preserved. Characters 1, 2, and 3 are arbitrary. Character 14 is not necessarily a diagnostic trait because lack of fusion of pelvic elements is ontogenetic, indicative of the individual's age, not its phylogenetic relationships. Characters 8, 10, 12,
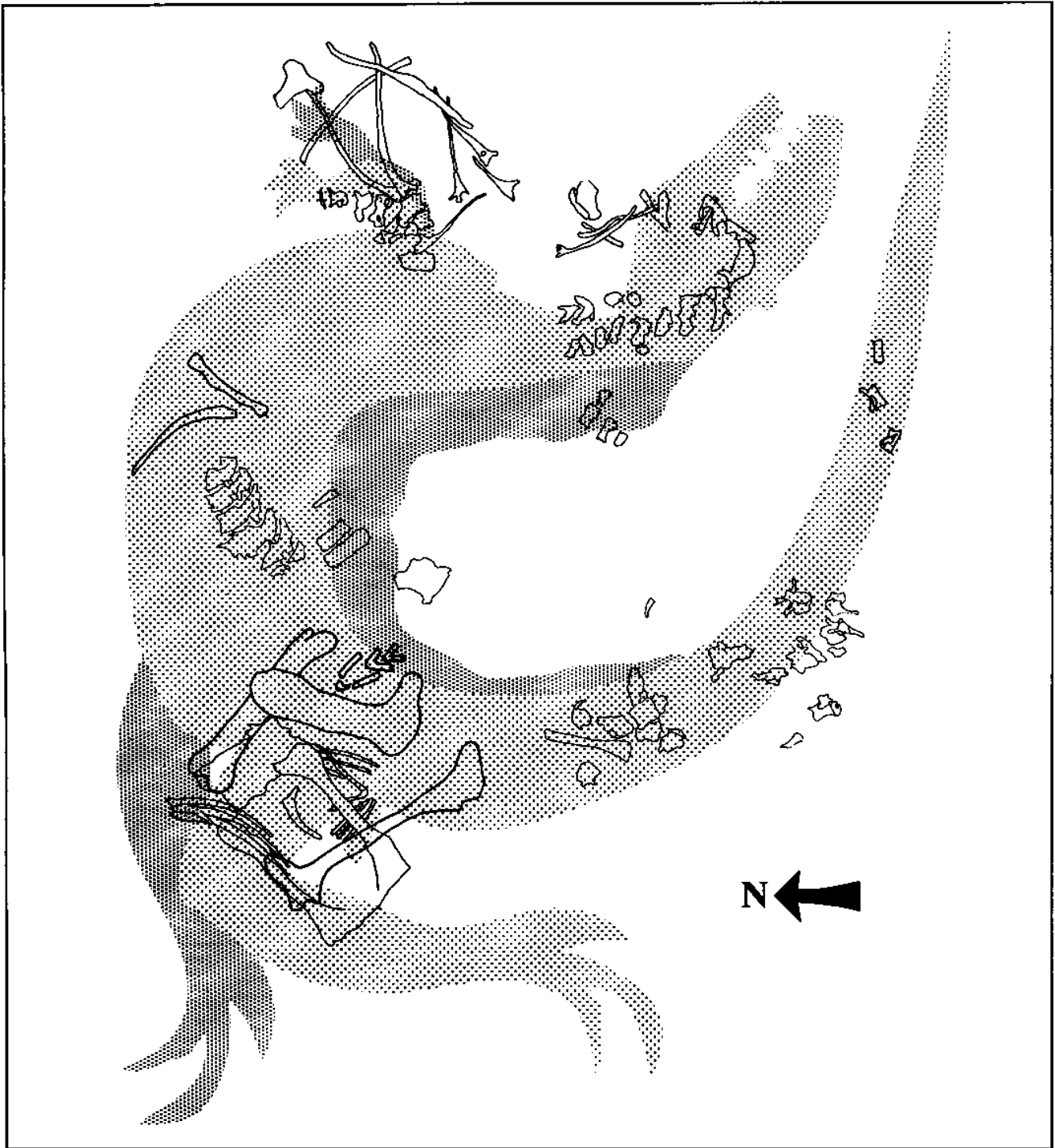
Figure 3. Schematic diagram showing preburial position of *Acrocanthosaurus* specimen SMU 74646 based on positions of elements as found in the field. Compare with Figure 2.

15, and 16 may have been diagnostic at the time of initial description but have since been discovered in a wide variety of theropods and are therefore not diagnostic at the species level. Character 18 is unclear because pinching of metatarsal III to various degrees occurs in different theropods, and each form may have phylogenetic significance (for example, possession of an hourglass-shaped metatarsal III that is visible in proximal view versus the nearly complete or complete elimination of metatarsal III in proximal view as in the Arctometatarsalia [Holtz, 1994, 1995]).

A unique characteristic of *Acrocanthosaurus* is the robust and elongate neural spines (character 1) for which the animal was named. The neural spines of SMU 74646 are virtually identical to those of the holotype in morphology. Both

also possess the peculiar triangular cranial projections on the cervical spines and have an abrupt change in cervical spine morphology at the eighth cervical vertebra (see below). The pattern and placement of fossae and foramina on the neural arches of the cervical and cranial dorsal vertebrae are also virtually identical. These are unique among the known Theropoda and confirm that SMU 74646 belongs to *Acrocanthosaurus atokensis*.

Note on Terminology

All osteological terms in this paper are the English equivalents of standard Latin names. Directional terms used follow the convention described by Clark (1993; also L. Witmer, personal communication, 1995), in which the terms anterior and posterior are avoided in favor of cranial and caudal. For the skull and mandible, wherein cranial becomes redundant, the term rostral is used. Within appendages, the tail, and individual bones, proximal and distal are used to describe the positions of features with respect to others in the same appendage or bone, but the positions of features with respect to the anatomical position of the body as a whole follow the standard convention, using cranial, caudal, dorsal, ventral, medial, and lateral, and combinations thereof. Dorsal, ventral, medial, and lateral retain their familiar meanings. Taxonomic names that lack a formal description are bracketed by quotation marks.

There is some confusion in the literature regarding whether foramina and canals leading into the interior of many dinosaur bones are pneumatic. There is some historical and structural precedence for viewing such openings, particularly in the vertebrae, as pneumatic (Britt, 1993). Numerous workers interpret such foramina as pneumatic without question; much of this interpretation appears to be based on assumed homology with Foramina pneumatica (= pneumatopores) of avians. The analysis presented herein refers to openings on the bones of *Acrocanthosaurus* simply as fossae and foramina, though it is acknowledged that they likely had a pneumatic function. A more detailed review of this overall problem, as well as a systematic nomenclature for individual fossae and foramina in avian and non-avian theropod crania is given by Witmer (1987, 1990, 1997) and in postcrania by Britt (1993). All abbreviations are listed in Appendix 1.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1886

TETANURAE Gauthier, 1986

NEOTETANURAE Sereno et al., 1996

ALLOSAUROIDEA Currie and Zhao, 1993

ACROCANTHOSAURUS Stovall and Langston, 1950

ACROCANTHOSAURUS ATOKENSIS Stovall and Langston, 1950

HOLOTYPE: OMNH 8-0-S9.

PARATYPE: OMNH 8-0-S8.

REFERRED SPECIMEN: SMU 74646 (FWMSH 93B-9).

REVISED DIAGNOSIS: Theropod dinosaur with coossified frontals and parietals; bifurcate jugal process of palatine; pronounced, laterally-projecting knob on surangular shelf; large caudal surangular foramen; reduced divisory ridge in mandibular glenoid; continuous apical denticulation on teeth; pleurocoelous fossae and foramina pronounced on all presacral and sacral vertebrae; presacral, sacral, and proximal caudal vertebrae with elongate (≥ 2.5x centrum length) neural spines possessing pronounced inter- and supraspinous ligament insertion sites with numerous associated asymmetrical fossae and foramina; cervical vertebral centra with camellate interiors; cervical vertebral neural spines with triangular cranial processes that insert into caudal overhangs; abrupt transition from craniocaudally broad to narrow neural spines at 8th cervical vertebra; large, centrally-placed pleurocoelous fossa with two foramina on axis; reduced distal neural spine on axis; large epipophyses on axis; cranial dorsal vertebrae with multiple fossae and foramina on lateral surfaces of neural spine; medial and caudal dorsal vertebrae transverse processes with strong dorsocaudal angulation, deep fossae on lateral surfaces separated by very thin laminae, arched pre- and postzygapophyseal facets, prezygapophyseal facets contiguous with hypantral facets; caudal dorsal vertebrae

Table 1. Comparative measurements (in mm) of selected elements between SMU 74646 and OMNH 8-0-S0 (holotype) and OMNH 8-0-S8 (paratype).

Element	OMNH 8-0-S9	OMNH 8-0-S8	SMU 74646
Fifth cervical vertebra, total height	287	—	341
Second caudal vertebra, centrum length	—	128	124
Femur	—	(left) 1153[e]	(right) 1090
Distal MT II, mediolateral width	—	86	97

Notation: — = measurement unavailable; [e] = estimate
Measurements of holotype and paratype taken from Stovall and Langston (1950).

with neural spines strongly angled cranially; rudimentary pleurocoelous fossae on proximal caudal vertebrae; multiple foramina located within proximal and distal fossae on neural spines of proximal caudal vertebrae; accessory transverse processes on medial caudal vertebrae; sagittal portion of gastralia consisting of single element; ischium with deep, elongate, ovoid fossa on proximal, dorsocaudal surface.

DESCRIPTION

Cranium

The only skull elements preserved in SMU 74646 are the right palatine, the left ectopterygoid, a partial left jugal, the caudal end of one mandible, and two teeth.

Palatine

The right palatine (3-24) is a light, thin, tetraradiate bone, with the four processes conjoining to form a relatively small body (Fig. 4). It measures 311 mm across its longest dimension, from the preserved end of the maxillary process to the end of the medial process, and 124 mm in the greatest preserved dimension, from the base of the maxillary process to the top of the vomeropterygoid process. The dorsal margin is strongly depressed with both the vomeropterygoid and, to a lesser extent, the jugal processes projecting well above the extent of the depression. The presence of a subsidiary palatal fenestra is unknown because the pterygoid is not preserved.

A large, expanded vomeropterygoid process extends rostrally and medially. This surface is the origin of the M. pterygoideus, pars dorsalis (Witmer, 1997). The medial side of the process is rough but not grooved, so the nature of its contact with the opposite palatine is unclear.

The thin, tapering maxillary process projects rostrally, ventral and lateral to the vomeropterygoid process. Together, the maxillary and vomeropterygoid processes bound the caudal end of the internal choana. As both processes are long, it appears that the choana was bounded primarily by the palatine with only a small contribution on the rostral end from the maxilla and vomer. The medial side of the maxillary process is marked by several grooves and ridges for articulation with the maxilla, implying that the joint permitted little motion.

The jugal process projects laterally and dorsally, caudal to the maxillary process. It is laterally compressed, dorsoventrally expanded, and bifurcate. The superior and inferior wings of the process are broken, but the superior appears to be larger than the inferior.

The region on the lateral side where the jugal, ascending, and maxillary processes converge (Fig. 4B) houses a deep, ovoid fossa, that Witmer (1997) terms the palatine pneumatic recess. The fossa opens dorsally and laterally. This opening appears to have continued into chambers both within the pterygoid process and the jugal process itself, and possibly even into the vomeropterygoid process (obscured by matrix). A depression on the lateral surface of the jugal process is bounded both dorsally and ventrally by broken ridges of bone that mark a shallow canal that feeds into the opening.

Immediately rostral to this large opening is another, smaller opening that leads rostrally into the dorsal margin of the maxillary process.

The medial process, like the maxillary process, is long, tapering, and increasingly laterally compressed. At its base, it is invaded ventrally by a large, blind, triangular fossa (Figs. 4A, C). When the palatine is viewed laterally, the medial process appears to bisect the notch created by the bifurcation in the jugal process (Fig. 4B). The medial and jugal processes bound the rostral end of the palatine fenestra.

Ectopterygoid

The left ectopterygoid (3-10) is virtually complete (Fig. 5). It is a triradite bone with hooked processes, giving it the
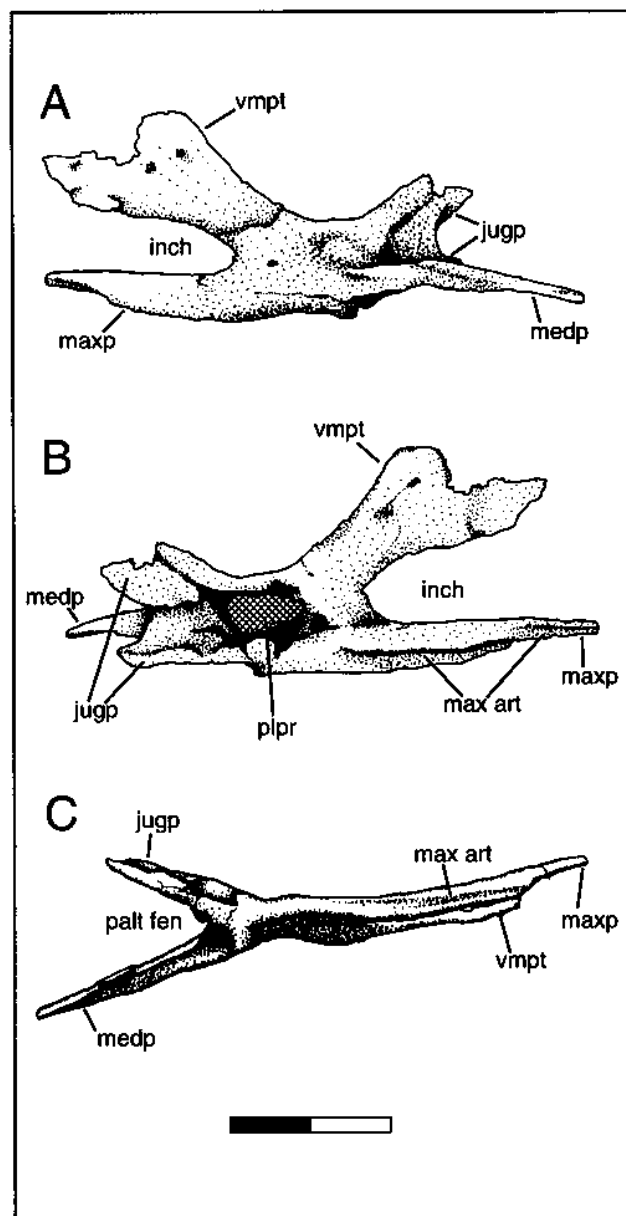

Figure 4. Right palatine of *Acrocanthosaurus*, SMU 74646 3-24 in (A) medial, (B) lateral, and (C) ventral view. Cross-hatching represents matrix. Scale bar = 10 cm.

"triskelion shape" seen in a broad spectrum of theropods (Molnar et al., 1990). The broad, thin pterygoid process hooks rostrally and dorsally, the jugal process caudally, and the ectopterygoid flange caudally and medially. It measures 152 mm mediolaterally and 184 mm rostrocaudally.

The pterygoid process lacks all outer edges, so the extent and shape cannot be determined. There is a small pit on the dorsal surface that does not penetrate the thin bone, similar to but situated somewhat more dorsally and caudally than one described in *Deinonychus* (Ostrom, 1969). The function of the pit is uncertain, but it is probably not associated with the insertion of the M. pterygoideus, pars dorsalis, as Ostrom (1969:27) suggested, but that Witmer (1997) shows is only associated with the palatine and pterygoid.

The ectopterygoid flange is relatively shallow and tapers gradually to its distal end. The broken dorsomedial edge indicates the presence of a thin lamina of bone that spans the

pterygoid process and ectopterygoid flange and overhangs the ectopterygoid pneumatic recess. A particularly deep portion of this recess invades the base of the jugal process; an identical feature can be seen in the holotype. The recess is limited ventrally by a pronounced lip of bone that bounds the entire fossa, gradually diminishing in size until disappearing under the pterygoid process (Fig. 5C). Inferior to this lip on the ectopterygoid flange is a second shallow, thin lamina of bone.

The jugal process emerges from the main body flattened dorsoventrally, but as it hooks caudally, it becomes flattened mediolaterally and fairly thin. This portion of the process is angled slightly dorsally as well. The lateral surface of this portion of the process bears several oblique and horizontal grooves for articulation with the jugal (3-31). This articular surface spans the length of the cranial-caudally oriented portion of the process.
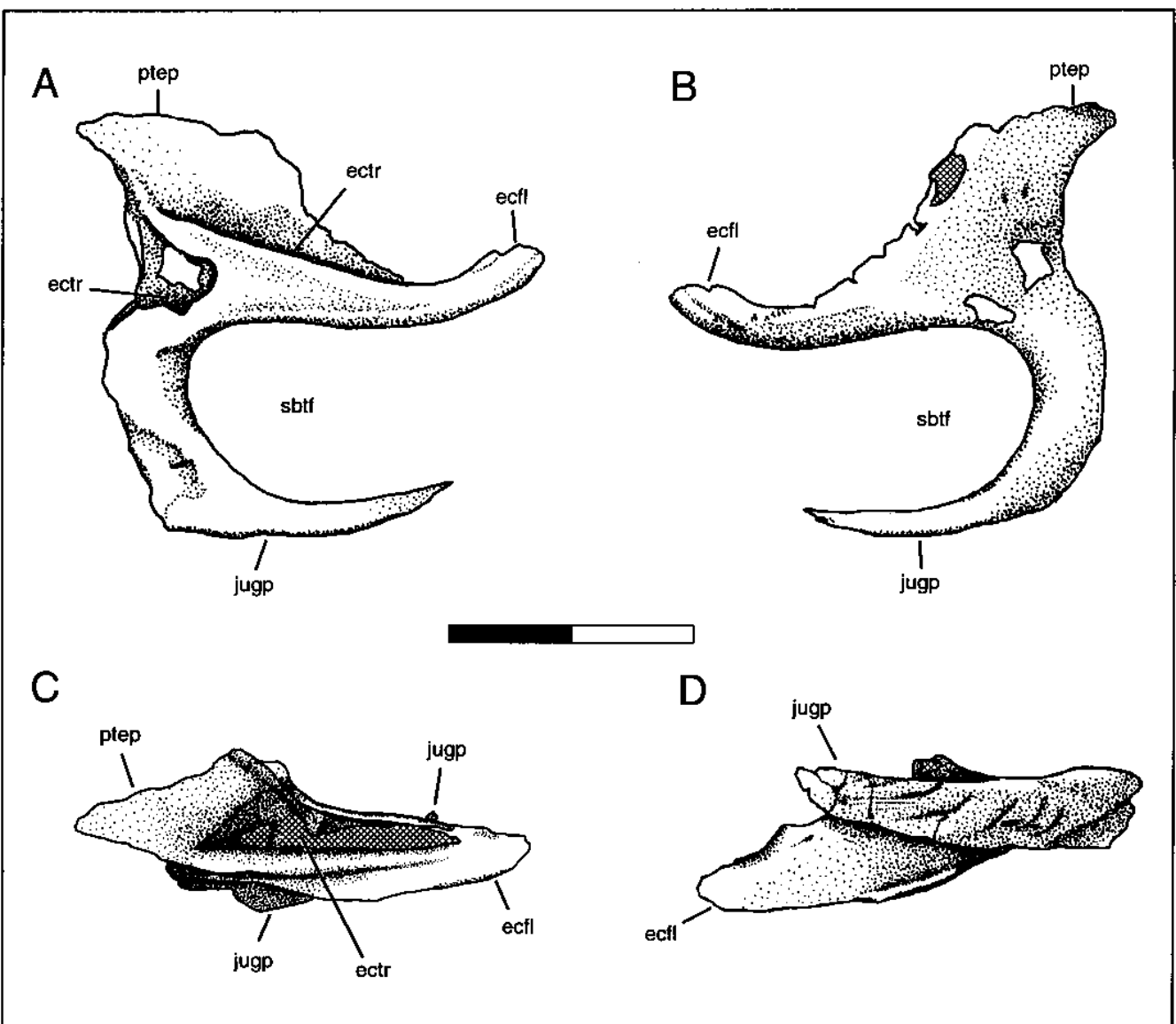

Figure 5. Left ectopterygoid of *Acrocanthosaurus*, SMU 74646 3-10 in (A) dorsal, (B) ventral, (C) medial, and (D) lateral views. Cross-hatching represents matrix. Scale bar = 10 cm.

Jugal

The left jugal (3-31) is represented by the main body only, lacking the majority of the maxillary, postorbital, and quadratojugal rami (Fig. 6). It is identifiable as the jugal, however, by the presence of the ventral limit of the orbit and articulation on the medial surface with the ectopterygoid (3-10). The preserved portion measures 315 mm long and 83.5 mm high.

Although most of the dorsal margin of the bone is missing, the ventral margin is mostly intact. The body of the jugal lacks an expanded lobe and is therefore shallow beneath the orbit. From the base of the postorbital process caudally, the bone is transversely thin (9.5 mm at the thinnest point), but the body of the jugal rostral to the postorbital process is much thicker, particularly along the ventral margin where it measures 39 mm.

The ventral surface of the entire rostral end of the jugal bears a broad, dorsally concave sulcus of variable depth that diminishes gradually and twists slightly laterally to terminate below the cranial margin of the postorbital process (Figs. 6A, D). It appears that it did not extend to the rostral limit of the

maxillary process because that portion is ovoid in cross-section, not narrowly chevron-shaped as it is where the sulcus is more prominent. This furrow may have been part of the articular surface for the jugal process of the maxilla. No similar sulcus is visible in the holotype. The reason for this difference is unclear.

Although the bulk of the maxillary process of the jugal is missing in 3-31, the jugal of the holotype (OMNH 8-0-S9) displays a deep jugal pneumatic recess (Stovall and Langston, 1950). Witmer (1997) reports that this opening leads to chambers deeper within the various rami of the jugal; it is hollow at least as far caudally as the postorbital process in the holotype. The broken portion of the maxillary process of 3-31 immediately rostral to the orbital margin bears a small, ovoid opening that appears to lead more deeply into the body of the jugal (Fig. 6B), thus indicating that the maxillary process was also invaded by diverticula. A small but deep medial jugal foramen marks another point at which the body of the jugal was invaded. The exact extent of the invasion remains undetermined. In contrast to the other rami, the postorbital processes of neither 3-31 nor the holotype appear to have been invaded by diverticula.

The ventral margin of the orbit is parabolic in shape, with both rostral and caudal margins sweeping rather steeply away from a vertical midline. The ventral limit of the orbit appears to extend further ventrally than the lateral temporal fenestra when the long axis of the body is horizontal. The dorsolateral surface of the preserved portion of the quadratojugal process is slightly recessed. The prongs for articulation with the quadratojugal are broken.

Mandible

As with the skull, most of the lower jaw is missing. The portions preserved in SMU 74646, all from the right side, are more complete than those of OMNH 8-0-S9, however. Included are a partial surangular (3-30), a partial prearticular (3-33), and a complete articular (3-32) (Fig. 7). All these elements are fused together, although a part of the prearticular was broken from the main bone mass and found separately. A partial splenial was found separately and in two pieces (3-3 and 3-16) (Fig. 8).

Surangular

The preserved portion of the surangular is dorsal and caudal to the external mandibular foramen, the margins of which are not preserved (Fig. 7). The part of the surangular rostral to the mandibular glenoid is dorsoventrally tall, laterally compressed, and sinuous in cross-section. The rostral portion of the dorsal margin of the surangular bears a shallow groove. The surangular, from the mandibular glenoid caudally, is comparatively dorsoventrally compressed and intricate. The preserved portion of the surangular measures 141 mm dorsoventrally, 137 mm mediolaterally (through the medial process) and is 290 mm long.

Rostrally, a large shelf of bone projects laterally, probably an expanded insertion site for the pterygoideus musculature (Gauthier, 1986). Immediately lateral to the rostral end of the
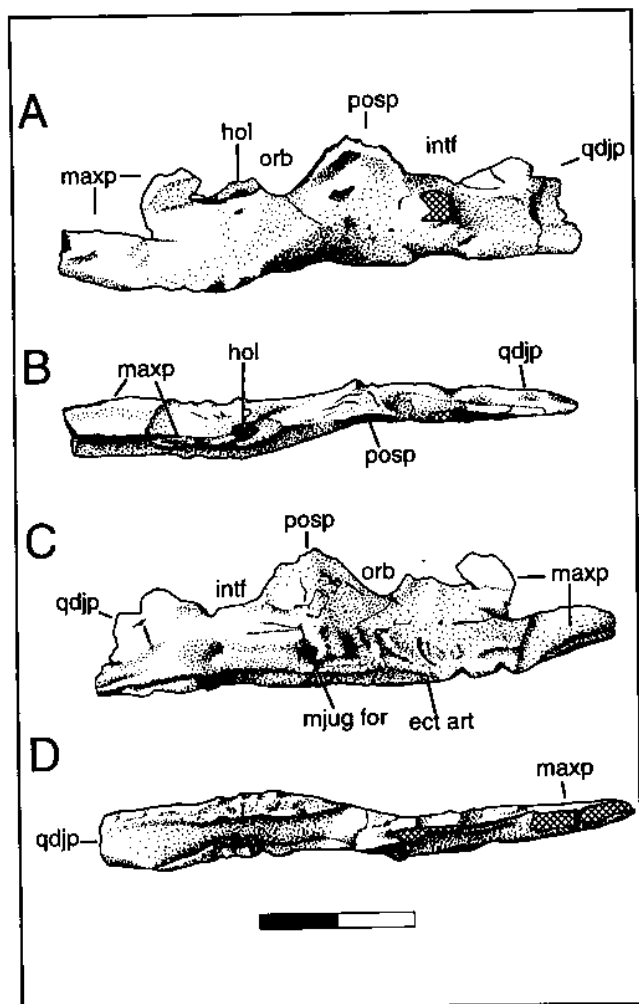

Figure 6. Left jugal of *Acrocanthosaurus*, SMU 74646 3-32 in (A) lateral, (B) dorsal, (C) medial, and (D) ventral views. Cross-hatching represents matrix. Scale bar = 10 cm.

glenoid, this shelf swells, forming a rough, laterally-projecting knob (Fig. 7B). Caudal to this, the shelf dies out rapidly. Though missing in 3-32, the preserved portion of the surangular in OMNH 8-0-S9 preserves the dorsal margin of a relatively large caudal mandibular fenestra (Stovall and Langston, 1950).

A deep excavation, the adductor fossa, is bounded laterally and ventrally by the surangular body and ventromedi-

ally by the prearticular. The steep ventral inclination of the prearticular with respect to the dorsal margin of the surangular forms a large surface for insertion of the M. adductor mandibularis (*per* Madsen, 1976).

The lateral mandibular glenoid is constricted transversely. Rostrally, it rises and terminates in a low ridge that continues onto the medial process. The caudal border of the lateral mandibular glenoid rises sharply. Behind the glenoid is a short spine, broken on all but the caudal edge; a similar spine is present on the articular (see below). There is a dorsoventrally-oriented groove on the lateral surface between the spine and the caudal margin of the surangular (Figs. 7A, B).

Articular

The articular (Fig. 7) is 162 mm long rostrocaudally. Overall, it is wedge-shaped, becoming mediolaterally compressed caudally and ventrally. Its rostrodorsal margin slopes forward fairly steeply, and is in direct contact with the medial process of the surangular along its entire length. The ventral margin nests in a groove on the prearticular and is not visible in ventral view.

The articular portion of the mandibular glenoid is almost square in dorsal profile, measuring 72 mm at its widest point. The rostral end abuts the medial process of the surangular. Unlike the glenoid of *Allosaurus* (Gilmore, 1920; Madsen, 1976), which is divided into approximate halves by a pro-
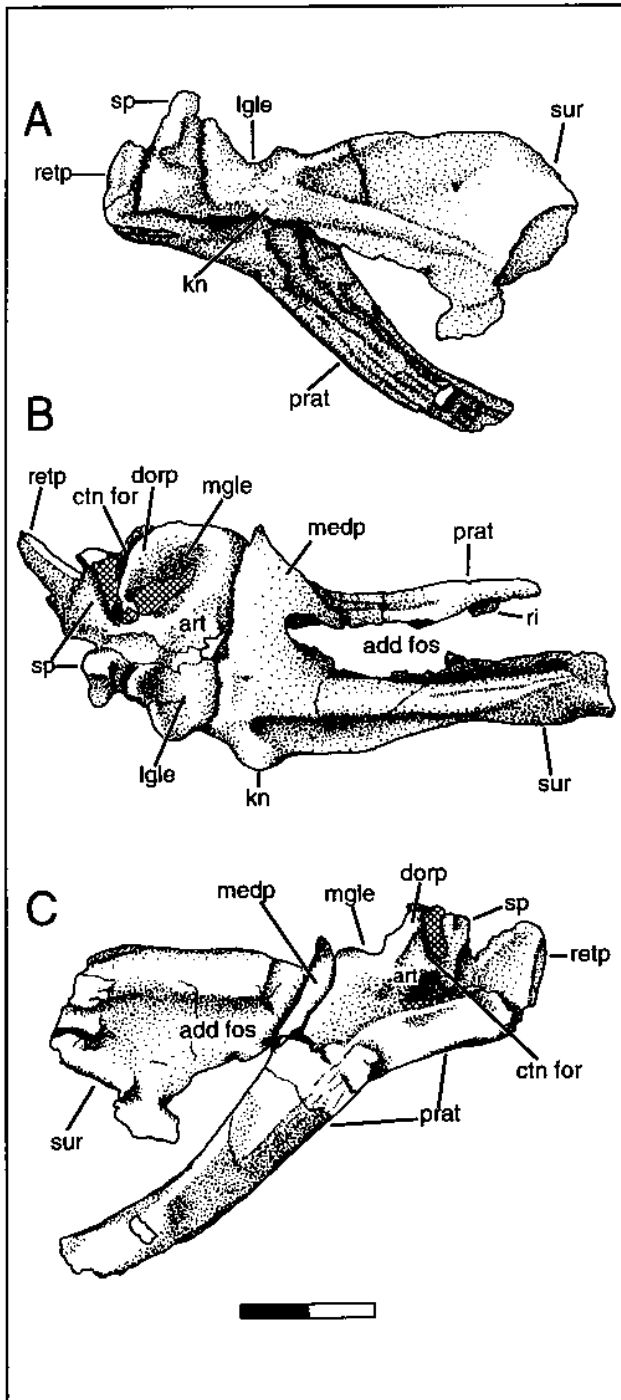

Figure 7. Caudal end of the right mandible of *Acrocanthosaurus*, SMU 74646 3-31/3-33 in (A) lateral, (B) dorsal, and (C) medial views. Cross-hatching represents matrix. Scale bar = 10 cm.
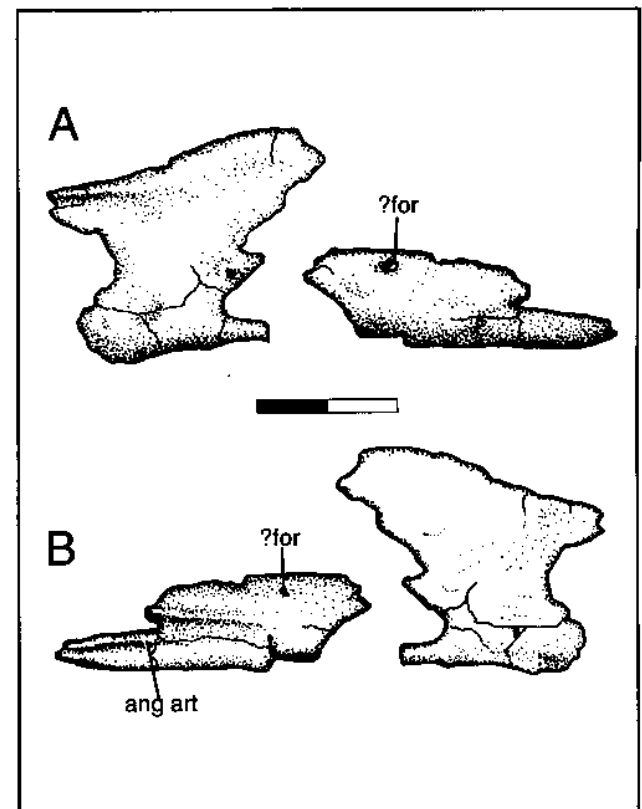

Figure 8. Fragments of ?right splenial of *Acrocanthosaurus*, SMU 74646 3-3 and 3-16 in (A) medial and (B) lateral views. Scale bar = 10 cm.

nounced, oblique ridge, the glenoid of *Acrocanthosaurus* is a much simpler cup possessing only a low ridge. The articular portion of the glenoid sits slightly more caudal than the surangular portion. The entire glenoid measures 112 mm across at its widest point.

Caudal to the depression, the bone rises sharply into a tall, rostrocaudally compressed dorsal process (Fig. 7C). Immediately behind the dorsal process is a deep, rostrocaudally narrow cleft between the glenoid and a tall, triangular, dorsally-projecting spine on the rostral end of the retroarticular process. The spine, similar to the one on the surangular, was undoubtedly taller than the dorsal process because the broken edge is equal in elevation to the top of the unbroken dorsal process. Caudal to the spine, the long retroarticular process angles medially. The dorsal edge of the process becomes transversely thin, and then thickens towards its rear end.

Towards the medial side of the articular, on the caudal surface of the dorsal process, is a small foramen. Similar openings in other theropods are interpreted as entrance sites of the chorda tympani nerve (Witmer, 1990; Currie and Zhao, 1993). There is no indication that *Acrocanthosaurus* possessed an antarticular ossification, as in *Allosaurus* (Madsen, 1976) and *Bagaraatan* (Osmólska, 1996).

Prearticular

The ventral surface of the preserved portion of the prearticular wraps around the ventral portion of the articular (Figs. 7A, C) and thickens rostrally. From its contact with the articular, the prearticular curves gently ventrally and medially before curving dorsally. The preserved portion is 341 mm long and 60.5 mm tall.

The lateral surface of the prearticular is concave laterally except for a pronounced, triangular, laterally-projecting ridge of bone (Figs. 7A, B). The ridge begins below the contact of the surangular medial process and the prearticular. It rapidly becomes more pronounced rostrally.

Splenial

Two pieces (3-3 and 3-16) were found, one atop the other (Fig. 8). One of these, 3-3, is the caudal process of the right splenial. The element is concave laterally, particularly so along the ventral margin, where it would wrap below the angular. In general, the concavity of the fragment is interrupted only by a low ridge that runs along and parallel to the top of the angular facet. The caudal extension of the angular facet is complete, but between it and the aforementioned ridge the bone thins, suggesting that a notch existed in this location.

The medial surface of the fragment is rough but virtually featureless. Towards the dorsal margin of the fragment, there is a small hole where the bone has been punctured. Surrounding the puncture, the bone is naturally indented. Thus, the puncture is either a second natural foramen or it is a puncture through a small, imperforate pit. Neither of these openings is in the same location as the rostral mylohyoid foramen housed in the splenial of *Sinraptor* (Currie and Zhao, 1993). The larger fragment, 3-16, does not demonstrably belong to the splenial, but its intimate association with 3-3 is suggestive.

Dentition

Two teeth were recovered with SMU 74646: one virtually complete (Fig. 9) and one fragmentary tip. The virtually complete tooth, specimen 1-1, includes a part of the root. The

A **B**
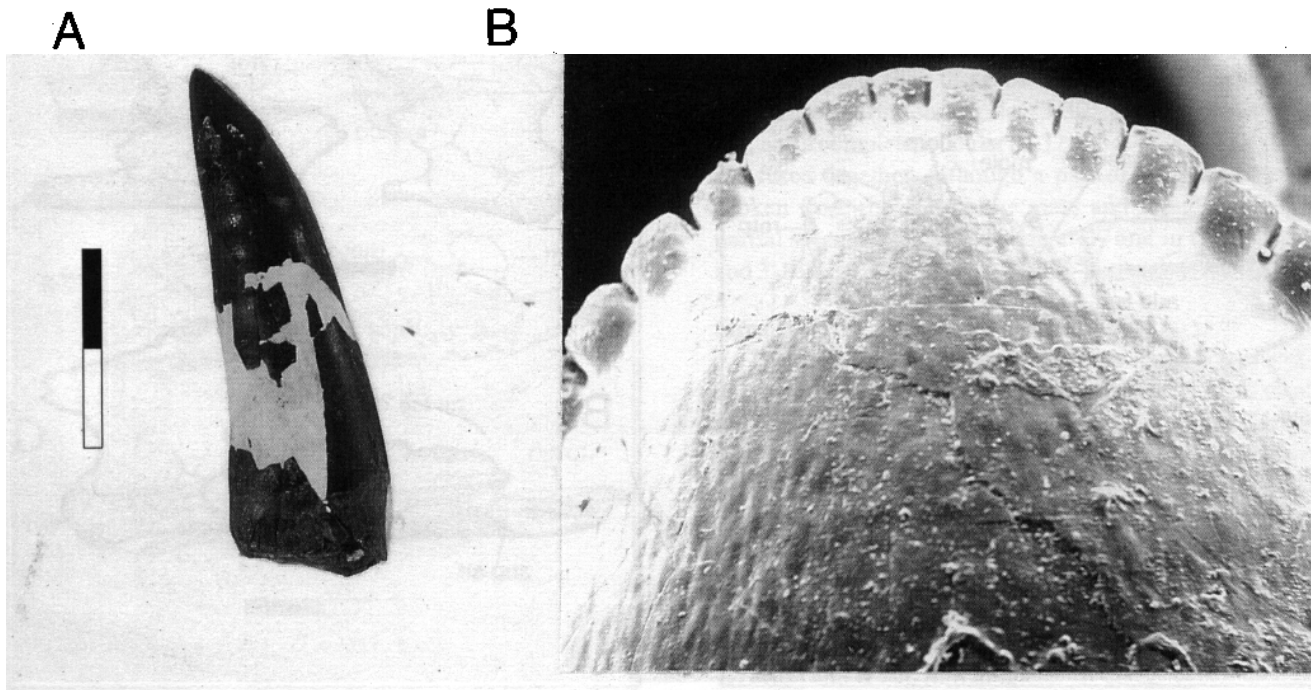
Figure 9 (*above and opposite page*). Tooth of *Acrocanthosaurus*, SMU 74646 1-1. (A) Entire tooth. Scale = 4 cm. (B) SEM photograph of tip of tooth, showing apical denticulation. Denticles of the rostral carina in (C) side view and (D) rostral view. Reflective ridge across top of denticles in (C) is artifactual. Denticles of caudal carina in (E) side view and (F) caudal view. Scale bar = 1 mm.

C

D

E

F
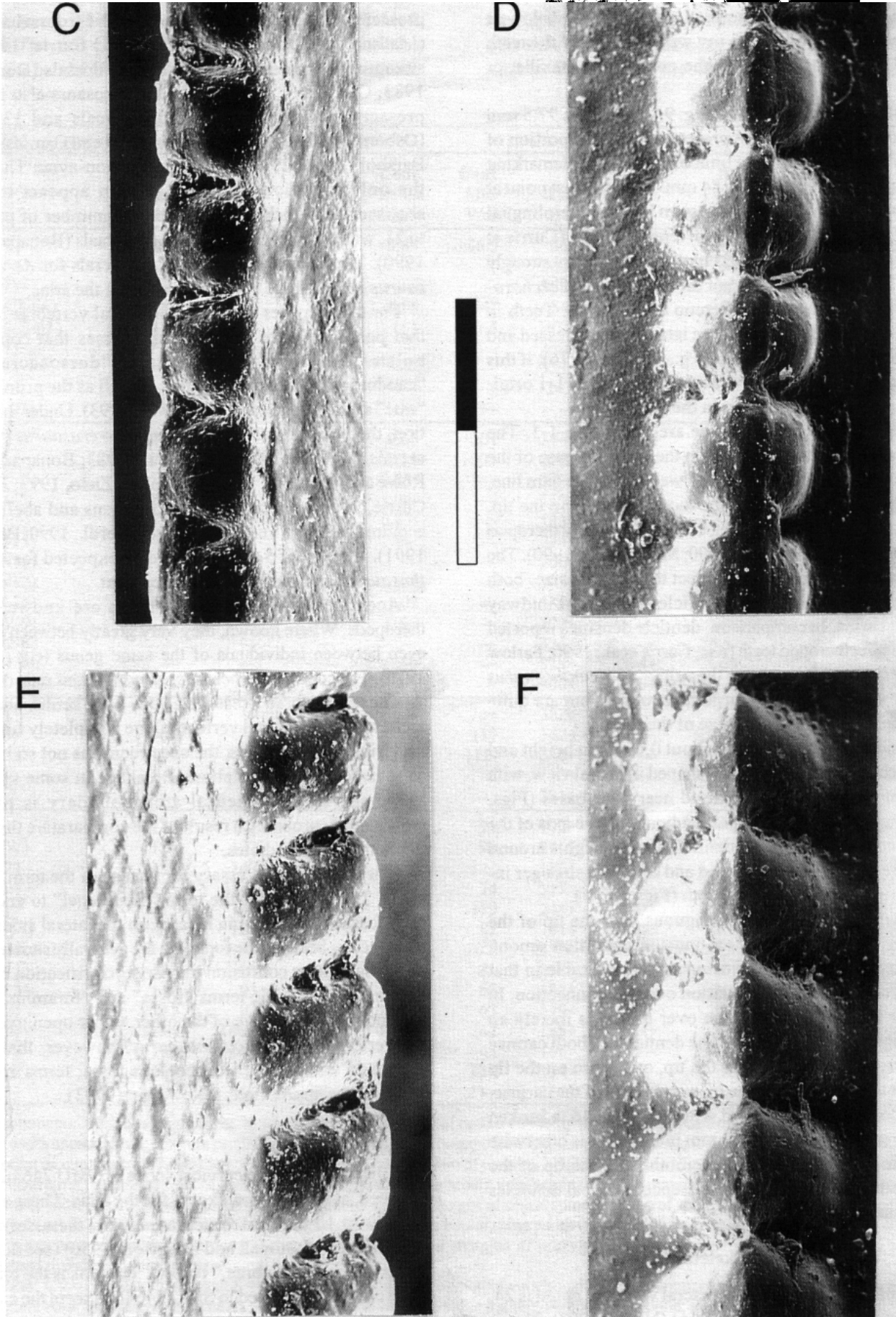
partial root implies this is not a shed tooth. Because no tooth-bearing bones have yet been described for *Acrocantho-saurus*, and no teeth were described with either the holotype or paratype, it is impossible to say with certainty if the teeth from SMU 74646 originated in the premaxilla, maxilla, or dentary.

The virtually complete tooth (Fig. 9A) measures 97.5 mm from tip to base, although the preserved base is a portion of the root; when measured to the limit of the enamel (demarking the gum line in life), the tooth is 84 mm. At the widest point at the base, which coincides with the gum line, the labiolingual width is 19.5 mm; the fore-aft basal length (FABL [Currie et al., 1990; Farlow et al., 1991]) is 31 mm. The tooth is not strongly recurved. There is no wrinkling of the enamel as in *Carcharo-dontosaurus* (Stromer, 1931; Sereno et al., 1996). Teeth in theropods commonly become more laterally compressed and more strongly recurved caudally (e.g., Madsen, 1976); if this consistency holds true in *Acrocanthosaurus*, then 1-1 origi-nated in a more rostral position in the skull.

Both rostral and caudal carinae are present on 1-1. The concave caudal carina extends from the tip to the base of the enamel; the rostral carina terminates well above the gum line, covering approximately $^3/_5$ of the tooth length from the tip. Neither carina displays any offset, common on many theropod premaxillary teeth (Currie et al., 1990; Molnar et al., 1990). The denticles are quite small with respect to the tooth size: both carinae possess just under 11 denticles per 5 mm midway down each carina. In comparison, denticle densities reported in many smaller theropod teeth (e.g., Currie et al., 1990; Farlow et al., 1991) are much greater than this. *Acrocanthosaurus* denticles may be absolutely larger than others, but are quite small compared to the overall size of the tooth.

The caudal denticles average about 0.6 mm in height and are cartouche (rounded rectangle)-shaped in lateral view, with bodies that are slightly compressed near their bases (Figs. 9C, D). They are set virtually perpendicular to the axis of the carina. In contrast, the rostral denticles, with heights around 0.5 mm, are parallelogram-shaped and display a stronger in-clination towards the tip of the tooth (Figs. 9E, F).

The carinae meet and are contiguous over the tip of the tooth (Fig. 9B). This is not an unusual condition among theropod teeth, but *Acrocanthosaurus* is remarkable in that there is no cessation of denticulation over the connection. In most other theropods, the bridge over the tip is merely an enamel ridge, lacking denticles. The denticles of both carinae in 1-1 decrease in size towards the tip, and those on the tip are smaller than those along the more proximal of the carinae.

The second tooth associated with SMU 74646, a broken tip numbered 2-14, measures 32 mm in height. It is otherwise comparable to the more complete tooth 1-1. The tip of the second tooth is damaged, so the presence of apical denticles is indeterminate.

Axial Skeleton

The primitive ornithodiran presacral vertebral count is 24, with 9 cervical and 15 dorsal vertebrae (Novas, 1993). This is the presumed condition in *Herrerasaurus* (Novas, 1993).

Ceratosaurians have either 23 (Colbert, 1989) or 24 (Welles, 1984). Primitive tetanurines and allosauroids have 23 presacrals divided into 9 cervical and 14 dorsal vertebrae (Madsen, 1976; Britt, 1991; Zhao and Currie, 1993), but sinraptorids have 10 cervicals and 13 dorsals (Dong et al., 1983; Currie and Zhao, 1993). Coelurosaurs also retain 23 presacrals, nominally with 10 cervicals and 13 dorsals (Osborn, 1916; Ostrom, 1978; Barsbold and Osmólska, 1990; Barsbold et al., 1990). Amongst the non-avian Theropoda, the only variation from this pattern appears to be the abelisaurids, which have reduced the number of presacrals to 21, with 10 cervicals and only 11 dorsals (Bonaparte et al., 1990). The expected number of presacrals for *Acrocantho-saurus* is 23; all are represented except the atlas.

For the purposes of this paper, sacral vertebrae are those that possess ribs or transverse processes that contact and bolster the ilium. This includes "dorsosacrals" and "caudosacrals" of some authors, as well as the primitive two "true" sacrals (Welles, 1984; Novas, 1993). Under this defini-tion, theropods more derived than *Herrerasaurus* possess 5 sacrals (Madsen, 1976; Dong et al., 1983; Bonaparte, 1986; Rowe and Gauthier, 1990; Currie and Zhao, 1993; Zhao and Currie, 1993), but many coelurosaurians and abelisauroids acquired >5 sacral vertebrae (Barsbold et al., 1990; Bonaparte, 1991). A count of 5 sacrals would be expected for *Acrocan-thosaurus*, and pieces of all are present.

Accurate caudal vertebral counts are known for few theropods. Where known, they vary greatly between taxa, and even between individuals of the same genus (e.g., Madsen, 1976). The count in *Acrocanthosaurus* remains uncertain.

Those vertebrae preserved with both centra and neural arches (e.g., the dorsal vertebrae) are completely fused, with no visible sutures. Thus, the specimen was not so immature as to have unfused vertebrae. Breakage in some specimens along the centrum-neural arch boundary is probably taphonomic, probably a result of the comparative thinness of the bone of the pedicles.

Clarification is necessary for the use of the term "pleuro-coel." This paper uses the term "pleurocoel" to encompass both fossae and foramina located on the lateral sides of ver-tebral centra because the foramina are generally situated within the fossa. Where confusion may arise, clarification by emen-dation of the specific terms "fossa" and "foramina" is used to denote one exclusive of the other. Other openings exist in the vertebrae of *Acrocanthosaurus*, however, that are not contained within the pleurocoelous fossa; terms applied to these, where appropriate, follow Britt (1993).

Cervical Vertebrae

All vertebrae of the cervical series of SMU 74646 are rep-resented, at least in part, except for the atlas. There appear to have been 10 cervical vertebrae, *contra* the assessment of the holotype by Stovall and Langston (1950) (see discussion under "Dorsal Vertebrae," below). The axis is the only com-plete cervical preserved in SMU 74646. Except the axis, most the cervical elements, particularly the neural spines, of SMU 74646 were found in approximate articulation. However, de-

grees of disarticulation, such as between the centra and their neural arch elements, increases caudally in the sequence. Measurements of the cervical vertebrae are given in Table 2.

AXIS: The axis (3B-1) is well preserved (Fig. 10). Most notably, the height of the neural arch is much greater in com-

parison to the centrum length, including the odontoid process, than in any other theropod, an autapomorphy of *Acrocanthosaurus*. The odontoid is a rough, rounded process that is fused to the centrum, although the suture is still visible. The process is conical, although the dorsal surface,

Table 2. Vertebral measurements (in mm) of SMU 74646.

Vert. # (Spec.#)	Cent. Ln.	Cent. Caud. Wd.	Cent. Caud. Ht.	Cent. Ht/Ln Ratio	Cent. Mid Wd.	Ttl. Ht.	N. Sp. Ht.	N. Sp. Ln.	N. Sp. Wd.	Prez. Wd.	Epi. Wd.
CV2 (3B-1)	101	92	90	0.89	46.5	351	245	63	59	75	180
CV3 (3-45)	—	—	—	—	—	307+	256	68	47.5	154^e	146^e
CV4 (3-51)	—	—	—	—	—	308+	274	80	37	150^c	152^c
CV5 (3-54/3-66)	158	156^e	91.5	0.58	54^e	341	232	91	36	136^e	152^e
CV6 (3-60/ 3-61)	180	128^e	87+	0.48+	79.5	363^m	268^m	76	39	—	134^e
CV7 (3-59)	—	—	—	—	—	250+	250+	81	42	—	—
CV8 (3-46)	—	—	—	—	—	325+	244+	54	55	—	—
CV9? (3-46)	—	—	—	—	—	124.5	124.5	54+	41-	—	—
CV10? (4-23)	213+	—	—	—	—	—	—	—	—	—	n/a
D1?(4-21)	295	110^e	136	0.46	201	344+	—	—	—	—	n/a
D2 (4-20)	268	136^e	137.5	0.51	100+	252+	—	—	—	—	n/a
D3 (4-17)	159+	—	132	0.83-	—	372+	231+	108+	—	—	n/a
D4 (4-29)	123+	—	128	1.04-	—	259+	—	—	—	—	n/a
D5 (4-25)	152+	—	133	0.87-	—	133+	—	—	—	—	n/a
D6 (A1-2-15)	—	—	120+	—	—	274+	—	—	—	—	n/a
D7 (A1-2-11)	—	—	—	—	—	266+	—	—	—	140^e	n/a
D8 (A1-2-12)	115+	—	—	—	—	303+	—	95-	—	—	n/a
D9 (A1-2-14)	135	138^e	137.5	1.02	—	335+	—	—	—	105^e	n/a
D10 (A1-2-9)	144	134^e	138.5	0.96	—	320+	—	—	—	—	n/a
D11 (A1-2-8)	—	—	—	—	—	325+	—	76.5-	—	122^c	n/a
D12 (A2-1/1)	—	—	—	—	—	519+	394+	60	39	—	n/a
D13? (A2-1/4)	—	—	—	—	—	340+	210+	—	—	—	n/a
S1 (2-15-1)	170	—	—	—	76+	382+	—	—	—	—	n/a
S2 (2-15-2)	160	—	—	—	117	342+	—	63.5+	—	130^e	n/a
S3 (2-15-3)	160	173-	108+	0.68-	112-	340+	—	—	—	—	n/a
S4 (2J-1)	—	—	—	—	—	120+	—	—	—	—	n/a
S5 (2J-2)	—	—	—	—	—	281+	—	—	—	109+	n/a
CD1 (1-6)	117	173	161?	1.38?	94	172+	—	—	—	—	n/a
CD2 (1C/W)	124	132	145	1.17	93	296+	151+	82	66	—	n/a
CD5 (1-22)	139	147	140	1.01	122	183+	—	—	—	80^e	n/a
CD6 (1-12)	135	126^e	122	0.90	74	315+	145.5+	75.5	18	53^e	n/a
CD8 (1-4)	135	146	152	1.13	119	244+	270+	68.5	17+	41^c	n/a
CD 15 (1-17)	140.5	109	126	0.90	82	314	148	74.5	16	81	n/a
CD16 (1-19/ 1-25)	150	99+	105	0.70	70^m	323^{m,p}	187^m	67	10	89	n/a
CD17 (1-11)	142	109	126.5	0.89	81	212+	74+	74	13	90	n/a
CD18 (1-13)	141	93	108	0.77	68	182+	—	—	—	90	n/a
CD19 (1-2)	141	92	102+	0.72+	63	179+	—	—	—	93	n/a
CD22 (1-3)	125+	80+	95+	0.76+	62	185+	79+	76-	13	93	n/a
CD28 (K1)	133	66+	84	0.63	42	108+	—	—	—	—	n/a
CD29 (K2)	131	71	56+	0.43+	33+	134+	48+	90	9.5	78^e	n/a
CD30 (K3)	128+	66+	77+	0.60+	31+	110+	—	—	—	—	n/a

Measurements: centrum length (cent. ln.) = distance from margin of caudal cup to tip of cranial ball; centrum caudal width (cent. caud. wd.) = maximum width of caudal cup; centrum caudal height (cent. caud. ht.) = distance from highest portion of caudal centrum cup beneath vertebral foramen to lowest point on cup; centrum height:length ratio (cent. ht/ln ratio) = ratio of centrum height to centrum length; mid-centrum width (cent. mid. wd.) = width of centrum at maximum point of constriction (not including pleurocoel); total height (ttl. ht.) = maximum height of vertebra from top of neural spine to ventral-most point of centrum; neural spine height (n. sp. ht.) = height of neural spine from top of spine to dorsal edge of neural canal; neural spine length (n. sp. ln.) = minimum craniocaudal length of neural spine; neural spine width (n. sp. wd.) = minimum mediolateral thickness of neural spine; prezygapophyseal width (prez. wd.) = distance between lateral margins of prezygapophyses; epipophyseal width (epi. wd.) = distance between lateral margins of epipophyses

Notation: CV = cervical; D = dorsal; S = sacral; CD = caudal; ? = position of vertebra in sequence approximate; — = measurement not possible; + = incomplete bone; measurement taken on preserved portion with true value higher; - = incomplete bone; measurement taken on preserved portion with true value probably lower; n/a = measurement not applicable; ^{e} = estimate; measurement taken from endpoint to midpoint of statistic and doubled; ^{m} = minimum value; measurements taken on two or more separate pieces and added; ^{p} = measured region marred by pathology.

just below the vertebral foramen, is depressed and slightly concave dorsally.

The axial intercentrum (= hypocentrum) is completely fused with the axial centrum. The intercentrum projects slightly further forward than the odontoid process. Its ventral margin is arched, but the ventral-most points lay in a plane parallel to the ventral margin of the centrum.

The main body of the axial centrum is strongly compressed mediolaterally, especially along the bottom where it creates a pronounced keel. The ventral margin is strongly arched dorsally. The articular faces are perpendicular to the horizontal axis of the centrum.

The pleurocoel on the side of the axis consists of two small but deep, subcircular foramina set into a single, craniocaudally ovoid fossa. The fossa is located just ventral to the diapophysis and is roughly centered on the centrum. The openings on the right side are larger than the left; those on the left are separated by a robust pillar of bone, whereas those on the right only by a thin lamina. This kind of asymmetry in the size of foramina on either side of any vertebra's long axis is pervasive (see below; Britt [1993:197]). A second small opening, the infrapostdiapophyseal foramen, is found at the dorsocaudal end of the diapophysis, leading into the neural arch complex dorsally.
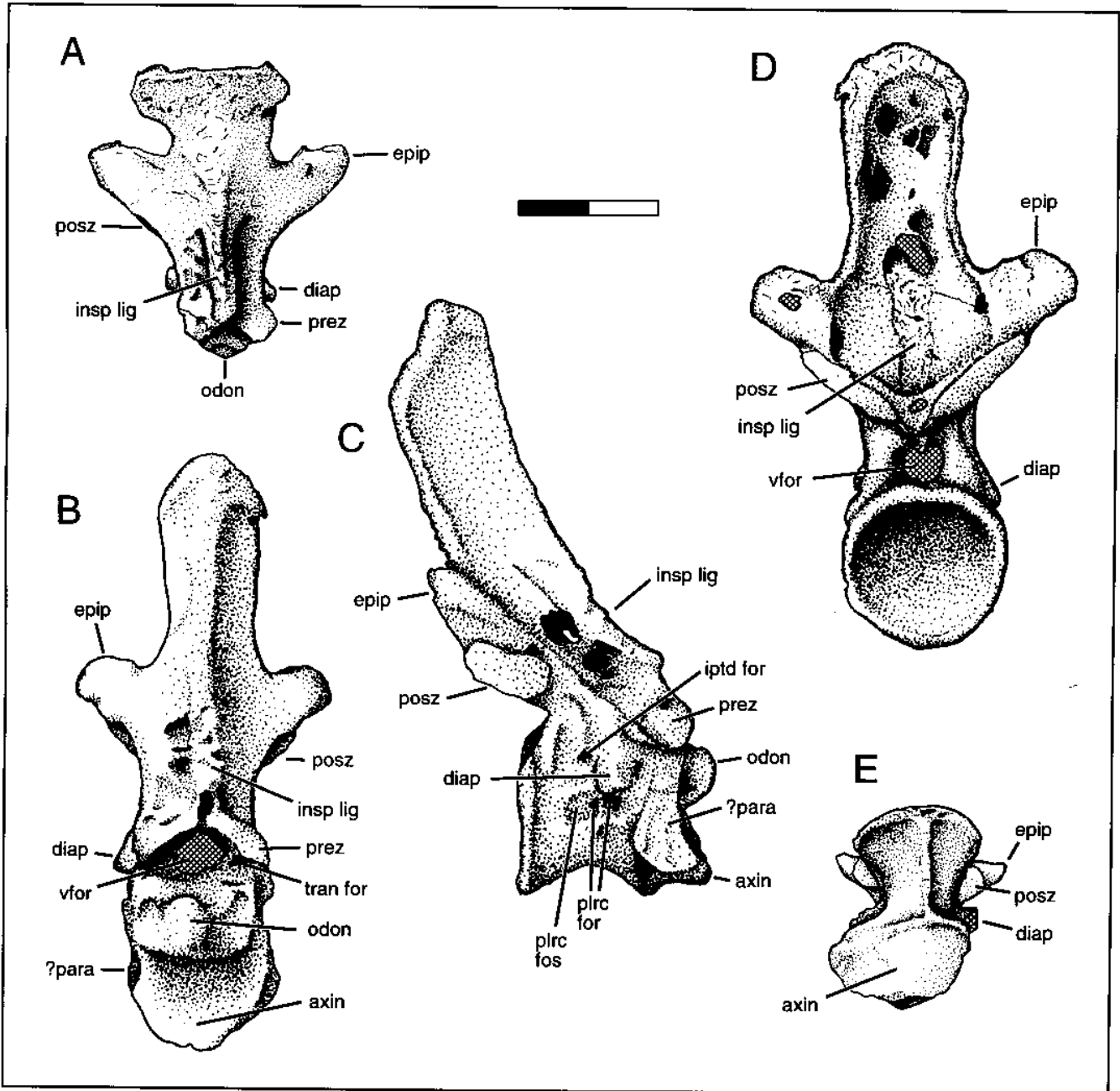

Figure 10. Axis of *Acrocanthosaurus*, SMU 74646 3B-1 in (A) dorsal, (B) cranial, (C) right lateral, (D) caudal, and (E) ventral views. Cross-hatching represents matrix. Scale bar = 10 cm.

The axial prezygapophyseal articular facets are subcircular in shape. They lie close to the sagittal plane, just dorsolateral to the vertebral foramen. They overhang the vertebral foramen both laterally and cranially and are sharply downturned from the horizontal plane. At least the right prezygapophysis is invaded by diverticula, that were visible in a break. The prezygapophyses protrude farther cranially than any part of the neural spine. Just dorsal to both the vertebral foramen and prezygapophyses, at the base of the neural spine, is a tall, mediolaterally narrow foramen that likely connects with the openings on the proximal portion of the spine (see below).

The prezygapophyses overhang narrow, craniomedially-oriented canals, that are perhaps analogous to the transverse foramina in the cervical vertebrae of mammals, and housed the vertebral arteries and veins immediately prior to their joining the spinal cord in entering the foramen magnum. The presence of similar canals in other theropods is undocumented. The axis of *Acrocanthosaurus* does not possess accessory hypantrum-hyposphene articulations.

The postzygapophyses are large, ventrolaterally-facing ovals slightly offset from the main body of the neural arch, forming a sort of plateau. They are connected medially by a short transverse ridge of bone, behind which is a deep pocket (Fig. 10D). The rugose strip for attachment of the interspinous ligaments continues into the pocket, lines its floor, and curls dorsally and caudally onto the top of the short ridge between the postzygapophyses. Prominent epipophyses, roughly triangular in shape, project dorsolaterally from the neural arch complex; the distal ends hook caudally. The epipophyses are invaded by foramina that open medially into the caudal concavity of the neural spine.

The axis of *Acrocanthosaurus* has small but well-formed, cylindrical diapophyses that project ventrally, laterally, and slightly cranially from the base of the neural arch. The regions where parapophyses would have been are broken on both sides.

The neural arch assembly sweeps dorsally and slightly caudally from the centrum. Thick but laterally short laminae of bone extend dorsocaudally to connect the prezygapophyses to the postzygapophyses and epipophyses. The neural spine is, in cross-section, shaped like a squat, rounded Y and is concave caudally. The cranial edge of the spine forms a mediolaterally thick ridge that runs from the summit to a point just above the opening above the vertebral foramen (Figs. 10A-C). The cranial margin of this ridge is rough, particularly at the proximal and distal ends, for attachment of the supraspinous and interspinous ligaments, respectively.

The lower end of the ridge, beneath the attachment surface for the interspinous ligamenture, overlies a series of foramina (Figs. 10A-C). As with the pleurocoelous foramina, the distribution, sizes, and shapes of the openings are asymmetrical on the right and left sides. Some of these are contiguous from the right to left side, leaving just a bridge of bone supported by an irregular set of struts spanning over the openings (Figs. 10A, C). At least some of these openings probably communicate with the tall, deep opening at the base

of the neural spine, just above the vertebral foramen. The more distal openings lead into the neural spine dorsally. Two more openings, set into a deep fossa overhung by an irregular process, open ventromedially into the neural spine on the upper left side, just below the summit and towards the caudal edge (Figs. 10A, B, D). These have no natural parallel on the right side.

The summit of the neural spine (Figs. 10A, B, D) is only slightly expanded beyond the rest of the spine. The sides of the spine are vertical distally, but flare laterally towards the epipophyses roughly midway to the centrum. The bone surface in most of the concavity is smooth, contrasting with the rugose margins of the spine and epipophyses. At a point level with the point where the lateral margins flare outwards, an irregular bony spur in the midline marks the distal end of a long, rectangular area of marked rugosity for attachment of the interspinous ligaments. The dorsocaudal surface of the summit is rugose, marking the attachment of the supraspinous ligaments. The region on the caudal surface between the attachment sites of the supraspinous and interspinous ligaments is smooth and riddled with fossae and foramina (Fig. 10D), as noted by Britt (1993:265). There is no symmetry to their placement, but they are concentrated near the summit.

POSTAXIAL CERVICAL VERTEBRAE: The third (3-45) and fourth (3-51) cervical vertebrae (Fig. 11) are represented primarily by neural arch elements, including the spines and the zygapophyses of the right side. The fourth preserves a small piece of the caudal centrum cup. The neural spines of both are curved laterally to the right; this may be the result of plastic deformation, but no other part of the elements, or any other element in the vicinity, shows signs of any such diagenetic alteration, so the curvature may be congenital for this specimen.

The prezygapophyses of the postaxial cervicals are large and subtriangular in shape. Each prezygapophysis extends far cranial to the neural spine, mounted on a short, dorsally-curving process that is connected by a mediolaterally thin lamina to the diapophysis. This lamina covers the infraprediapophyseal foramen in later vertebrae. The postzygapophyseal facets are large and ovoid to subtriangular in shape. The medial extent of each facet is close to the sagittal plane.

The postzygapophyses are, as on the axis, capped by large epipophyses. The preserved epipophysis is larger on the fourth cervical than the third, where it forms fully half of the supporting process. The epipophysis is long enough on the fourth cervical that, when articulated with the fifth, the epipophysis actually overlaps the neural arch of the fifth cervical. On both the third and fourth vertebrae, the epipophyses are rough, unlike the smooth knobs on the axis. The epipophysis of the third vertebra has at least two small, subcircular foramina on the lateral surface, just above the postzygapophysis, while the fourth vertebra has two small, ovoid holes on the caudal surface, well above the postzygapophysis. There are no foramina opening into the epipophyses from the caudal surface of the neural spine as in the axis.

The neural spines of both the third and fourth cervicals, and of all the postaxial cervicals, are as tall as but much more

laterally compressed than that of the axis; they are also concave caudally. There is a pronounced, cranially-projecting, dorsoventrally oblong process that extends dorsally from the base of the spine to a point just less than halfway to the summit. This process corresponds to the strip on the caudal surface of each subsequent vertebra for the attachment of the interspinous ligaments. A short distance above the limit of this process, the cranial margin of the neural spine becomes concave, forming a notch that terminates beneath the triangular, cranial process. On the third vertebra, this process is located at the cranial edge of the spine's summit, but on the fourth, it is located well below the top of the spine. The bone surface between the interspinous process and the cranial process is smooth and pitted by foramina and fossae. The fourth spine displays no foramina, but does possess some small fossae.

The caudal surfaces of the spines, as in the axis, contain a series of irregular, asymmetrical fossae and foramina. The summit of each neural spine is rough and knobby and somewhat inflated laterally, particularly at the caudal end, where it projects well behind the main body of the spine and overhangs the pitted, concave region. The cranial process of the preceding vertebra inserts into this overhang, a pattern repeated with subsequent cervicals.

Because the left sides of the third and fourth cervical neural arches have been broken off, a small portion of the interior of the bone on that side is visible. The interior is riddled with small camellae of various sizes.

Figure 11. Third and fourth cervical vertebrae of *Acrocanthosaurus*. Third cervical, SMU 74646 3-45 in (A) cranial, (B) right lateral, and (C) caudal views. Fourth cervical, 3-51, in (D) cranial, (E) right lateral, and (F) caudal views. Cross-hatching represents matrix. Scale bar = 10 cm.

The fifth cervical (3-54/3-66, Figs. 12A-C) is more complete than either the third or fourth, consisting of the neural spine and the zygapophyses of the right side and the right half of the centrum. The centrum (3-66) was found separated from the neural arch assembly (3-54).

The centrum is strongly opisthocoelous. The cranial ball is separated from the main body of the centrum by a shallow groove. The caudal cup is depressed just below the vertebral foramen, giving the face a reniform outline similar to that

described by Sereno et al. (1996:991) for *Carcharodontosaurus*, although the face in the latter is much broader than in *Acrocanthosaurus*.

The fifth cervical lacks a ventral keel; thus, this feature was limited either to the axis or to the most cranial cervicals. Instead, the underside of the centrum houses a shallow, longitudinal groove that widens caudally and is bounded below the caudal cup by two low ridges. The ventral margin in *Acrocanthosaurus* is lightly arched, and the caudal cup projects further ventrally
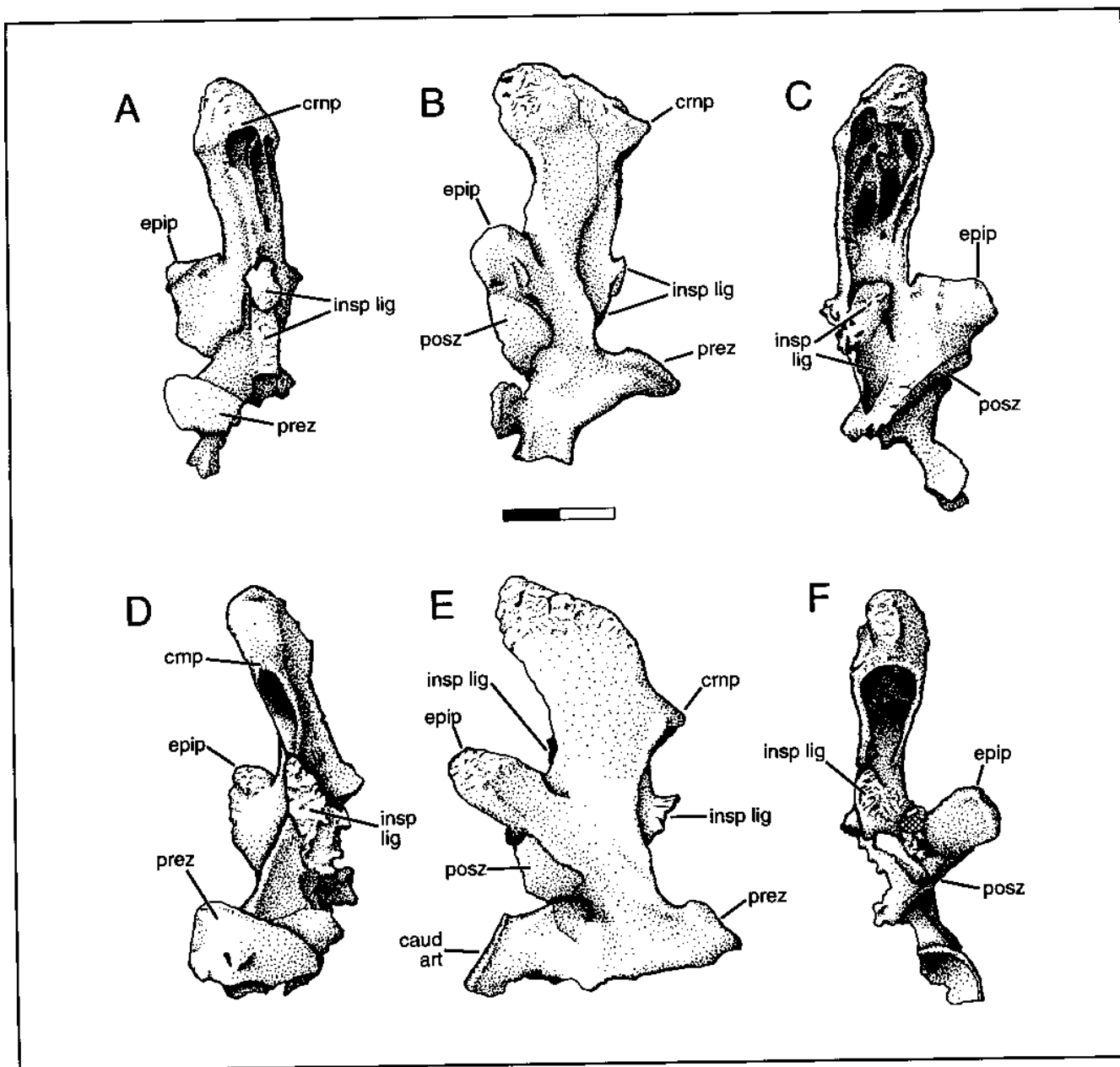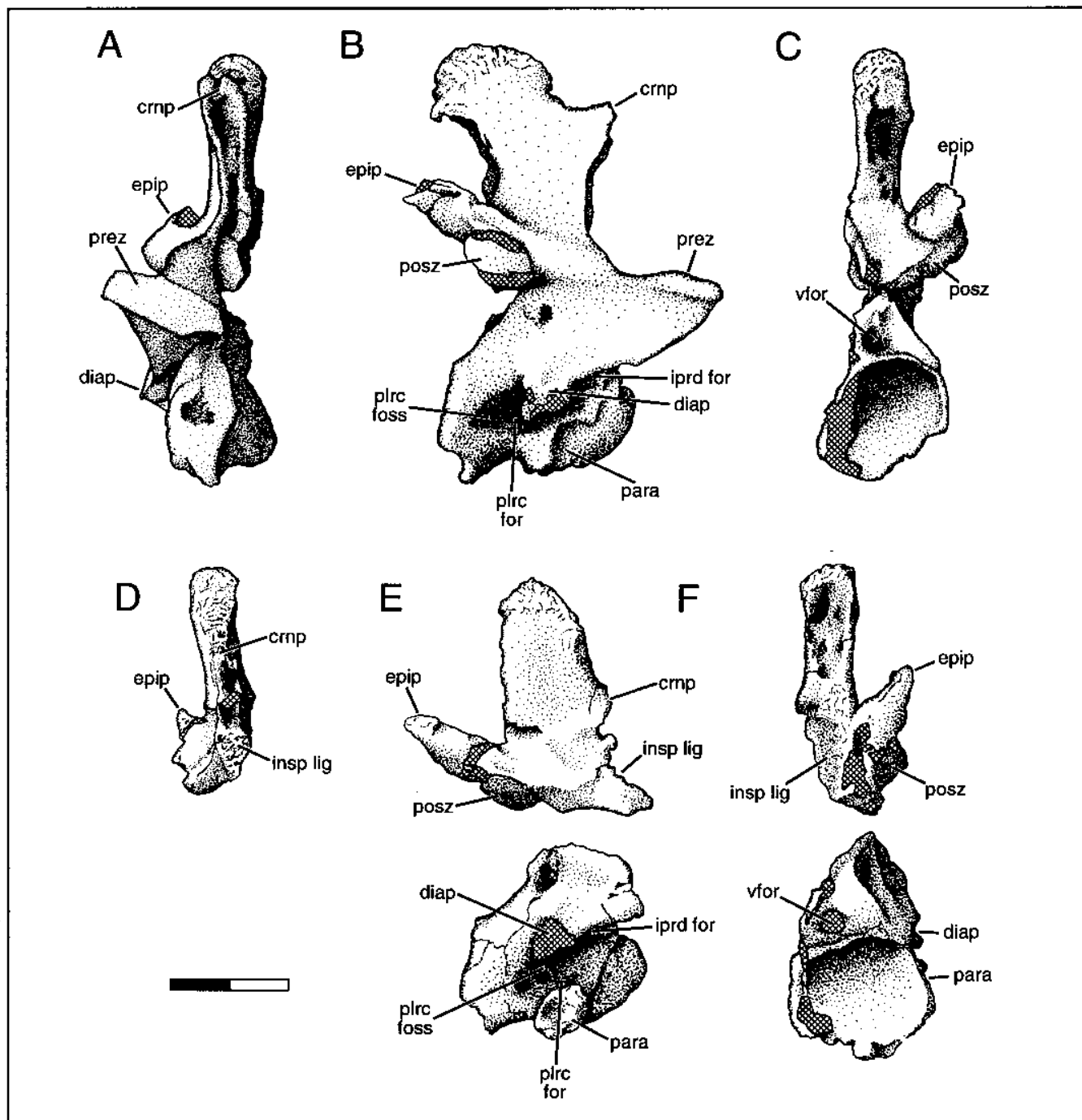

Figure 12. Fifth and sixth cervical vertebrae of *Acrocanthosaurus*. Fifth cervical, SMU 74646 3-54/3-66, in (A) cranial, (B) right lateral, and (C) caudal views. Sixth cervical vertebrae, 3-60, and neural spine, 3-61, in (D) cranial, (E) right lateral, and (F) caudal views. Cross-hatching represents matrix. Scale bar = 10 cm.

than does the cranial ball (Fig. 12B). The caudal face of the centrum in *Acrocanthosaurus* is just short of perpendicular to the long axis of the centrum, but the cranial ball has a marked ventral tilt (Fig. 12B). This feature would have given the neck of *Acrocanthosaurus*, at this point, a downward curve.

The diapophysis of the fifth cervical is oriented ventrolaterally and slightly caudally. Most of the parapophysis is missing, but its outlines can be discerned. It is a short, ovoid process projecting from the cranioventral portion of the centrum located slightly forward of the diapophysis.

The right side of the centrum, below and beneath the diapophysis and above the parapophyseal region, houses a single, large, shallow pleurocoelous fossa. The fossa runs virtually the entire length of the centrum. This differs from the fifth cervical of the holotype, in which the fossa appear to consist of two separate indentations separated by a substantial bar of bone; these differences are best viewed as individual variation. Since most of the cervical vertebrae of *Acrocanthosaurus* bear a single large pleurocoelous fossa with generally divided foramina, the condition in the holotype appears to be an exception, rather than the norm, and is unlikely to be homologous with the separate cranial and caudal pleurocoelous fossae of ceratosaurians (Rowe and Gauthier, 1990; Holtz, 1994).

A single, deep pleurocoelous foramen that tunnels medially and slightly cranially into the centrum is located towards the caudal end of the fossa. The passage does not traverse the centrum because there is no trace of it on the broken left side. A second opening, the infradiapophyseal foramen, leads dorsally into the neural arch, and is hidden beneath the arch of bone that connects the diapophysis to the main body. A third opening, the infraprediapophyseal foramen, opens dorsocaudally. It is located just cranial to the diapophysis but is hidden in lateral view by the thin lamina of bone connecting the prezygapophysis to the diapophysis. Although not reported by Stovall and Langston (1950), the fifth cervical vertebra of the holotype, OMNH 8-0-S9, also possesses large, circular cranial peduncular fossae, as noted by Britt (1993).

The neural arch is similar to that of the fourth cervical, with large epipophyses. The spine is angled slightly caudally from the vertical. Like the preceding postaxials, there is a triangular cranial process projecting from the leading margin of the neural spine, but unlike those of previous vertebrae, this process is bifid and hooked dorsally (Figs. 12A, B). The cranial and caudal margins house large, irregularly spaced fossae and foramina. Although similar in overall morphology, the fifth spine in SMU 74646 is more rugose and has more pronounced processes than does that of the holotype, OMNH 8-0-S9 (Stovall and Langston, 1950:fig. 3), demonstrating that the neural spines were a region of individual variation in *Acrocanthosaurus*.

Still in articulation with the postzygapophysis of the fifth cervical was a fragment of the prezygapophysis of the sixth that fit with the larger portion of the prezygapophysis of 3-60, a disarticulated centrum found caudal to 3-66 (Figs. 12D-F). This specimen preserves the entire body plus a portion of the base of the neural arch complex except for much of the left

face. Like 3-66, it is strongly opisthocoelous, lacks a ventral keel, and has a ventrally-tilted cranial ball separated from the main body by a shallow groove. The pleurocoelous fossae on both sides are markedly different from those of previous vertebrae: they are divided into two, shallow, craniocaudally oblong depressions by horizontal laminae of bone, as in the fifth cervical centrum of the holotype (Fig. 13A). The dorsal part of the pleurocoelous fossa merges with the two openings under the diapophysis. These two openings are separated by a thin lamina.

A depression, possibly an infrapostzygapophyseal fossa, is located above and slightly caudal to the diapophysis (Fig. 12E, F). It contains two foramina separated by a thin oblique lamina; there is only a shallow, blind fossa in this position on the fifth cervical. The dorsal eversion of the caudal cup (giving it the reniform shape) is more pronounced in the sixth than the fifth vertebra. The parapophysis is quite large and projects laterally.

The preserved portion of the neural arch assembly of the sixth cervical differs from the fifth in that the lamina connecting the diapophysis to the prezygapophysis is tilted more laterally. The ovoid prezygapophyseal facet is longer craniocaudally than wide, unlike the broad, subtriangular facets of the preceding cervicals.

Centrum 3-60 had been sheared parasagittally and slightly obliquely prior to burial (Fig. 13F). It was acid prepared using the procedure outlined by Rutzky et al. (1994:162-3) to elucidate the nature of the internal system of camellae (Fig. 13). Camellae (singular: camella) are defined as "numerous small chambers...which are separated by thin trabeculae [and whose] outer walls tend to be thin;" they contrast with camerae (singular: camera) which are defined as "large chambers...separated from each other by laminae and [whose] outer walls tend to be thick" (Britt, 1993:23). Preparation revealed that the centrum, diapophysis, parapophysis, and neural arch, including the base of the neural spine, have camellate interiors. In general, the camellae exposed increase slightly in size dorsally. A few mural pores (small foramina between camellae and not open to the surface [Britt, 1993:264]) are visible (Fig. 13B).

Caudal to the fifth cervical, the neural spines of the succeeding cervicals are preserved in sequence, but the rest of the vertebral elements are scattered or missing. Behind the neural arch of the fifth cervical (3-54) is 3-61, which preserves the neural spine and a portion of the right postzygapophyseal ala (Figs. 12D-F). The spine undoubtedly belongs with the centrum 3-60, but they cannot be fitted together. The spine differs from that of the fifth cervical in having a much less concave caudal surface and a less craniocaudally expanded summit. The cranial face maintains convexity, however, and possesses a single large foramen. The base of the cranial process is broken. The caudal face possesses several fossae and a single foramen. The postzygopophysis maintains a large and prominent epipophysis.

The caudal face of the seventh spine in the sequence, 3-59 (Figs. 14A-C), like the spine of the sixth cervical, is flat. There are no large fossae on this face, although at least one

small foramen penetrates the spine beneath the small caudal overhang. A small, non-bifurcate, triangular cranial projection is maintained. An arched, caudoventrally tilted process of bone protrudes dorsocaudally from the region where the interspinous ligaments attach.

The last preserved specimen (3-46) includes spines attributed to both the eighth and ninth cervicals (Figs. 14D-G). The eighth is much narrower craniocaudally and broader mediolaterally than any of the aforementioned spines except the axis (Fig. 14F). This abrupt change in cervical spine morphology is in agreement with the holotype of *Acrocanthosaurus* (Stovall and Langston, 1950). This spine returns to the deeply concave caudal face of the more cranial cervicals. It retains a small caudal overhang. The concavity contains an indeterminate number of fossae and foramina, but all are concentrated at the distal end just beneath the overhang
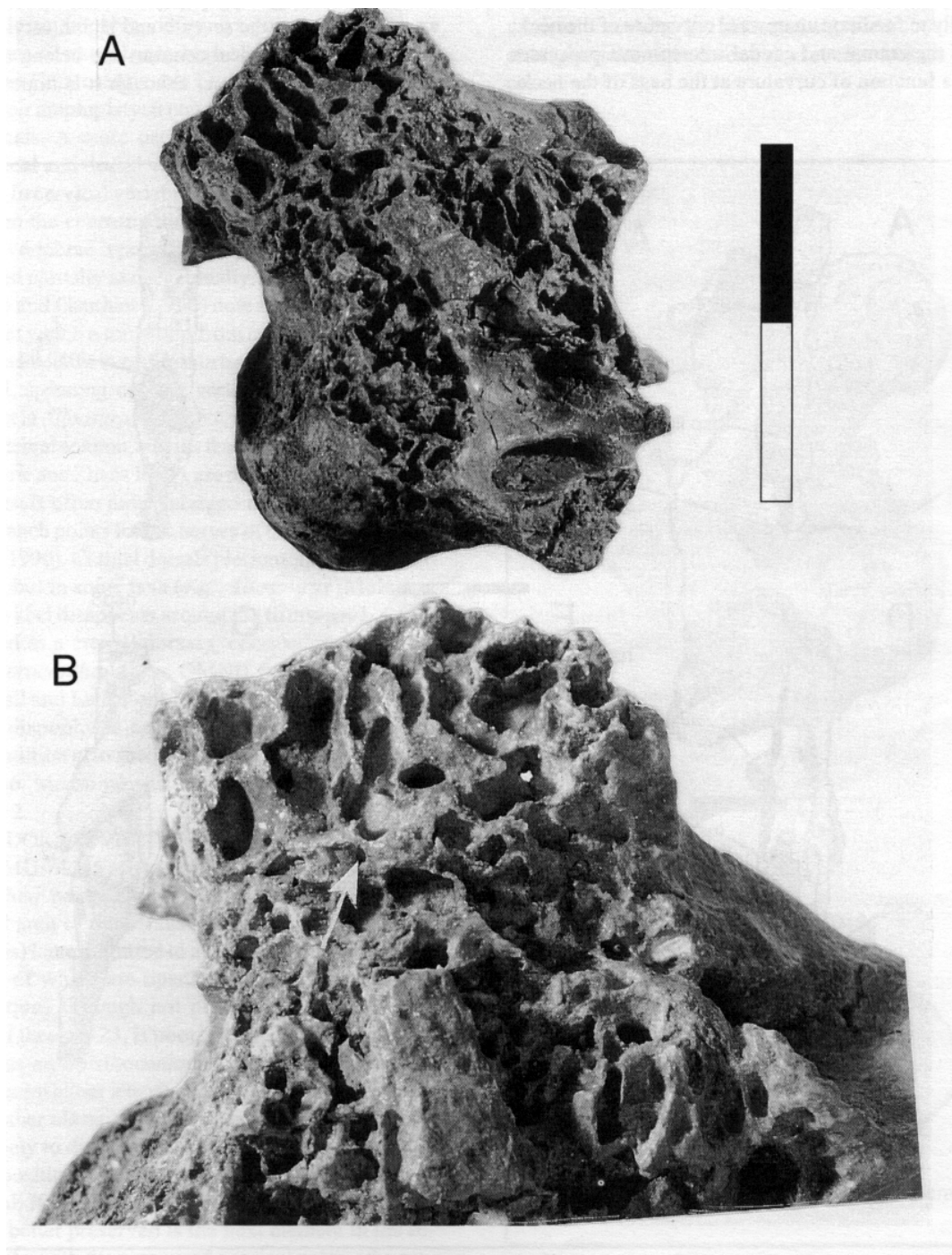
Figure 13. Left lateral view of centrum of sixth cervical vertebra of *Acrocanthosaurus*, SMU 74646 3-60. (A) View of sheared, left lateral surface, showing numerous camellae on interior of centrum and neural arch. Scale bar = 10 cm. (B) Close-up of camellae in neural arch. Arrow points to a mural pore.

(Fig. 14G). The cranial face, below the apical rugosity, is slightly concave. The summit of the spine on the cranial end is higher than at the caudal end, and tilts slightly forward from the vertical axis. There is no triangular projection as in all the preceding postaxial cervicals; however, towards the base, there is a rectangular projection for attachment of the interspinous ligamenture. The distal end of this process is lower than the distal end of the aforementioned caudal interspinous process. Stovall and Langston (1950:708) report that the spines of the caudal-most cervicals in *Acrocanthosaurus* angle cranially to facilitate an upward curvature of the neck; the offset of the cranial and caudal interspinous processes may also be a function of curvature at the base of the neck.

Adhering to the caudal face of 3-46 is a fragment of what appears to be the distal end of the ninth cervical neural spine. If this identification is correct, then it has been rotated 180° so that its caudal face is in contact with the caudal face of the eighth spine. Like the eighth, its summit is tilted cranially. The caudal face is deeply concave and houses a number of fossae, some of which contain small foramina (Fig. 14E). Unlike the preceding spine, however, the cranial face is strongly convex (Figs. 14F, G).

Two isolated right zygapophyseal assemblies (3-63 and 3-64) were found below the seventh and eighth cervical spines and behind the sixth cervical centrum and belong to the seventh, eighth, or ninth vertebrae, although it is impossible to place
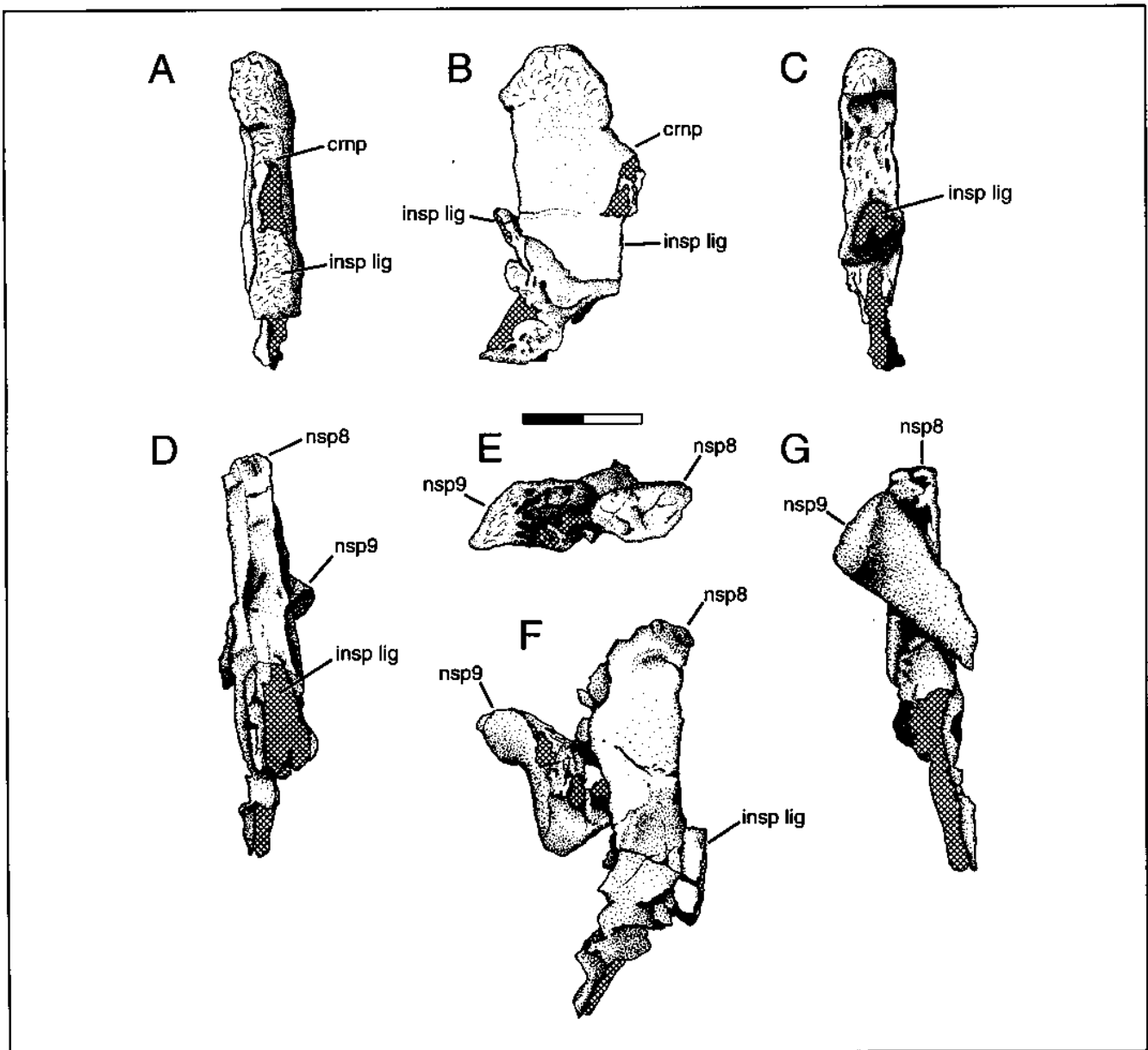
Figure 14. Seventh, eighth, and ninth cervical vertebral neural spines of *Acrocanthosaurus*. Seventh neural spine, SMU 74646 3-59 in (A) cranial, (B) right lateral, and (C) caudal views. Eighth and ninth neural spines, 3-46, in (D) cranial, (E) right lateral, and (F) caudal views. Cross-hatching represents matrix. Scale bar = 10 cm.

them precisely. They differ from the preceding assemblies (particularly the fifth, the last most completely preserved in the sequence) because the postzygapophyseal process does not bear a large epipophysis. There is a small, laterally compressed ridge of bone atop the postzygopophysis, but it is quite short compared to the epipophysis of the more cranial cervicals.

Dorsal Vertebrae

In the absence of articulated vertebrae and ribs, whereby rib morphology can be used to differentiate the last cervical from the first dorsal vertebra, defining a point of transition is difficult. In general, dorsal vertebrae of theropods more advanced than the Ceratosauria can be distinguished from the cervicals by their amphiplatyan condition, unlike the opisthocoelous cervicals. A more useful characteristic for distinguishing cervical and dorsal vertebrae is the position of the parapophysis. In cervical vertebrae, the parapophysis is situated entirely on the centrum, but in the caudal cervical and cranial dorsal vertebrae it progressively migrates dorsally to become situated partially and, eventually, entirely on the neural arch. Rowe and Gauthier (1990) note that it is difficult to define a point at which a transition from cervical vertebrae to dorsal vertebrae occurs in ceratosaurians because the transition is gradual, spanning up to 5 vertebrae. In contrast, the change is abrupt in *Allosaurus* (Gilmore, 1920). Further subdivisions of the vertebral column, such as those employed by Welles (1984) and Currie and Zhao (1993), are not used here.

Cranial dorsals often have enlarged neural canals due to the multiple branch points for the nerves of the brachial plexus (Molnar et al., 1990). Cranial dorsals plesiomorphically retain a ventral keel, but in some taxa (e.g., *Allosaurus* [Molnar et al., 1990]), the keel disappears around the fifth dorsal. A vertebra identified as a cranial dorsal ("cervicodorsal") in the holotype of *Acrocanthosaurus*, OMNH 8-0-S9, is opisthocoelous (Stovall and Langston, 1950); the latter authors also note that the diapophysis on this centrum is not directed laterally, a condition also seen in some of the cranial dorsals of SMU 74646. Measurements of the dorsal vertebrae are given in Table 2.

CRANIAL DORSAL VERTEBRAE: Five, possibly six, vertebrae from SMU 74646 are identified as cranial dorsals because either their parapophyses overlap both the centrum and the neural arch or their transverse processes (including the diapophysis) have migrated to a lateral orientation. Seven vertebrae, six of which are opisthocoelous, were found in linear association, although not precisely articulated. The most cranial of these, 4-23, is poorly preserved and only just recognizable as an opisthocoelous centrum, so this specimen may represent either a tenth cervical or a first true dorsal. The trend in other allosauroid theropods is for dorsal vertebral opisthocoely to disappear around the fifth dorsal, so the conservative position is to view the first of this sequence as a tenth cervical. If so, 13 dorsal vertebrae are expected.

Somewhat better preserved is the next element in the sequence, 4-21. As with the preserved cervical centra, the cranial ball of 4-21 is separated from the rest of the centrum by a shallow groove. The centrum retains a single, dorsoventrally

compressed foramen in the pleurocoelous fossa immediately above the parapophysis. There appears to be a strong ventral keel, but this is uncertain due to breakage. The base of the transverse process is directed laterally. A fragment of the neural spine rises dorsocaudally from the top of the element. Specimen 4-21 is interpreted as the first dorsal vertebra.

Caudal to 4-21 was another opisthocoelous vertebra, 4-20, by correlation the second dorsal vertebra (Fig. 15). Its opisthocoelous centrum has been plastically deformed, so the true orientations and locations of the parapophyses are unclear. Crushing has distorted the pleurocoels. There is a strongly pronounced ventral keel that lacks a ventral process (Fig. 15B).
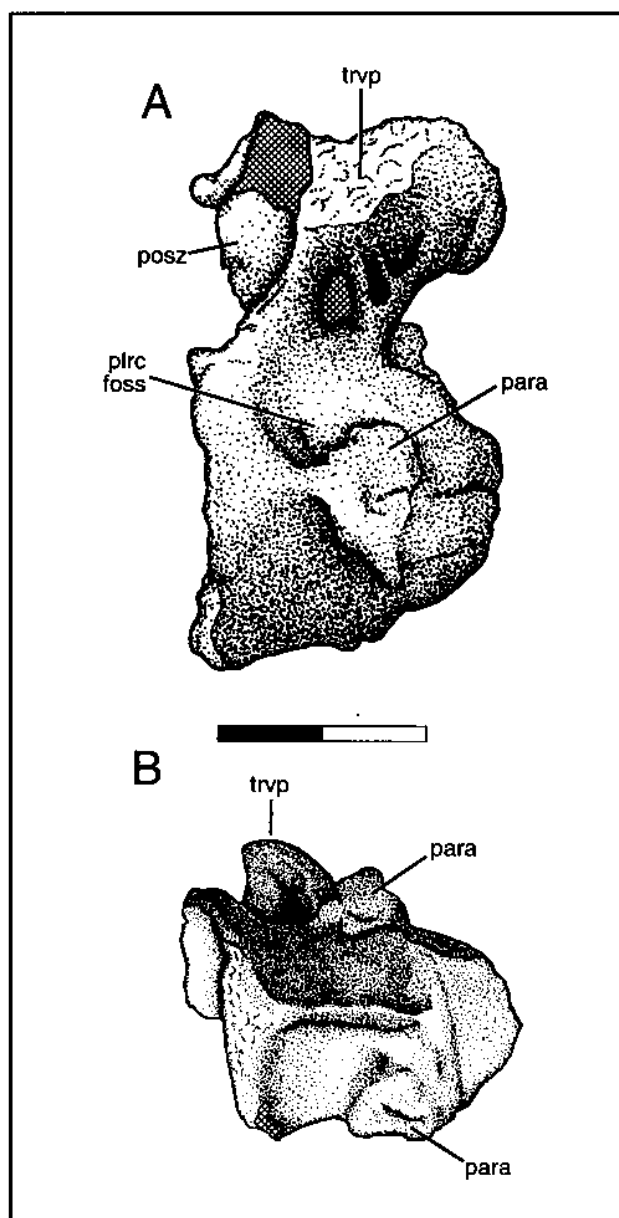
Figure 15. Second dorsal vertebra of *Acrocanthosaurus*, SMU 74646 4-20, in (A) right lateral and (B) ventral views. Cross-hatching represents matrix. Scale bar = 10 cm.

The neural arch sweeps forward from the dorsal margin of the centrum. There are three openings on the right lateral surface arranged linearly (Fig. 15A). The caudal and middle openings are foramina, while the cranial opening is a blind fossa. It is unclear if any or all of these fossae are homologous with the infradiapophyseal, infrapre- or infrapostdiapophyseal, or infraprezygapophyseal fossae or foramina of other theropods. Immediately above these openings, the base of a thick transverse process sweeps dorsally, caudally, and laterally, in contrast to the previous vertebra. Similarly, the base of the prezygapophyseal process projects craniodorsally. Another opening is located mediocaudal to the transverse process, set into a deep subconical fossa that separates the transverse process from the base of the neural spine. This fossa leads

craniomedially and is roofed by the postzygapophysis in all subsequent vertebrae (see below). In life, it would have housed the prezygapophysis of the subsequent vertebra.

Caudal to 4-20 was specimen 4-17, here considered the third dorsal (Figs. 16A, C, E). Like the previous two vertebrae, this element is also sheared into right and left halves, but unlike the latter, both halves are preserved. It differs from the previous two dorsals in that the parapophysis is greatly elongate dorsoventrally and borders the ventral margin of the neural arch, as expected in the progression towards the more caudal dorsals.

As in previous vertebrae, the cranial ball of the centrum is set off from the body by a shallow groove immediately cranial to the parapophysis. Unlike the groove on the cervical
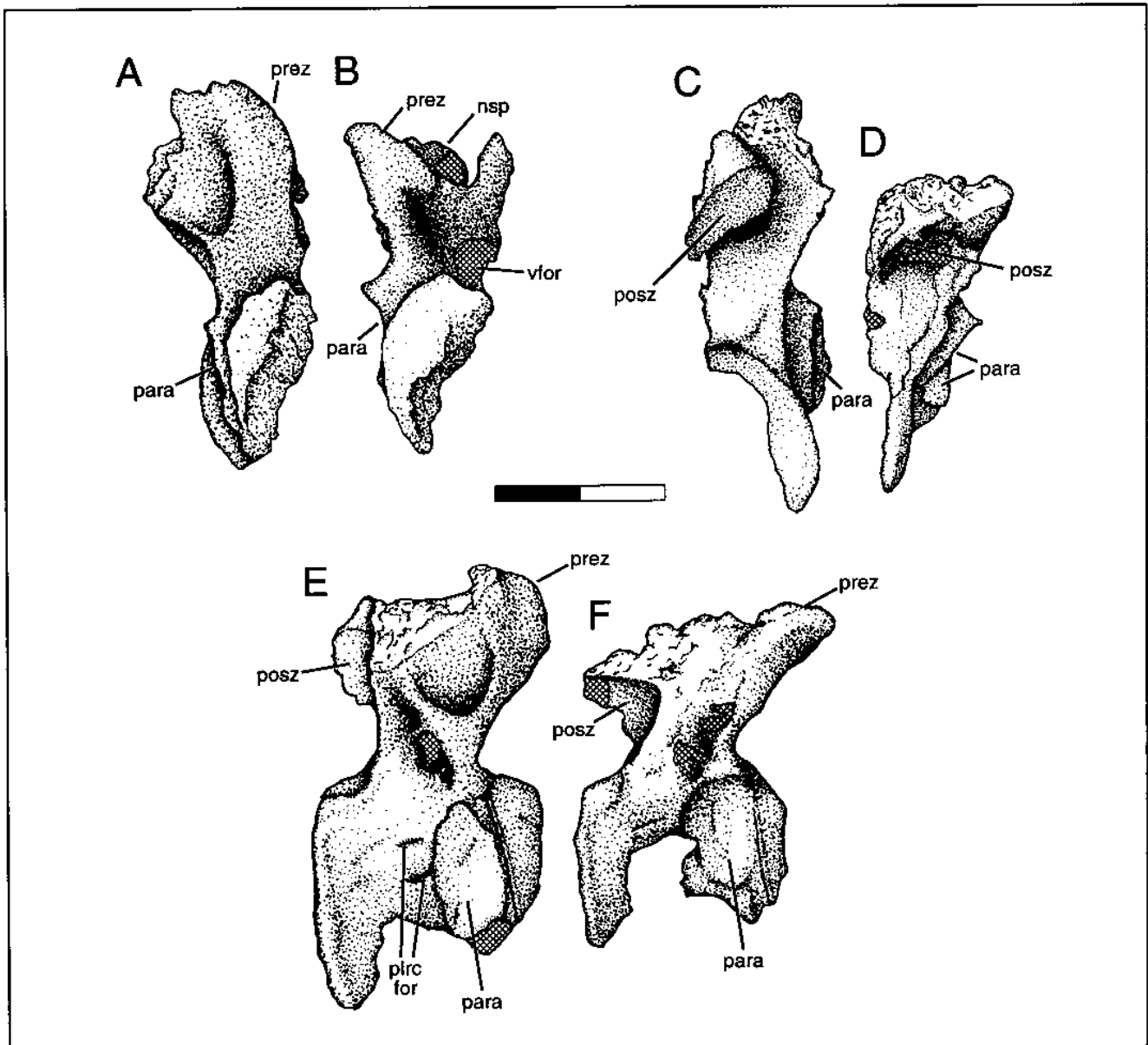
Figure 16. Third and fourth dorsal vertebrae of *Acrocanthosaurus*. Third dorsal, SMU 74646 4-17, in (A) cranial, (C) caudal, and (E) right lateral views. Fourth dorsal, 4-29B, in (B) cranial, (D) caudal, and (F) right lateral views. Cross-hatching represents matrix. Scale bar = 10 cm.

centra, however, it is oriented dorsocaudally. The centrum appears to have retained a ventral keel, but the shearing makes it difficult to ascertain its degree of pronunciation. Crushing has damaged the pleurocoels on both sides. Two dorsoventrally narrow and craniocaudally short slits reside atop one another on the right side, and possibly are the relics of pleurocoelous foramina (Fig. 16E).

The neural arch is similar in gross morphology to that of 4-20. Unlike 4-20, however, it has four openings (three caudal fossae and a blind, cranial pocket) that, instead of being arranged in a linear fashion as in 4-20, have a triangular layout (Fig. 16E). The base of the transverse process is swept more strongly dorsally in this specimen than in the preceding.

The process that bears the prezygapophyseal facet is deep dorsoventrally and angles craniodorsally. The facet is planar and tilted strongly ventromedially. The prezygapophysis of 4-17 is higher than the postzygapophysis; this configuration would provide the vertebral column with an upward curvature at this point.

Also as in 4-20, there is a large, deep opening mediocaudal to the transverse process, that is roofed dorsally and medially by the postzygapophysis. The articular facet is ovoid, planar, and steeply angled ventromedially.

The left half of 4-17 preserves a portion of the neural spine. Of this, only the right side contains some undamaged bone, that contains two shallow, blind fossae that open medially. Though incomplete, it is quite tall.

Specimen 4-29 (Figs. 16 B, D, F), found behind 4-17, exemplifies the continuing migration of the parapophysis, approximately one-fifth of which is borne on the neural arch. The dorsal migration of the parapophysis has rearranged the layout of the centrum, so that the pleurocoel now lies caudal to, instead of dorsal to, the parapophysis (Fig. 16F). The pleurocoelous foramen is divided internally into a larger cranial and smaller caudal openings by an irregular bar of bone. Three openings on the side of the transverse process are arranged in a linear fashion, as in the second dorsal.

The prezygapophysis is supported by a narrow, craniodorsally oriented pillar of bone. As before, it is higher than the postzygapophysis (Fig. 16F). The postzygapophyseal facet roofs a deep subconical pocket.

The last intact centrum of this sequence, 4-25, is the right half of a clearly opisthocoelous centrum (still encased in matrix) found caudal to 4-29, making it the fifth dorsal vertebra. In the same block of matrix is a fragment of bone oriented properly to be the cranial end of the sixth centrum. It conceivably belongs to dorsal A1-2-15 (see below). It is not clearly opisthocoelous; if it is not, then the transition from opisthocoely to amphicoely in the dorsal column of *Acrocanthosaurus* is abrupt.

MID-DORSAL AND CAUDAL DORSAL VERTEBRAE: Assessment of all vertebral elements caudal to the cranial dorsals is complicated by an artifact of their preservation: all the elements were sheared into left and right halves during collection and were preserved in two blocks, A1-2 and A2-1. Block A1-2 contained only the right halves of vertebrae, while A2-1 contained only left halves. Field and preparator's notes

explain that these two blocks fit together, but post-preparational separation of individual elements precludes determination of the degree of overlap between A1-2 and A2-1. Morphological differences indicate that the overlap is not total. Enough material is missing between the halves that no one piece can be fitted to another.

The right halves of block A1-2 (Fig. 17) include a sequence of six partial, apparently mid-dorsal, vertebrae in articulation. The most cranial of this sequence, A1-2-15 (Fig. 17A), consists of a partial neural arch, including most of the right transverse process, postzygapophysis, and caudal end of the centrum (which may represent the same element as the fragment noted above with 4-25). The transverse process sweeps strongly dorsocaudally. The postzygapophysis is large and, as in the cranial dorsals, forms the roof of a deep fossa. It differs from its cranial counterparts because it forms the entire roof of the fossa and, more strikingly, its facet is arched dorsally instead of being planar. Dorsal and lateral to the fossa roofed by the postzygapophysis is another opening (Fig. 18E). This fossa is squeezed out ventrally where the postzygapophysis meets the lateral support of the transverse process. Because it is lacking the cranial end of the centrum and the prezygapophyses, the relationship of this specimen with the last opisthocoelous dorsal (4-29) cannot be precisely determined. It is referred here to the position of the sixth dorsal.

Caudal to A1-2-15, a more complete vertebra, A1-2-11, is by correlation the seventh dorsal (Figs. 17B, D). The cranial face of the centrum is amphicoelous. As described in the holotype by Stovall and Langston (1950:710), the pleurocoelous fossa is deep but poorly demarcated. There are two pleurocoelous foramina, that are separated from each other by an oblique shelf of bone.

The parapophysis is located entirely on the neural arch, and is smaller than its more cranial counterparts. The transverse process is robust, triangular in lateral view, and is oriented dorsocaudally and, toward its distal end, laterally. The lateral surface of the neural arch of A1-2-11 is deeply excavated by an enormous fossa that is divided into two by a very thin, obliquely-oriented lamina of bone that runs caudally from the dorsal margin of the parapophysis to the lateral surface of the transverse process, just cranial to the postzygapophysis. Such a lamina is not mentioned or illustrated in the holotype of *Acrocanthosaurus* by Stovall and Langston (1950).

The prezygapophysis is dorsally convex. On the cranial face of the vertebra, just dorsolateral to the neural canal, the prezygapophysis is deeply excavated by a subconical cranial peduncular fossa (Fig. 17D). There is a deep, but narrow, V-shaped cleft between the complete right prezygapophysis and a fragment of the left; the prezygapophyseal facets of both continue into this cleft. This region represents a confluence of the prezygapophyseal and hypantral facets, as seen in the mid- and caudal dorsal vertebrae of *Allosaurus* and tyrannosaurids (Madsen, 1976; Molnar et al., 1990). No hyposphenes are preserved in SMU 74646. Unlike the more cranial dorsals, the postzygapophysis of A1-2-11 lies in roughly the same plane as the prezygapophysis.

The next (eighth) mid-dorsal, A1-2-12 (Fig. 17C), has a more complete centrum. The parapophysis and transverse process are virtually identical to those of A1-2-11. The prezygapophysis is incomplete, but the preserved portion faces dorsally and laterally, implying that, as in A1-2-11, the prezygapophyseal facet of A1-2-12 was convex dorsally, forming a condyloid joint. The postzygapophysis of A1-2-12 is lightly concave ventrally, not as pronounced as in A1-2-11. An elongate cleft narrowly separates the postzygapophysis from the lateral ramus of the transverse process. This gap persists in all subsequent dorsal vertebrae for which this region is preserved (Fig. 18E).

The next vertebra in the sequence, A1-2-14 (the ninth dorsal, Fig. 18A), is the most completely preserved of the series. Its centrum is amphicoelous, and, as before, the pleurocoel contains two foramina separated by an oblique lamina. A smaller crest of bone at the caudal end of the caudal foramen partially divides this opening further into a large cranial portion and a tiny caudal hole. The lamina that divides the fossa on the side of the transverse process is less than 1.4 mm thick. It is somewhat sinuous, drooping downwards approximately halfway along its length (Fig. 18A). Both above and beneath the lamina, the fossae empty directly into cancellous bone. There is no visible connection between the cranial and caudal foramina around the lamina, but passage via the microscopic pores of the cancellous interior is present.

As in the previous mid-dorsals, the prezygapophysis is convex dorsally and is underlain by a deep, subcircular, cranial peduncular fossa. This opening leads caudally, but does not penetrate into the lateral fossae of the transverse pro-

cess. The postzygapophysis is also arched; the fossa which its facet domes contains the broken prezygapophysis of the following vertebra (Figs. 18A, B).

The tenth and eleventh dorsal vertebrae (A1-2-9 and A1-2-8, respectively, Figs. 18B-E) are virtually identical to A1-2-14 in all discernible details. The tenth differs in that it lacks the subsidiary ridge dividing the caudal pleurocoelous foramen. The pleurocoel of A1-2-8 is incomplete. It differs from the previous dorsals in that the ridge connecting the parapophysis to the prezygapophysis is less steeply tilted dorsomedially than in the previous dorsals. A1-2-8 preserves, for the first time, the base of the neural spine. Dorsal to the transverse process and lateral to the neural spine, the vertebra is again deeply excavated (Fig. 18D), making the neural spine crescent-shaped in dorsal view. Within the fossa on the spine are two low, vertical ridges that divide the lateral surface into small fossae. These ridges do not persist dorsally, and grade into a smooth surface.

Opposing the preserved right halves of vertebrae from block A1-2 is a sequence of left halves from block A2-1, a natural series of six vertebrae. Most of the preserved elements are fragmentary. The centra are amphicoelous. The most complete element in the block, specimen A2-1/1 (Fig. 19B), preserves the only attached neural spine of all the dorsal vertebrae. The spine is remarkable in that it has a marked cranial inclination, roughly 23° from the vertical (assuming that the preserved caudal face of the centrum was, as in the preceding vertebrae, roughly vertical). The preserved left half of the spine is virtually straight and shows no sign of having suffered diagenetic distortion, so the angulation appears to
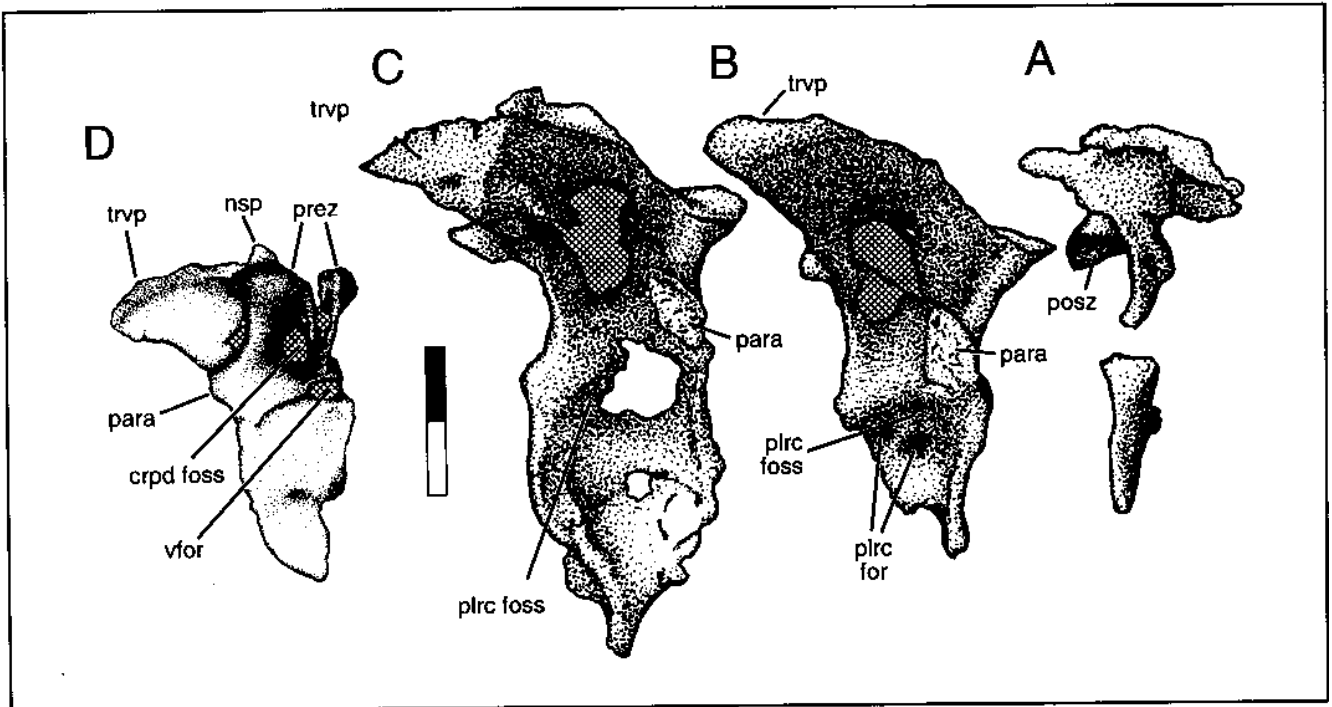
Figure 17. Sixth, seventh, and eighth dorsal vertebrae of *Acrocanthosaurus*, SMU 74646. (A) Sixth dorsal, A1-2-15, in right lateral view. (B) Seventh dorsal, A1-2-11, in right lateral and (D) cranial views. (C) Eighth dorsal, A1-2-12, in right lateral view. Cross-hatching represents matrix. Scale bar = 10 cm.

be genuine. This is further supported by the identical orientation of the postzygapophysis and partial neural spine of A2-1/4 (Fig. 19A), cranial to A2-1/1.

The base of the spine is formed by the union of the postzygapophysis and transverse process (broken in this specimen). The spine is narrow craniocaudally; its mediolateral width cannot be determined because the right half is missing. It appears to be less massive than the spines on more cranial dorsals. The caudal face of the spine is, at the base, strongly concave, forming a deep but narrow fossa that persists roughly one-fourth the distance to the preserved distal end. As in the cervical vertebrae, this fossa contains smaller, shallow fossae. Above this is a planar and moderately rugose surface, presumably part of the interspinous ligament attachment. There is also a small, ovoid, dorsocaudally-oriented foramen on the cranial margin of the neural spine, opposite the postzygapophysis (Fig. 19B).

Whereas the previous postzygapophyseal facets were merely arched, that of A2-1/1 is cupped like an inverted bowl. Unfortunately, no prezygapophyses are preserved in this sequence, so confirmation of a matching ball-shaped morphology cannot be

given. Like the previous dorsals, however, the postzygapophysis forms the roof of a fossa, but unlike its cranial counterparts, this fossa is more open laterally because the transverse process is not as strongly backswept. A narrow fossa remains between the postzygapophysis and the base of the transverse process.

Although the distal end of the transverse process is lacking, it is clear from the preserved portion that it resembled its cranial complements in possessing two deep fossae separated by an extremely thin lamina of bone, supporting their position as dorsal vertebrae. However, because of the more lateral than dorsolateral orientation of the process, the large fossa and divisive lamina are strongly inclined compared to those of the mid-dorsal vertebrae: the fossae lead dorsomedially rather than medially. This difference in orientation and location of the transverse process fossae, as well as the tilt of the neural spines, demonstrate that A2-1/1 and A2-1/4 do not correspond with any of the right halves from the A1-2 sequence. This would make A2-1/4 and A2-1/1 the twelfth and thirteenth (terminal) dorsal vertebrae, respectively.

ISOLATED NEURAL SPINES: Although most of the aforementioned dorsal vertebrae lack attached neural spines, sev-
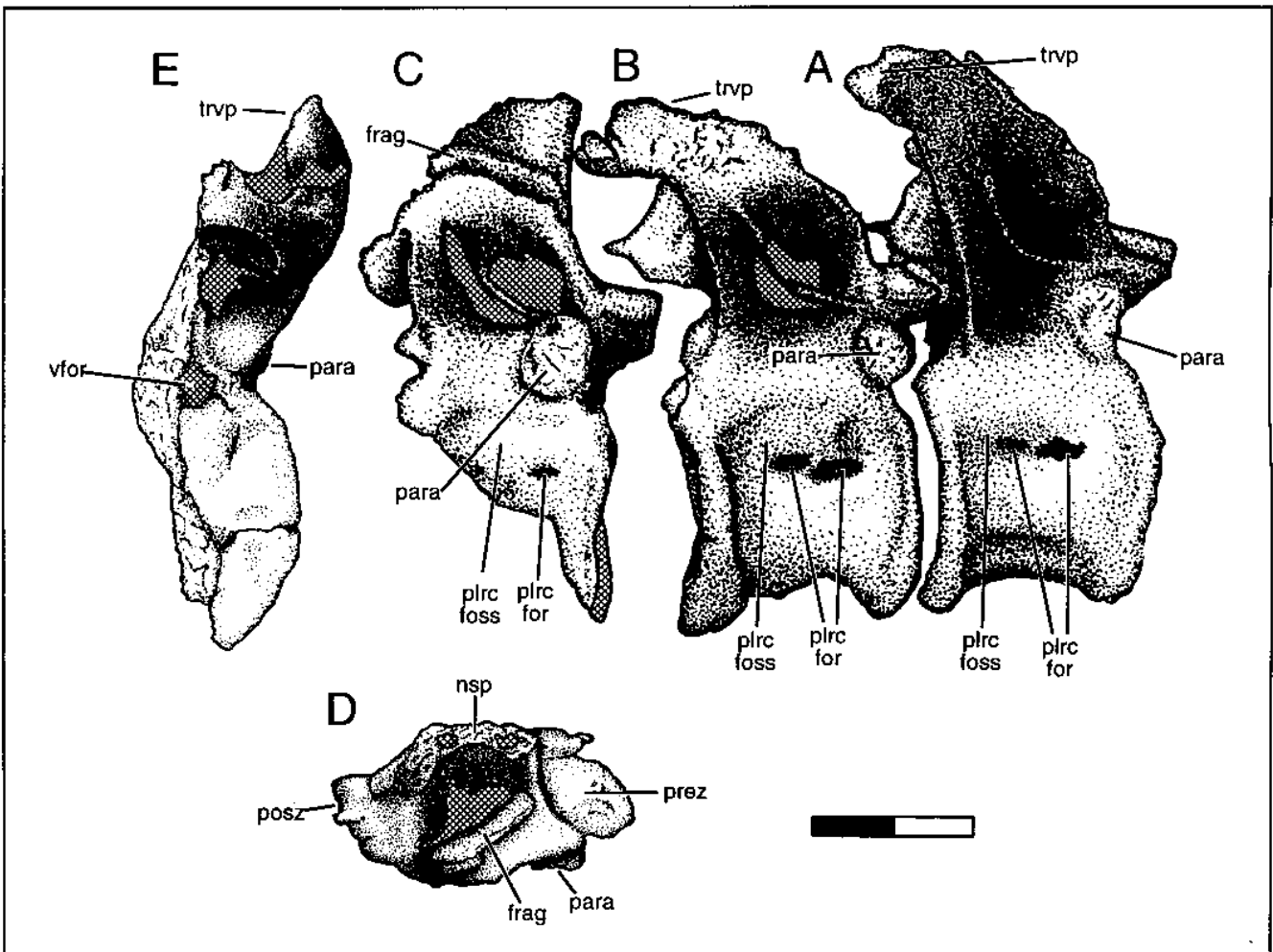
Figure 18. Ninth, tenth, and eleventh dorsal vertebrae of *Acrocanthosaurus*, SMU 74646. (A) Ninth dorsal, A1-2-114, in right lateral view. (B) Tenth dorsal, A1-2-9 in right lateral and (E) cranial views. (C) Eleventh dorsal, A1-2-8, in right lateral and (D) dorsal views. Cross-hatching represents matrix. Scale bar = 10 cm.

eral isolated neural spines were recovered from the same blocks. Their morphology provides an indication of approximate continuity.

Except for being distorted so that it bears a strong left lateral curvature, spine 3-29 (Figs. 20A, B) strongly resembles the spines of the mid- and caudal cervical vertebrae. It is craniocaudally short but mediolaterally wide, especially on the distal end. As with the spines of most of the cervical vertebrae, the caudal margin is strongly concave, and contains several shallow fossae. This concavity terminates abruptly distally beneath a rugose caudal projection, also as in the cervical vertebrae. The groove terminates proximally behind the flat, rough, interspinous ligament attachment site. On the cranial margin of the spine, there is a corresponding projection for the attachment of the forward interspinous ligaments. The distal end of the spine is inflated, knob-like, and rugose. Because of its similarity to the caudal cervical spines, 3-29 must have originated with one of the most cranial of the dorsal vertebrae, possibly even a tenth cervical.

Five partial neural spines appear to be from more caudal positions than 3-29 or 3-15. Of the five elements, three — 3-9, 3-12, and 3-26 — were found in a sequence that may be representative of their life positions. If the trend of possessing

prominent caudal overhangs on the distal end continues from the cervicals onto the dorsals, then of these three, 3-9 would be the most cranial and 3-26 the most caudal of the sequence. Spine 3-9 is grossly similar to both the cervical spines and the two aforementioned dorsal neural spines because it bears a slightly concave cranial margin and a strongly concave caudal one (Figs. 20C, D). Both margins also contain fossae. The summit is expanded craniocaudally, possessing a slight cranial projection and a more pronounced caudal overhang. Unlike the cervicals, however, the caudal overhang is not an abrupt projection of the spinal summit; instead, the caudal margin of 3-9 arcs gradually so that the distal end lies further caudally than the plane of the concavity. The preserved portion of this element measures 162 mm in length.

Spines 3-12 and 3-26 more closely resemble the dorsal spines figured for the holotype of *Acrocanthosaurus* OMNH 8-0-S9 (Stovall and Langston, 1950:plate 4, figs. 7-8). Specimen 3-12 does not possess cranial or caudal concavities; instead, the bulk of both margins are occupied by the prominent ridges for attachment of the interspinous ligaments that reach almost to the summit of the spine, unlike all previous spines. Above the attachment sites, on the cranial face, is a virtually flat, smooth region that continues all the way to the
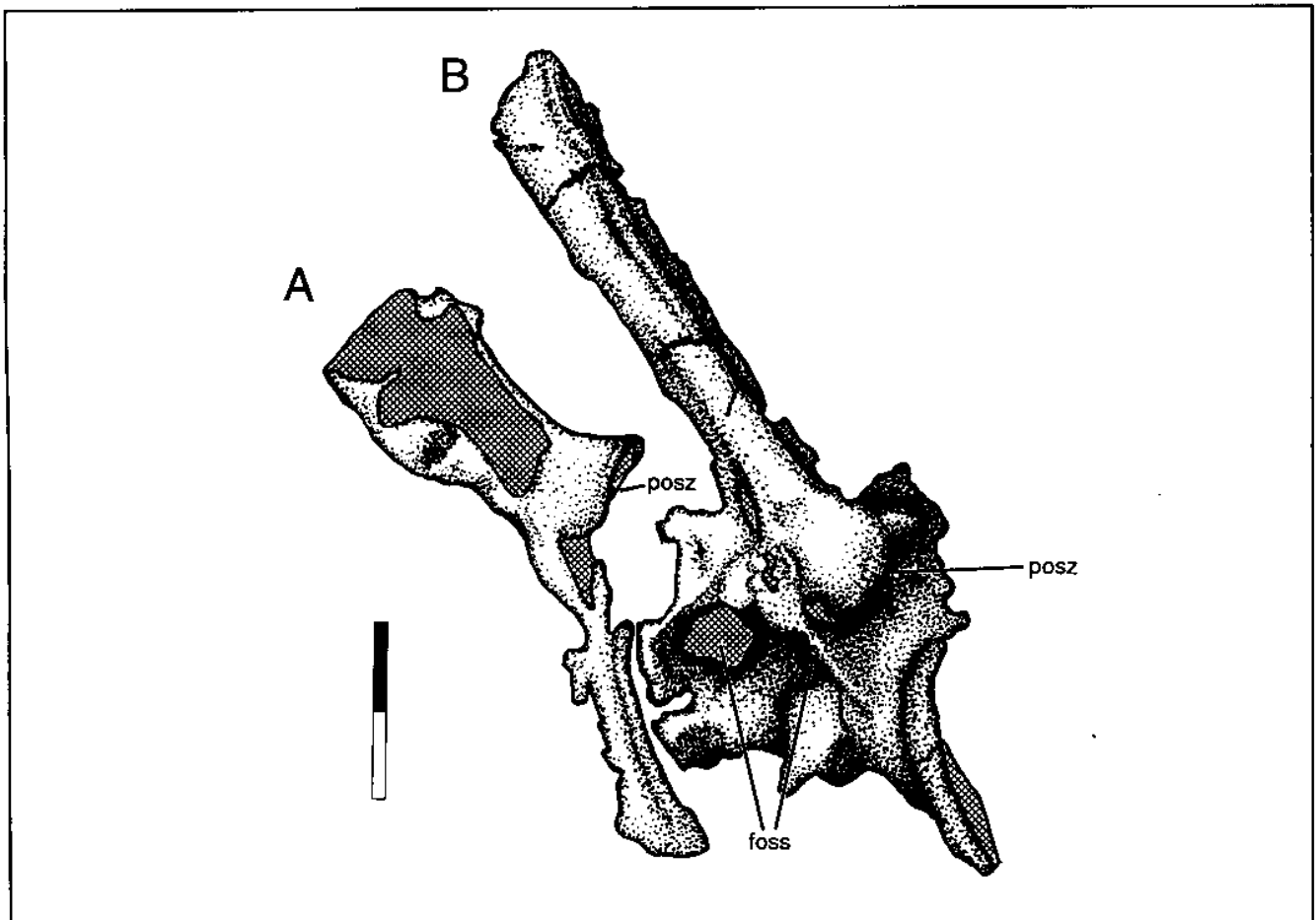
Figure 19. Twelfth and thirteenth dorsal vertebrae of *Acrocanthosaurus*, SMU 74646. (A) Twelfth dorsal, A2-1-4, in left lateral view. (B) Thirteenth dorsal, A2-1-1, in left lateral view. Cross-hatching represents matrix. Scale bar = 10 cm.

summit and is marred only by a few narrow, shallow fossae. The caudal face likewise contains fossae and a foramen. The summit is only slightly expanded. The third element of this series, 3-26, is similar to 3-12 in that both cranial and caudal faces bear prominent ridges of bone for interspinous ligament attachment. The shift in morphology from 3-9 to 3-12 and 3-26 appears to document an abrupt transition from vertebral neural spines of a "cervical-style" morphology to a more typical "dorsal-style" morphology.

The remaining two spines, 2A-3 and 2A-4, are similar in morphology to 3-12. Spine 2A-3 (Figs. 21A, B) measures 297 mm long and is different in that the ridges for interspinous ligament attachment are more prominent and extend even further towards the summit than in 3-12. It lacks the curvature of the caudal margin and has no caudal overhang. The interspinous ligaments attachment sites are bounded by numerous extremely narrow, vertically-oriented fossae, many of which contain foramina leading to the interior of the spine. The summit is rugose and expanded craniocaudally beyond the shaft of the spine, excluding ligament attachment ridges. The rugosities extend downwards to a point where they overlap the extent of the interspinous ligament attachments; thus, at this point in the dorsal vertebral column, it appears that there was some merging of the inter- and supraspinous ligamenture.

Specimen 2A-4, a 177-mm-long distal end of a spine, is similar to 2A-3 but is more massive (Fig. 21C). The interspinous ligament attachment ridges reach the summit of the spine. Specimen 2A-4 is unique in that there are numerous fossae and foramina (seven on one side, one on the other), that open laterally. Because of its greater mass, this spine is assumed to have been more caudal than any of the other isolated spines.

The expansive area for inter- and supraspinous ligamenture on the neural spines of *Acrocanthosaurus* implies that this taxon could not have possessed a fleshy sail, as has been reconstructed for other animals that have elongate dorsal neural spines (e.g., the pelycosaur *Dimetrodon* [Bailey, 1997]). Such sails, being vascularized by near-surface blood vessels and lacking prevalent ligament attachment sites and rugosities, have sometimes been interpreted as thermoregulatory devices. However, the pronounced and rugose attachment sites of *Acrocanthosaurus* indicate that the neural spines were enmeshed in ligamenture, and probably heavily muscled, more analogous to that of a buffalo than the sails borne by the aforementioned taxa (q.v., Bailey, 1997).

The vertebrae display specializations that would have limited movement in life. The cervical vertebrae had restricted lateral undulation and ventral flexion owing to the insertion of the cranial processes into the caudal overhangs of preceding vertebrae and the overlap of the epipophyses onto the bodies of the following vertebrae. The dorsal vertebrae were similarly limited by the "cup-and-socket" morphology of the zygapophyses, the insertion of the prezygapophyses into deep pockets, and by the extensive ligamenture. On the whole, the vertebral column of *Acrocanthosaurus* seems geared towards dedicated strength while forfeiting greater flexibility.

However, none of these features would impede craniocaudal motion of the column — indeed, the powerful ligamenture may have enhanced sharp craniocaudal movement by acting as powerful springs, absorbing shock during recoil. This would be necessary during lunging, and such behavior can be visualized as a predatory tactic in a carnivorous animal. Tall neural spines in the cervical region would also serve to allow the head to bob fore and aft somewhat at higher locomotory speeds, effectively transmitting kinetic energy along the sagittal plane during locomotion, a feature common to galloping, long-distance, endurance runners such as horses (Slijper, 1946; Wake, 1979). Horses also possess tall neural spines on the cranial dorsal vertebrae that limit lateral flexibility. Tall neural spines in ungulates (obligate quadrupeds)

Figure 20. Isolated neural spines attributed to the cranial dorsal region of *Acrocanthosaurus*, SMU 74646. Specimen 3-29 in (A) right lateral and (B) caudal views. Specimen 3-9 in (C) right lateral and (D) caudal views. Cross-hatching represents matrix. Scale bar = 10 cm.

develop over weight-bearing limbs in order to resist bending moments during locomotion (Slijper, 1946; Alexander, 1985; Bailey, 1997), but the spines of *Acrocanthosaurus* (probably an obligate biped) are high in the neck and over the pectoral girdle, which do not bear weight, so the function of the spines cannot be restricted just to loading. Added rigidity and strength is a more likely explanation and may have evolved as a means of strengthening the vertebral column against antagonistic stresses applied by prey animals larger than *Acrocanthosaurus* itself, possibly sauropods, during predation. This conclusion was also derived by Bailey (1997).

Sacral Vertebrae

Three massive though badly damaged vertebrae were found between the proximal ends of the pubes of SMU 74646. The entire mass is labeled 2-15 in the preparator's notes; they are emended with individual labels as 2-15-1, 2-15-2, and 2-15-3, from cranial to caudal. None of the vertebrae are fused; in fact, there are wide gaps between the articular facets of the centra in all three. Thus, *Acrocanthosaurus* did not possess a synsacrum; complete fusion of all other neural arches to their respective centra with no visible sutures argues against an interpretation of the lack of a synsacrum as an ontogenetic characteristic of *Acrocanthosaurus*. Madsen (1976:42) proposes that lack of fusion of the sacral vertebrae may be more common in females than in males, at least for *Allosaurus*. Measurements of the sacral vertebrae are given in Table 2.

All the sacral vertebral centra are amphicoelous. The left sides of 2-15-2 and 2-15-3 bear pronounced pleurocoels (Fig. 22B). On 2-15-3, the pleurocoel consists of a single,

craniocaudally elongate fossa containing two foramina. The foramina are much more widely separated than in previous vertebrae. The ventral surfaces of all three of these vertebrae are damaged, but none appear to have had a ventral keel.

The left side of 2-15-3 retains the base of a massive, fused complex consisting of the base of the neural spine and the transverse process. Beneath the circular, shield-like ventral portion of this sacral rib, at the cranial end of the vertebrae, there is a small parapophysis, separated from the prezygapophysis by a short shelf of bone. Although broken, the distal end of the parapophysis does not appear to have bolstered the sacral rib complex in life. Less of a similar complex is preserved on 2-15-2, but, unlike the previous vertebra, the postzygapophysis is present. Its close appression to the base of the neural spine and broken lateral surface indicates that it, too, was a part of the immense articular surface with the ilium.

Beneath and hidden by the sacral rib on 2-15-3 is a deep fossa that is subdivided into two smaller fossae by a shelf of bone. This configuration is reminiscent of the double fossae seen on the sides of the transverse processes of the dorsal vertebrae, though the dividing shelf is significantly thicker on the sacral. As in the caudal dorsal A2-1/1, the fossae open more dorsomedially than on the mid-dorsal vertebrae. Sacral vertebra 2-15-2 preserves a divided fossa in a similar location, but compared to that of 2-15-3, it is much shallower, narrower mediolaterally, and not as extensive craniocaudally.

The left prezygapophysis of 2-15-3 contrasts sharply with those of the preceding dorsal vertebrae because it is concave, rather than convex. As preserved, it faces dorsally and
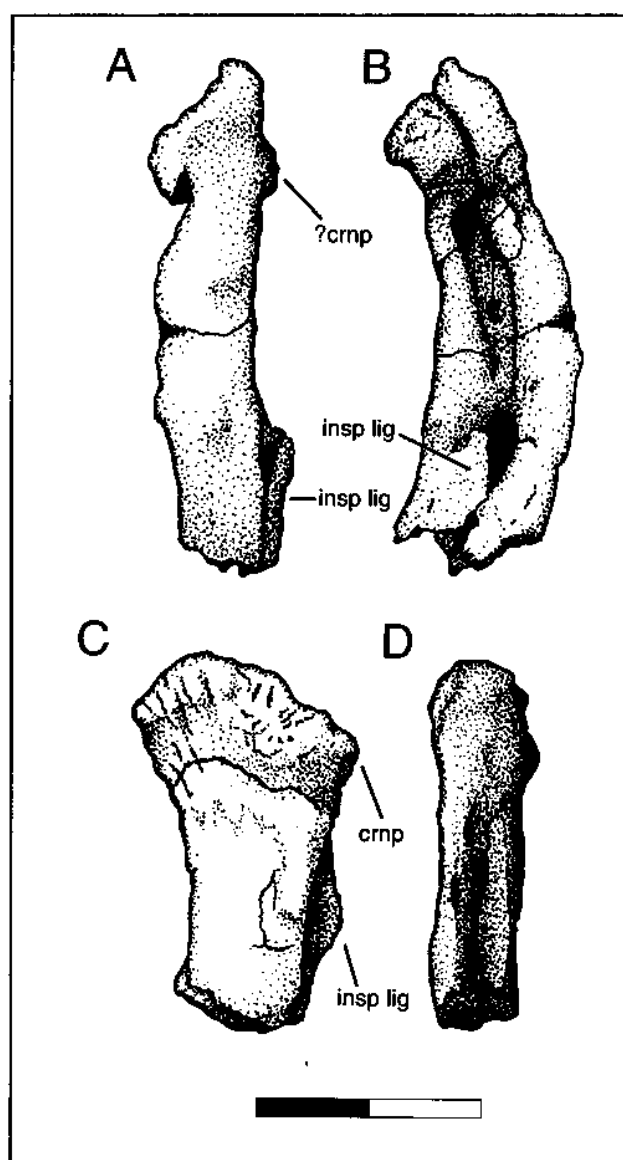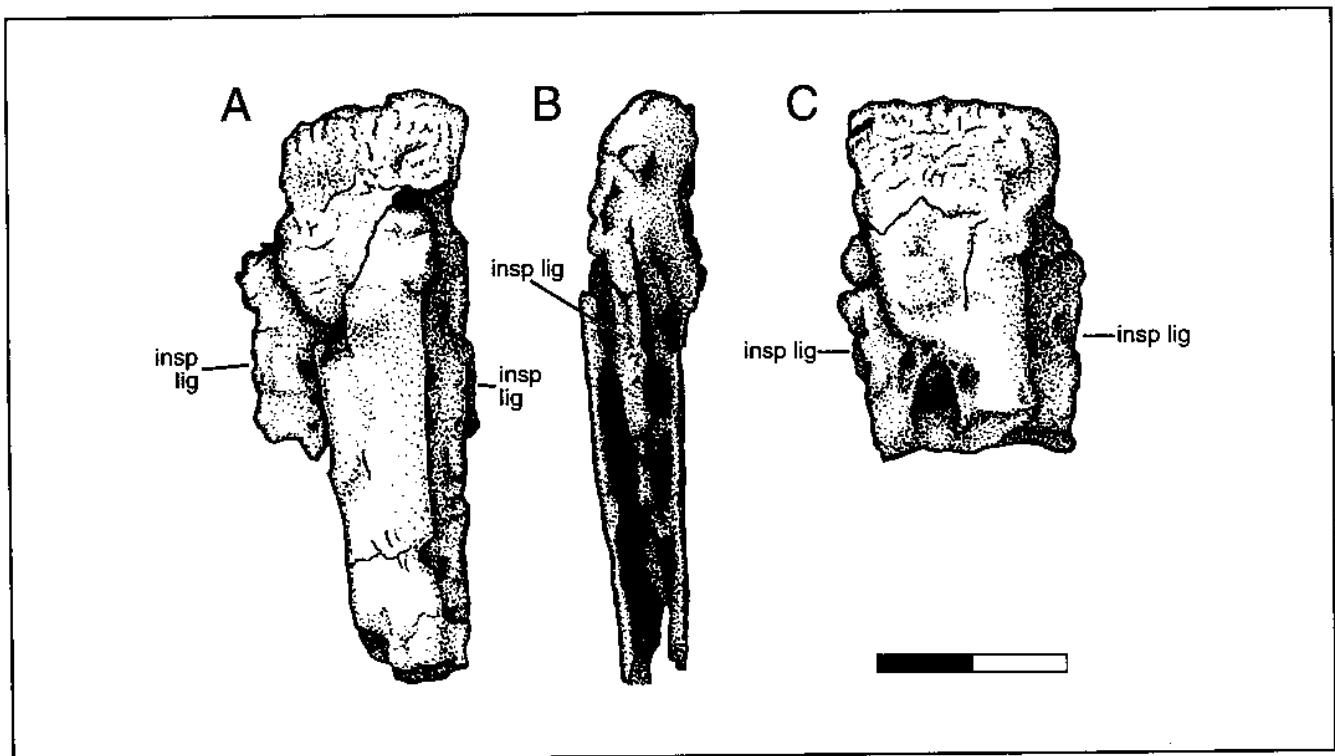

Figure 21. Isolated neural spines attributed to the mid- or caudal dorsal region of *Acrocanthosaurus*, SMU 74646. Specimen 2A-3 in (A) lateral and (B) ?cranial or ?caudal views. Specimen 2A-4 in (C) lateral view. Scale bar = 10 cm.

slightly laterally, but the lateral component may be an artifact of preservation because the process may have been reoriented by compression against the centrum of 2-15-2, against which it rests. The prezygapophysis of 2-15-2 is more planar and faces dorsally. The prezygapophyses are separated from the sacral rib complex by narrow gaps, similar to the hypantral facets on the dorsals. The postzygapophyses, present on 2-15-2, are ventral-facing cups.

The cranial and caudal margins of the bases of the neural spines house deep fossae; the cranial excavations are so deep as to give the neural spine bases a T-shaped cross-section, with the broad part of the T at the caudal end. The lateral surface of 2-15-3, at least on the cranial end (where it is not subsumed into the complex of the sacral rib), is excavated as well.

By possessing large articular surfaces with the ilia, 2-15-2 and 2-15-3 are probably the two "true" (ancestral) sacral vertebrae, and occupy the positions of second and third sacrals, respectively, as outlined by Huene (1926) for *Eustreptospondylus* and Welles (1984) for *Dilophosaurus*. Vertebra 2-15-1, by default, must be the first sacral.

Two other vertebral fragments, both unlabeled either on the specimen or in the preparator's notes, were found in the vicinity of the three articulated vertebrae mentioned above. They are given the labels "2J-1" and "2J-2," again from cranial to caudal, for reference in this thesis. Of the two latter fragments, 2J-2 is the more complete, consisting of the cranial end of a centrum and neural arch complex. The centrum is very large, especially compared to the dorsals, and is more similar to the previously described sacrals. Both prezygapophyses are preserved, as is most of the neural arch above the centrum. Dorsal and lateral to the vertebral foramen are two cranial peduncular foramina, as in the dorsal vertebrae. Between these foramina, and dorsal to the vertebral foramen, there is a vertical groove bounded by two thin ridges of bone, again reminiscent of the conjoined prezygapophyseal and hypantral facets on the mid-dorsals but much narrower. Small foramina on the cranial edges, one on the medial side of the left prezygapophysis and two on the right, lead into the prezygapophyses.

The prezygapophyseal articular facets are slightly convex dorsally, similar to the mid- and caudal dorsals, but unlike the more cranial of the sacral vertebrae. Just caudal to the right prezygapophysis, on the lateral side of the vertebra, is a craniocaudally elongate fossa. Possibly this is homologous with the two foramina described in sacral vertebra 2-15-3.

A specimen, 2A-8, found with some of the dorsal neural spines discussed previously, clearly consists of two sacral neural spines that are similar in gross morphology to the isolated dorsal neural spines 2A-3 and 2A-4. The cranial and caudal margins possess vertical ridges for insertion of the interspinous ligaments; as in 2A-4, these extend to and merge with the rugose summits. On one of the sacral spines, the border between this ridge and the spine proper is interrupted by several foramina, as in 2A-3 and 2A-4. Unlike the dorsal neural spines, however, the sacral spines are much narrower mediolaterally and much longer craniocaudally; this may be

due to postmortem compaction. The two spines are fused together distally but not proximally. D. Chure (personal communication, 1997) notes that fusion of sacral neural spines typically proceeds from distal to proximal in theropods.

Because of disassociation and absent material, these two spines cannot be placed with any specific sacral vertebrae. Although in some specimens all five sacral neural spines are fused together (Gilmore, 1920:plate 8), Madsen (1976:plate 24, figs. E and G) illustrates only the sacral spines of the
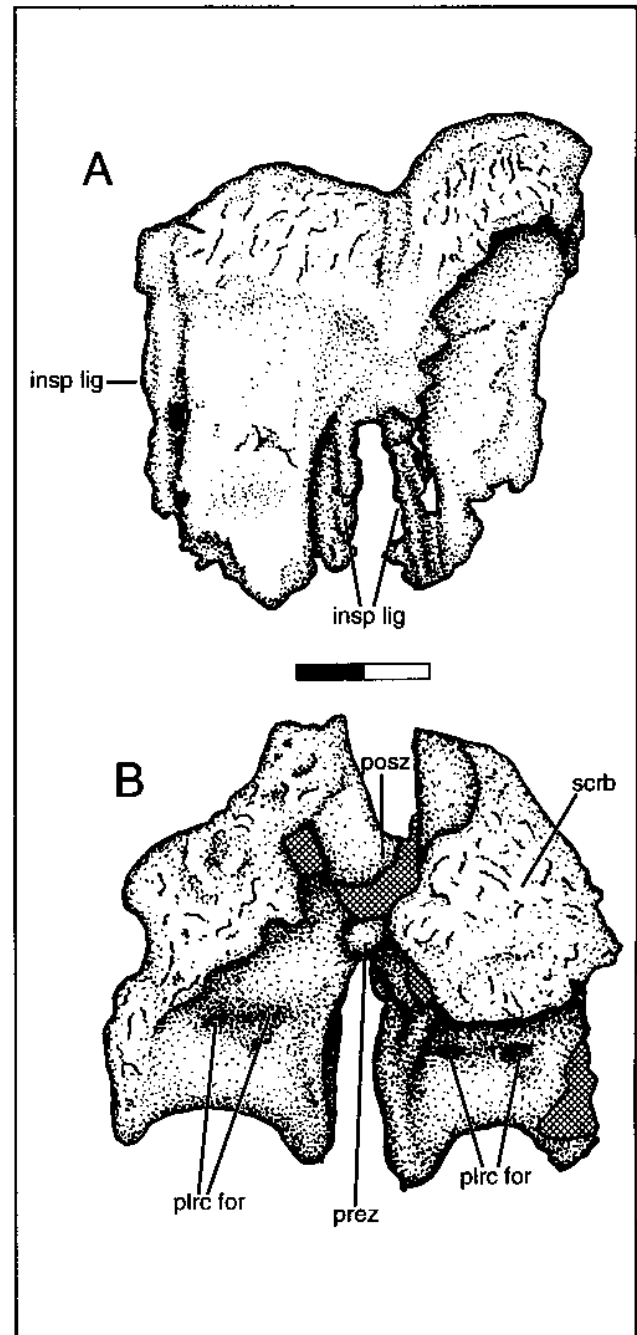
Figure 22. Sacral vertebral elements of *Acrocanthosaurus*, SMU 74646. (A) Sacral neural spines, 2A-8, in lateral view. (B) Second, 2-15-2, and third, 2-15-3, sacral vertebral centra and neural arches in left lateral view. Cross-hatching represents matrix. Scale bar = 10 cm.

second and third sacral vertebrae of *Allosaurus* fused together. The two spines of 2A-8 are tentatively referred to the second and third sacral vertebrae of *Acrocanthosaurus*.

Caudal Vertebrae

Except in the autapomorphic tails of some maniraptoriforms (e.g., avians) and *Herrerasaurus* (Novas, 1993), the centra of theropod caudal vertebrae tend to become relatively more elongate distally (Molnar et al., 1990). Simultaneously, transverse processes and neural spines decrease in size and ultimately may disappear altogether. As described first by Russell (1972) and emphasized by Gauthier (1986), vertebrae with these traits occur beyond a "transition point" between the more mobile proximal caudal vertebrae and the stiffened, less mobile distal caudals. This point is defined between the last caudal with transverse processes and the first with significantly elongate prezygapophyses (Russell, 1972) and, to a lesser degree, an alteration from elongate, ventrally-directed chevrons to "boat-like," proximodistally-oriented bones (Gauthier, 1986). In non-abelisauroid ceratosaurians, this point occurs well distal to the halfway point of the tail and is contained within a gradual transition zone; in the Tetanurae, the transition point occurs more abruptly and closer to the proximal half of the tail (Gauthier, 1986). In the Coelurosauria (Holtz, 1994; Sereno et al., 1994, 1996), 15 or fewer caudal vertebrae possess transverse processes, placing the transition point much closer to the base of the tail. As a result of the relative elongation of the caudal centra, more distal caudals display proximodistally shortened neural arches: the centrum protrudes distally (and sometimes proximally, as well) beyond the extent of the arch, and increasingly so with more distal positioning in the sequence.

Only proximal and medial caudal vertebrae are preserved in SMU 74646; no distal caudals could be identified. Measurements of the caudal vertebrae are provided in Table 2.

PROXIMAL CAUDAL VERTEBRAE: One isolated, amphiplatyan (slightly amphicoelous) centrum, 1-6, is short proximodistally and strongly compressed mediolaterally. Unlike all previous vertebrae, the pleurocoelous fossa is not deep and does not contain pleurocoelous foramina. Instead, tiny nutrient foramina are visible a short distance below where the neural arch would have been. The ventral surface of the centrum is damaged. Because the neural arch is lacking, it is impossible to determine which face is proximal and which is caudal. Unlike all other preserved caudal centra, both faces lack chevron facets, a typical feature of the first caudal.

Four further caudal vertebrae from SMU 74646 are candidates for proximal caudals. These specimens, 1-4, 1-12, 1-22, and 1C/W, are more robust than the other caudals. Stovall and Langston (1950:712) note that the second and third caudal vertebrae are differentiable from the remainder of the caudal sequence in being "gently procoelous and slightly wedge-shaped in lateral aspect." Of the proximal caudal vertebrae preserved in SMU 74646, only specimen 1-12 (Figs. 23A-C), meets the latter criterion because the proximal face is concave while the distal face is virtually flat. All other preserved centra of the caudal sequence, including 1-4, 1-22,

and 1C/W, are amphicoelous. Specimen 1-12 cannot be the second or third vertebra, however (see below).

The left side of 1-12 is intact and displays a rudimentary pleurocoelous fossa (Fig. 23B). As confirmed by Stovall and Langston (1950) in the paratype of *Acrocanthosaurus*, the fossa is shallow and located dorsal to the midline of the centrum. There are small nutrient foramina at the proximal and distal ends of the fossa. Specimens 1C/W, 1-4, and 1-22 are similar to 1-12 in possessing a shallow, rudimentary pleurocoelous fossae with pinhole-sized openings at their distal end. The presence of rudimentary pleurocoelous fossae reinforces the concept that these three vertebrae are indeed proximal caudals. Britt (1993:198) notes that foramina that exist primarily for the entrance and egress of circulatory vessels and nerves are inflated in size when invaded by diverticula that generally follow the vessel and nerve tracks; thus, the enlarged pleurocoelous foramina described on the presacral and sacral column are nutrient foramina that have been invaded by such diverticula. Invasion was insufficient in the proximal caudals to create inflated foramina in the shallow fossae.

The centra of 1-4 and 1-22, in lateral view, possess a slight parallelogram shape, with the dorsal edge of the proximal articular face overhanging the ventral margin. The proximal end of the centrum of 1C/W is angled as in the former two vertebrae, but the distal face is markedly less so, lending the vertebra a more wedge-shaped, quadrilateral profile that more closely resembles that of the more distal caudals. Paul (1988:102) notes that the proximal caudals of most theropods are "beveled," which arches the base of the tail dorsally. However, the proximoventral angle of the proximal face of the four vertebrae from SMU 74646 would, when articulated (and assuming symmetry of the intervertebral bursae), produce a downward curve, not an upward one.

In lateral view, the ventral margin of all four centra are arched dorsally at the proximal end. The distal end is on a slightly lower plane than the proximal end. Specimens 1C/W and 1-4 possess ventral grooves (Fig. 23E). These grooves were possibly associated with the caudal artery and vein; the absence of the groove on the chevron facets marks where the vessels left close appression with the centra to enter the haemal canal of the chevrons.

The chevron facets on all four centra are beveled triangles. The distal facets are somewhat less pronounced than their proximal counterparts in 1-12 and 1C/W. The proximal facets are more strongly angled than the distal ones. The proximal facets lack foramina for articulation of accessory chevron prongs as in some *Torvosaurus* caudals (Britt, 1991).

The neural arches of 1-4, 1-12, and 1C/W span roughly the proximal three-fourths of the centra; the arch of 1-12 spans slightly less than the other two. The transverse process is flat and sweeps distally. The transverse processes of 1C/W are more complete than those of 1-12 (Figs. 23A, D) but are similar in possessing a mild dorsal arching at their bases. They angle distally from the perpendicular of the neural spine. Inset from the proximal and distal margins are shallow grooves that parallel the axis of the process.

The prezygapophyses differ between 1-4 and 1-12 in that the articular facet of 1-4 is much more steeply angled ventromedially than that of 1-12. In this respect, 1-4 is much more similar to the more distal caudals. Only vertebra 1-12 preserves a partial postzygapophysis, and it shows no sign of having a ventrally-projecting "hyposphene-like process" as noted by Stovall and Langston (1950:713) for the first three caudals of *Acrocanthosaurus* paratype 8-0-S8. The prezygapophysis in 1-12 protrudes only a short distance beyond the centrum face. Its articular facet is angled only slightly ventromedially. There is no infraprezygapophyseal foramen. The postzygapophyses angle ventrolaterally and protrude slightly from the base of the neural spine. Their articular surfaces are small and angle slightly dorsolaterally.

The neural spine of 1-12, though incomplete, is not particularly robust, especially in comparison to the spines of the axis and cranial cervical vertebrae, indicating that it originated further caudal than the initial several caudals, that bear long neural spines in the paratype. It is mediolaterally quite thin, especially so proximally. The proximal edge bears a narrow, matrix-filled groove, the bordering walls of that sweep downward to connect to the prezygapophyses (Fig. 23A), identical to the condition in the paratype.

Distally, between the postzygapophyses, 1-12 has a narrow but deep, tear-drop-shaped fossa that terminates a short distance above the zygapophyses, giving way to the interspinous ligament attachment (Fig. 23C). As with its proximal counterpart, the walls bordering this depression form thin
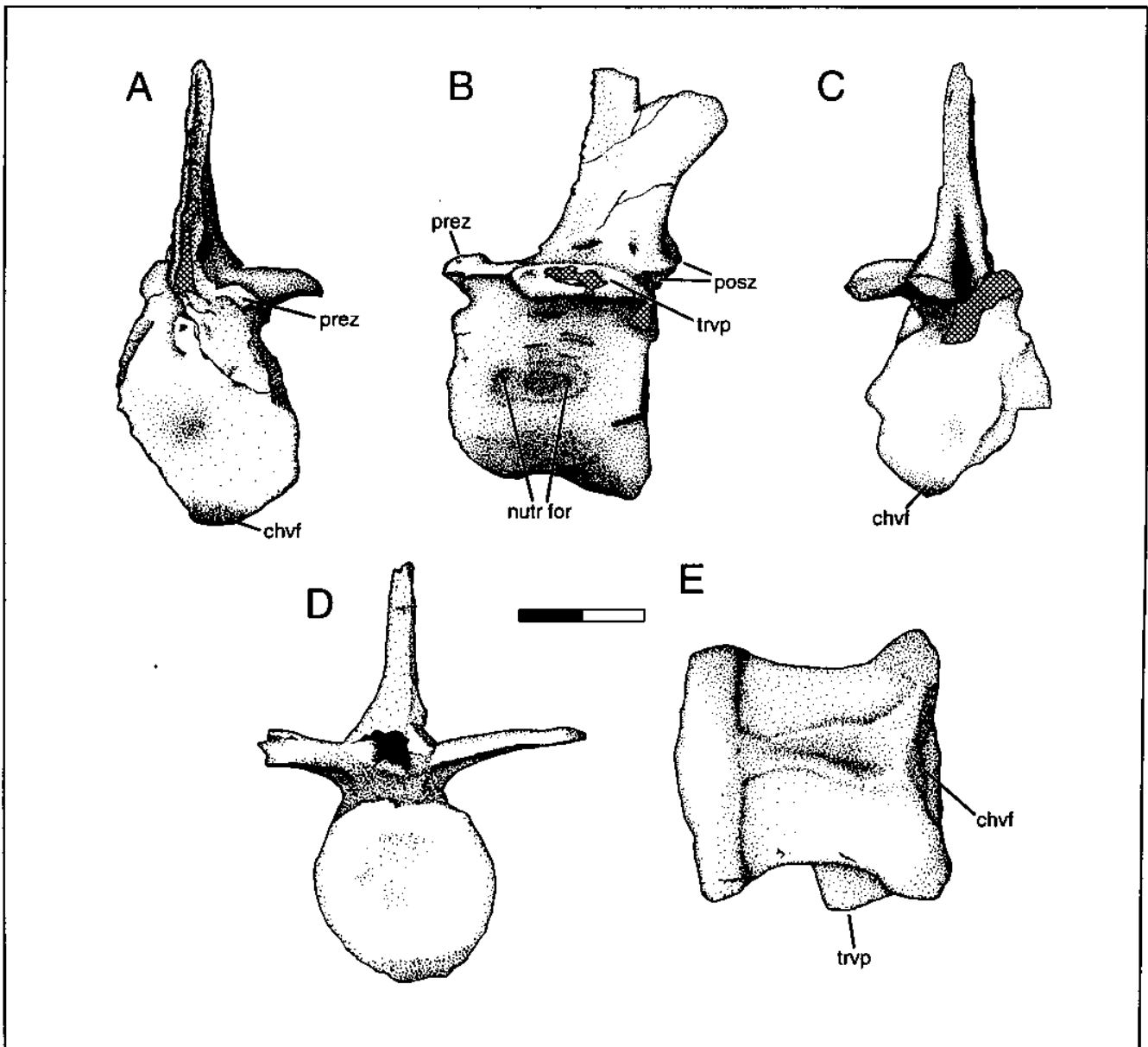
Figure 23. Proximal caudal vertebrae of *Acrocanthosaurus*, SMU 74646. Eighth caudal, 1-4, in (A) proximal, (B) left lateral, and (C) distal views. Scale bar = 10 cm. (D) second caudal, 1C/W, in caudal view. (E) sixth caudal, 1-12, in ventral view. Cross-hatching represents matrix.

ridges that support the zygapophyses. This deep cavity contains smaller, asymmetrically placed openings. There are two on either side: large ventral openings and smaller dorsal ones. The lamina separating the openings is much more robust on the right than on the left.

The spine of 1-12 is angled slightly distally from the vertical, unlike the vertical spines of the most proximal caudals of the paratype, OMNH 8-0-S8. The distal end of the spine is missing. Just above the base of the left side of the neural spine, a small foramen leads ventrally into the base of the spine (Figs. 23A, B). This foramen in bounded laterally by a short ridge of bone. A similar foramen was noted in the paratype of *Acrocanthosaurus* by Britt (1993:198). The right side of 1-12 is damaged, and no foramen can be discerned, but the short lateral ridge is still present.

The spine of 1C/W is more fragmentary than that of 1-12, but is much wider at the base, especially the distal end (Fig. 23D). Neither the proximal nor distal margins are preserved, but the ridges that lead from the broken proximal edge to the bases of the prezygapophyses are thicker than those of 1-12, implying that 1C/W is more proximal in the caudal sequence than 1-12.

The wider neural spine base of 1C/W strongly implicates this vertebra as the most proximal of the four, despite the slight procoely of 1-12. All preserved neural spines are less robust than those of the most proximal caudals in OMNH 8-0-S8. The distal tilt of the neural spine of 1-12 indicates that it one of the most distal of the four vertebrae; the steep tilt of the prezygapophyseal facet on 1-4 also places it more distally in the sequence. 1C/W is referred to the position of second caudal, 1-22 the fifth, 1-12 the sixth, and 1-4 the eighth.

MEDIAL CAUDAL VERTEBRAE: The next largest caudal preserved in SMU 74646, 1-17 (Fig. 24C), lacks only the right transverse process. The centrum lacks any indication of a pleurocoelous fossa, but tiny nutrient foramina are visible on both sides, located near the proximal and distal ends. Like the more proximal caudals, its ventral margin is dorsally arched, with the arch skewed slightly proximally. Both the proximal and distal faces are vertically oriented. A well-developed, shallow ventral groove is present (Fig. 24E) that terminates just behind the proximal chevron facet. Each prezygapophysis bears a low, horizontally-projecting ridge that runs backwards to join with the proximal margin of the transverse process. At the point where this ridge joins with the lateral surface of the prezygapophysis, it swells, becoming thickened dorsoventrally and more prominent laterally. This projection is probably homologous to the small "accessory transverse processes" seen on the more distal medial caudals (see below). The postzygapophyses project a short distance from the base of the neural spine and overhang the centrum.
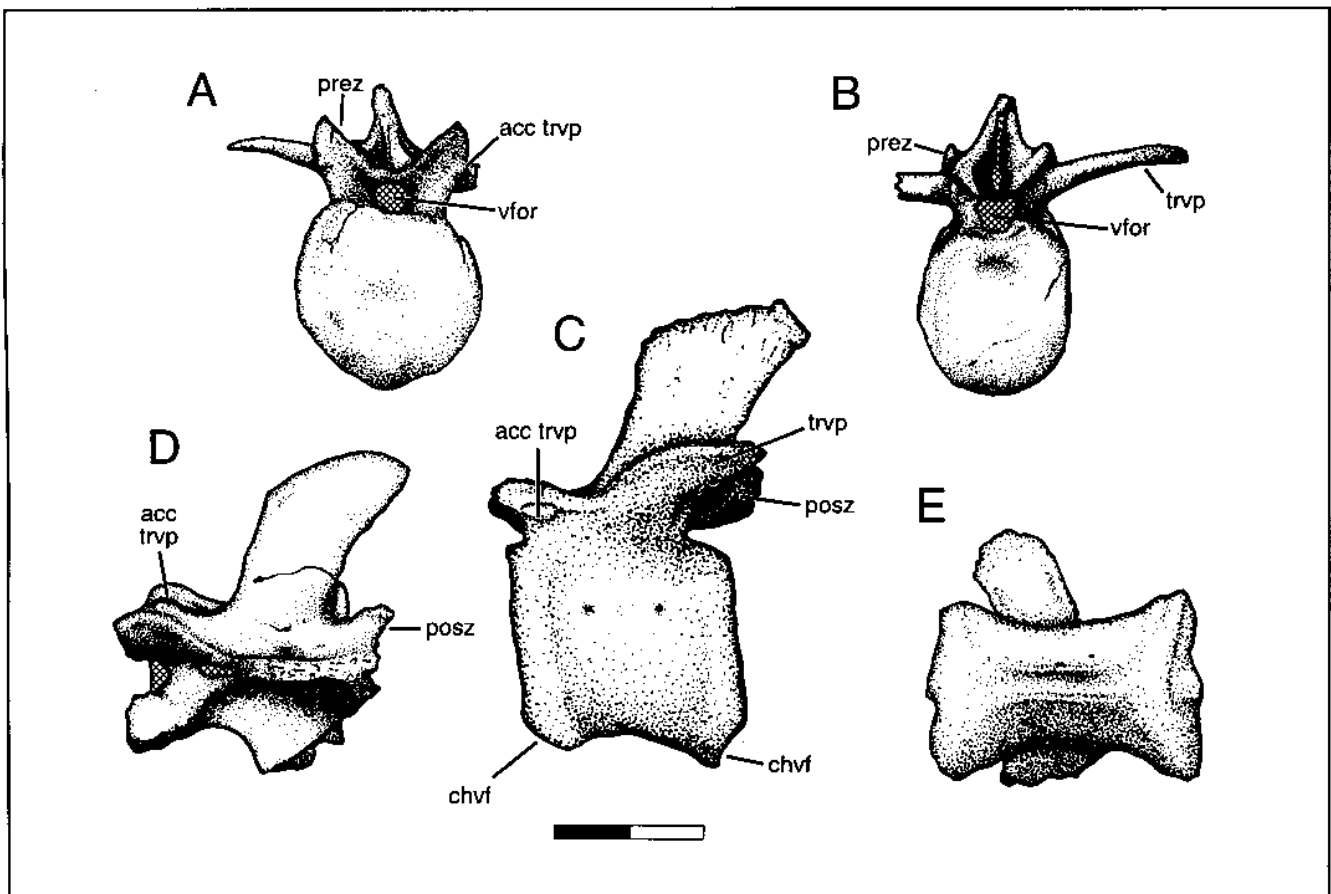
Figure 24. Medial caudal vertebrae of *Acrocanthosaurus*, SMU 74646. Sixteenth caudal, 1-19, in (A) proximal, (B) distal, and (E) ventral views. (C) Fifteenth caudal, 1-17, in left lateral view. (D) Seventeenth caudal, 1-11, in dorsal view. Cross-hatching represents matrix. Scale bar = 10 cm.

The transverse processes, again similar to those of the most proximal caudals, arch dorsally and sweep distally in dorsal view (Fig. 24D). The shallow grooves on the ventral side of the process (Fig. 24E) are still present but not as pronounced as those of 1C/W. The distal end of the right transverse process is expanded, particularly on the distal edge, to form a moderate curve laterally in dorsal view.

The neural spine is one of few intact in SMU 74646 and is much shorter than the spines of the proximal caudals of the paratype OMNH 8-0-S8. It is thin proximally, but retains a deep sulcus bounded by two thin ridges that become the dorsomedial margins of the prezygapophyses. The distal end is slightly wider and also possesses a deep, tear-drop-shaped depression. The left side bears a small, ventromedially-directed foramen set into a shallow fossa at the base of the spine, as in 1-12.

Similar to 1-17 in most respects are 1-19/1-25 (Figs. 24A, B, E; Fig. 25A) and 1-11 (Fig. 24D). Both are relatively complete. The transverse processes are similar to that of 1-17 in that the

distal end is rounded laterally. The distal end of the neural spine, which displays a pathology in 1-19/1-25, was found separately (1-25, Figs. 25B, C). 1-19/1-25 differs from 1-17 and 1-11 in that the proximal face of its centrum is angled proximoventrally, while the distal face is more or less vertical. This would lend the tail at this point a slight downward curve. 1-11 and 1-19/1-25 are estimated to have originated in the twelfth and thirteenth caudal positions.

The grooves on the proximal and distal margins of both neural spines contain fossae and foramina (Figs. 24A, B) similar to those described above for 1-12. Above the dorsalmost extent of these fossae and foramina, the grooves shallow and become rugose, indicating the insertion points of the interspinous ligaments.

There are no foramina on the lateral sides of the bases of the spine, as in 1-12, but a shallow fossa occupies this position on the right side of 1-19/1-25 (Fig. 25A). Towards the pathologic distal end of the spine, the proximal margin abruptly jogs distally before resuming its predominantly dorsal orien-
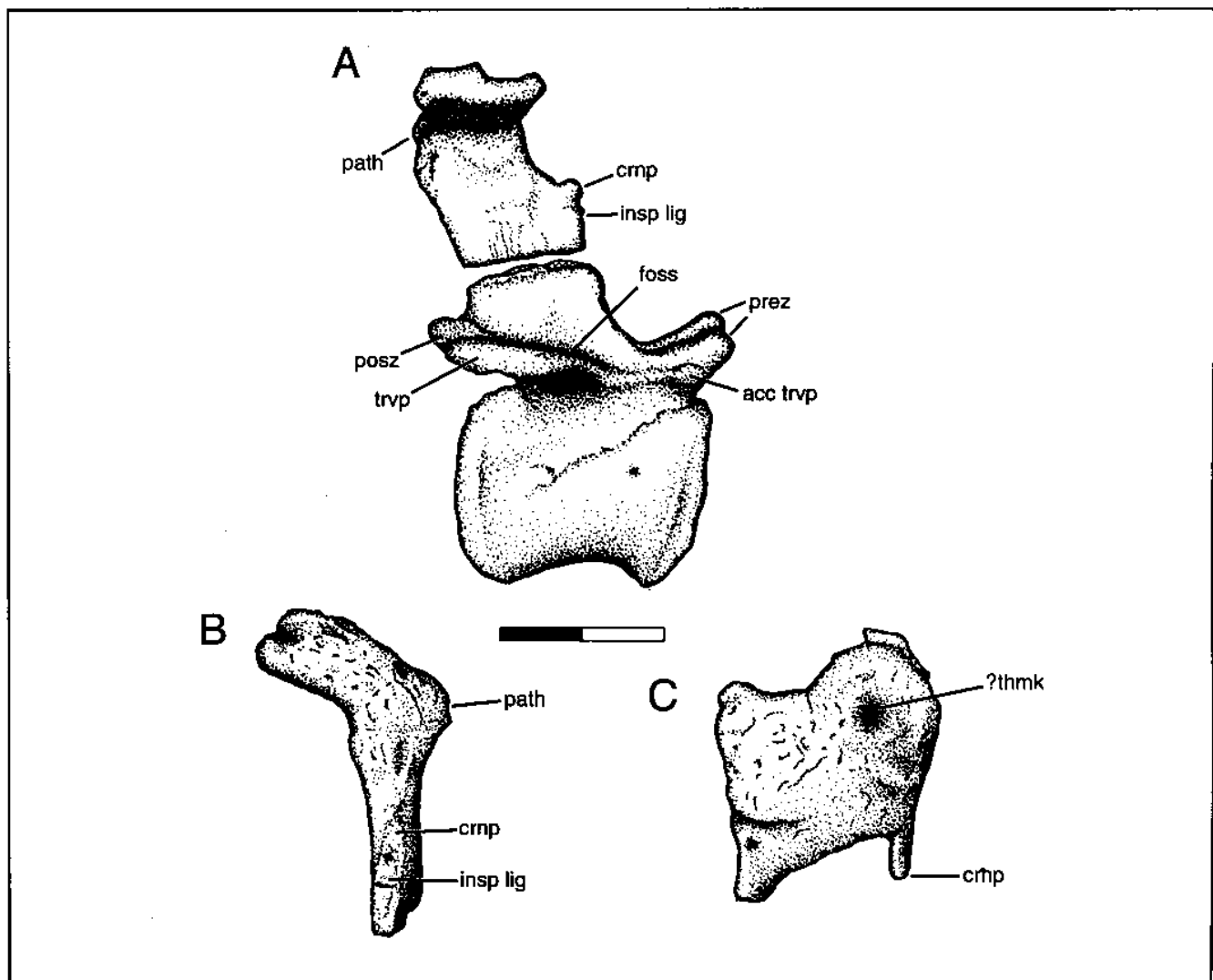
Figure 25. Sixteenth caudal vertebra and pathologic neural spine of *Acrocanthosaurus*, SMU 74646. (A) Centrum, 1-19, and neural spine, 1-25, in right lateral view. Scale bar = 10 cm. Pathologic neural spine in (B) proximal and (C) dorsal views. Not to same scale as (A).

tation, forming a distinct cranial process. This "stair-step" morphology is also noted by Stovall and Langston (1950:713) in some caudals of OMNH 8-0-S8.

The distal end of the spine, 1-25, is bent sharply to the right. At the base of the bend on the left side is an amorphous, rugose mass of bone. The right surface of the neural spine below the bend is heavily striated. Because non-mammalian and non-avian (presumably including other dinosaurs) vertebrates do not form secondary cartilage at the site of fractures (Rothschild and Martin, 1993 and references cited therein), non-displaced, healed fractures tend to have smooth-surfaced, inflated structures (e.g., Rothschild and Martin, 1993:216, fig. 19-4); this is represented on many of the ribs of SMU 74646 (see below). The rugosity and disfigurement of the thick mass at the base of the bend in 1-25 is more consistent with an infected, displaced fracture (1993:217, fig. 19-5). There is a rounded, smooth-walled, blind pit on the dorsal surface of the bone; this may represent a healed bite mark. As illustrated by Stovall and Langston (1950:plate 4, fig. 10), many of the caudal neural spines of the paratype specimen of *Acrocanthosaurus* are also bent; however, none of the bends in these specimens display inflated, rugose textures indica-

tive of healing, so the bends in those specimens are more likely diagenetic than pathologic.

Three other vertebrae from SMU 74646, numbered 1-2, 1-3, and 1-13, are similar to 1-19/1-25 in overall morphology (though they lack evidence of neural spine pathologies), but are smaller. The only outstanding difference is in 1-3: the proximal edge of the transverse process angles sharply backwards, giving the distal end of the process a triangular shape as in 1-11 (Fig. 24D). These specimens are attributed to the region of the 15th-22nd caudals.

The remaining three caudal vertebrae are much smaller than any of those aforementioned. They were collected in near-surface, soft sediment, and do not bear specimen numbers. For the purposes of this thesis, they are designated K1, K2, and K3, of which K2 is the most complete (Fig. 26). Because they retain small transverse processes, they must be from a region proximal to the "transition point." The presence of neural spines is also indicative of their origin far forward of the distal caudals.

The centra of these three vertebrae are low, long and do not possess pleurocoels. Both proximal and distal faces are more laterally constricted than any of the preceding verte-
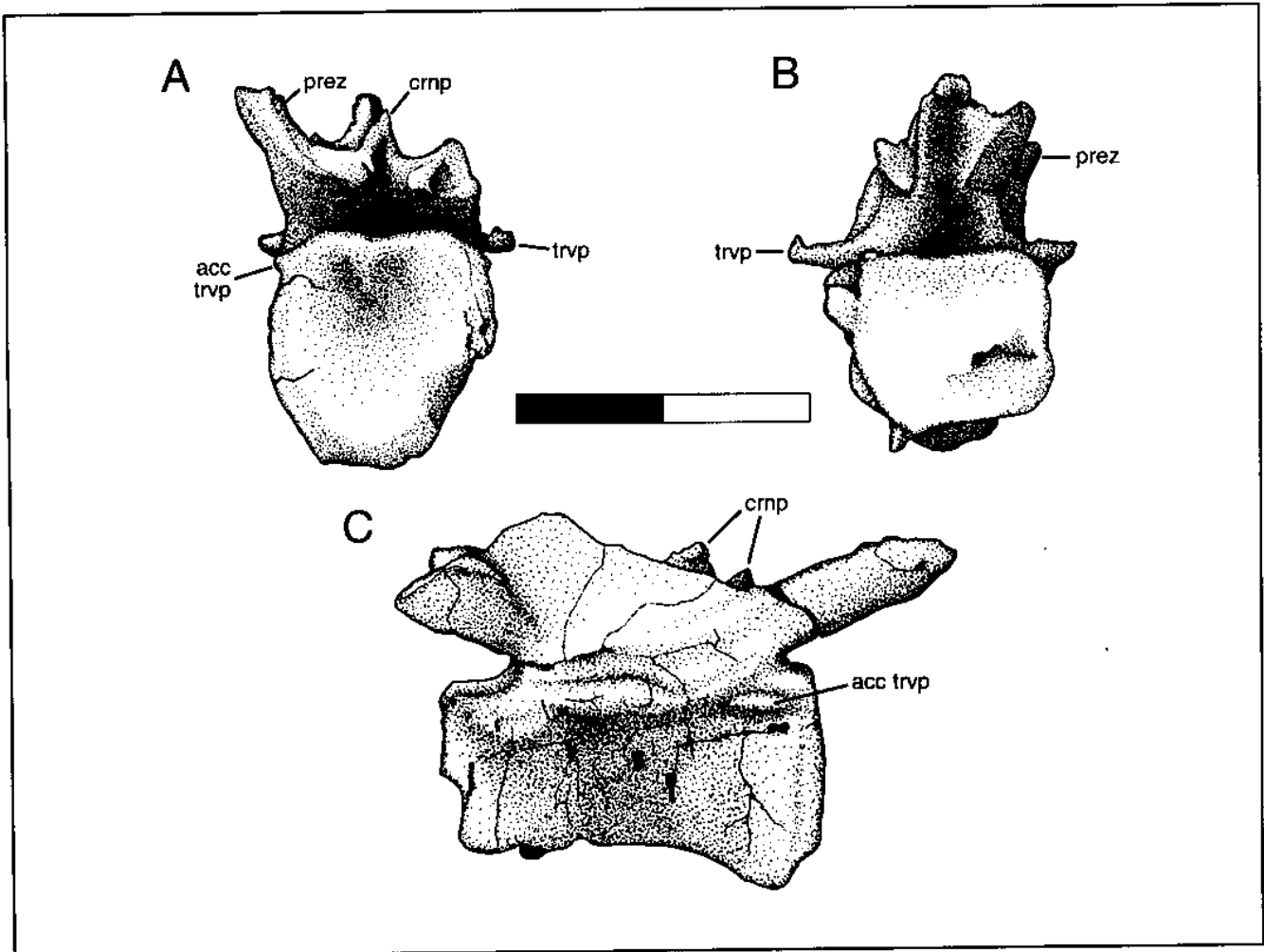
Figure 26. Twenty-ninth caudal vertebra of *Acrocanthosaurus*, SMU 74646 K2, in (A) proximal, (B) distal, and (C) right lateral views. Scale bar = 10 cm.

brae. The proximal faces are more concave than in the preceding vertebrae, though overall the centra are still amphicoelous. A shallow, ventral groove, evident only on K1, spans the entire distance between the chevron facets.

The neural arch on K2 spans two-thirds the centrum length, and remains concentrated towards the proximal end. K2 possesses short, stubby transverse processes (Figs. 26A, B); broken surfaces indicate their presence on K1 and K3 as well. As in the aforementioned proximal caudals, a low ridge connects the proximal margin of the transverse process to the prezygapophysis, but in the medial caudals, the ridge changes from a horizontal orientation on the centrum to a ventrolateral orientation on the prezygapophysis. Just below the notch formed where the prezygapophysis and neural arch separate from the centrum on the proximal end, there is a short, dorsoventrally flat "accessory transverse process" that parallels but is much shorter than the transverse process. Its homologue on K1 is smaller still.

The neural spines are not fully preserved on any of the three medial caudals. However, the preserved portion on K2

indicates that the spine was divided into a proximal (cranial process) and distal (neural spine) portion, similar to that of *Allosaurus* (Madsen, 1976) and noted by Stovall and Langston (1950:713) in the paratype of *Acrocanthosaurus*, thus retaining a low "stair-step" morphology as in 1-19.

Ribs

Numerous ribs and rib fragments were found scattered through the blocks of SMU 74646. These include cervical and dorsal ribs, and gastralia. Measurements of all ribs are provided in Table 3.

CERVICAL RIBS: Seven unambiguous cervical ribs are preserved with SMU 74646: five from the right side and two from the left. None are fused to the cervical vertebrae. One rib (3-13) can be adequately articulated with both the fifth and sixth cervical centra. When in articulation, the rib is directed caudally and laterally and would have spanned at least three vertebrae (based on the length of the sixth cervical centrum).

The smallest preserved cervical rib fragment (3-17, Fig. 27A) must be from one of the most cranial cervicals. It is

Table 3. Rib measurements (in mm) of SMU 74646.

Rib # (Spec. #)	Ln.	Ht.	Cap.-Tub. Span	Cap.-Tub. Angle (°)
CV2r (3-17)	83+	54	48+	n/a
CV4l (3-8)	318+	—	—	n/a
CV4r (3-11)	285+	83	68	n/a
CV5l (3-1)	425+	—	—	n/a
CV5r (3-13)	558+	92	68	n/a
CV7l (4-16)	330+	106	117.5	n/a
CV8r (4-19)	425+	116	122	n/a
CV9l (4-4)	679+	150	150	n/a
CV9r (4-18)	624+	122	122	n/a
D2 (A1-4/2C-9)	757+	n/a	197	59°
D2 (2C-4)	884+	n/a	163	54°
D3 (A1-5/2C-2)	510+	n/a	203	41°
D3 (A1-2/2C-1)	753+	n/a	229^m	—
D4 (A1-1/4-12)	554+	n/a	144+	—
D5 (4-15/4-16)	994+	n/a	210+	68°
D5 (4-12)	875+	n/a	—	—
D6 (4-10)	1086+	n/a	183+	59°
D6 (4-11)	1003+	n/a	204	53°
D7r (2-18)	632+	n/a	—	—
D8r (2-19)	656+	n/a	—	—
D8l (2-23)	535+	n/a	—	—
D9r (2-24)	600+	n/a	—	—
D10r (2-39)	779+	n/a	—	—
D11r (2-40)	653	n/a	—	—
D12l (2-36)	415+	n/a	150	49°
D12r (2-41)	451+	n/a	156	52°
D13? (2-42)	321	n/a	117	44°
D13? (2-43)	176+	n/a	122	$60°^P$
(A1-6)	—	n/a	228+	—
(A1-16)	—	n/a	244+	—

Measurements: rib length (ln.) = distance from top of cranial process (on cervical ribs) or tuberculum (on dorsal ribs) to end of rib; rib height (ht.) = maximum distance from tuberculum to tip of cranial process (cervical ribs only); capitulum-tuberculum span (cap.-tub. span) = maximum distance between capitulum and tuberculum; rib curvature (rib curv.) = degree of rib curvature

Notation: CV = cervical; D = dorsal; r = right; l = left; ? = position of rib in sequence approximate; — = measurement not possible; n/a = measurement not applicable; + = incomplete bone; measurement taken on preserved portion with true value higher; - = incomplete bone; measurement taken on preserved portion with true value probably lower; ^{m} = minimum value; measurements taken on two or more separate pieces and added; ^{P} = measured region marred by pathology.

unlikely to be an atlantal rib because, where known in theropods (e.g., *Herrerasaurus* [Sereno and Novas, 1993] and *Carnotaurus* [Bonaparte et al., 1990]), they are single-headed. Possibly it belongs to the axis, but breakage on the axial vertebra and of the capitulum on the rib fragment makes this impossible to verify. Between the bases of the capitulum and tuberculum on the distal side is a deep but narrow fossa. The capitulum and tuberculum are connected by a very short ridge of bone.

Two similar ribs, 3-11 and 3-13, are substantially larger than 3-17, but similar in overall morphology (Fig. 27B). In each, the capitulum and tuberculum are ovoid in shape, with their long axes oriented approximately 90° to each other. The tubercular and capitular heads are inflated well beyond their respective necks and, like 3-17, are connected by a short ridge of bone. Both possess deep fossae between the bases of the capitula and tubercula on the medial side of the rib (Fig. 27H) and at the base of the capitula, tucked behind the short lamina of bone that connects the tuberculum and the cranial process (Fig. 27G). A third and much shallower fossa is present between the base of the capitulum and the cranial process on the ventral side of the rib. The capitulum is significantly smaller than the parapophysis of the fifth cervical, so the rib probably originated with the third or fourth.

The capitular head of 3-13 bears a sizable opening leading laterally into the neck of the capitulum (Fig. 27C). The shaft of 3-13 is flattened proximally and ovoid distally, but the flattened portion of 3-13 bears a thin, pronounced, aliform lamina connecting to the tuberculum and not seen in the previous ribs (Fig. 27C). This lamina terminates abruptly a short distance from its origin.

The rest of the cervical ribs are all clearly from the caudal end of the sequence. Ribs 4-4, 4-16, 4-18, and 4-19, remain triradiate and thus are cervical, but mark the beginning of the transition to dorsal rib morphology. In each, the tuberculum is more pronounced than in the preceding cervical ribs and is set more widely apart from but is still connected to the capitulum by a lamina of bone. The medial fossa between the tuberculum and capitulum has been broadened by the migration of the tuberculum and thus appears much shallower. The body of each rib is flattened for the entirety of its preserved length, and there is a pronounced dorsal lamina connecting the tuberculum to the shaft. In rib 4-18, the capitulum, tuberculum, and cranial process surround in a roughly equilateral fashion a deep, triangular fossa (Fig. 27J). The shafts of both ribs are flattened but concave medially, bearing distinct costal grooves.
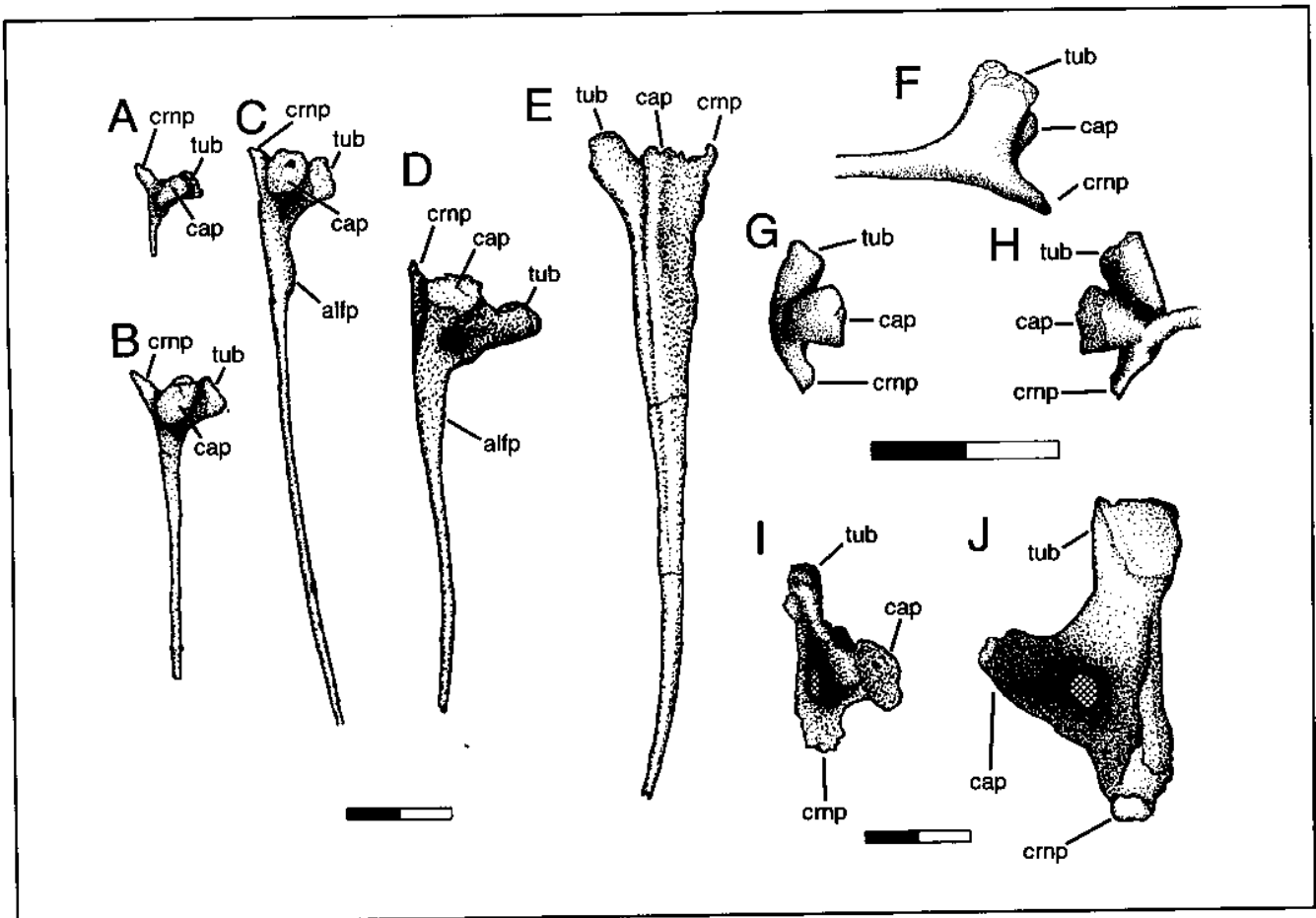
Figure 27. Cervical ribs of *Acrocanthosaurus*, SMU 74646. (A) Right axial rib, 3-17, in medial view. Right fourth cervical rib, 3-11, in (B) medial, (F) lateral, (G) cranial, and (H) caudal views. (C) Right fifth cervical rib, 3-13, in medial view. Right eighth cervical rib, 4-19, in (D) medial and (I) cranial views. Left ninth cervical rib, 4-18, in (E) medial and (J) cranial views. Cross-hatching represents matrix. Scale bars = 10 cm.

DORSAL RIBS: Several dorsal ribs are present in SMU 74646. None are complete, but a few are virtually so, lacking only the distal extremities. Many of the ribs appear to have been plastically deformed, possessing sinuosities, and several display pathologies (discussed below). As indicated in the description of the dorsal vertebrae (above), *Acrocanthosaurus* appears to possess 13 dorsal vertebrae, that would bear 26 ribs. Nineteen ribs complete enough for identification plus two isolated capitula (thus 73-81% of the total number of ribs) are represented in SMU 74646; a large number of undiagnostic head and shaft fragments, primarily from blocks 2C and 2C-D, probably represent the remaining ribs.

None of the ribs were found in direct articulation with dorsal vertebrae, so it is impossible to determine their exact positions. However, there are some consistencies across the Theropoda with regard to costal traits that allow for the approximate placement of the preserved elements. In most theropods, the longest dorsal rib co-occurs with the fourth, fifth or sixth dorsal vertebra (Molnar et al., 1990); they then shorten rapidly and become more strongly recurved caudally. The shaft, however, tends to be the widest just cranial to the longest rib (Lambe, 1917; Dong et al., 1983; Bakker et al., 1992; Currie and Zhao, 1993). The tuberculum of the rib is

more pronounced and generally larger in the cranial ribs than in the more caudal ones (Parks, 1928a). The capitular necks tend to become more gracile caudally, and often shorten or angle more obliquely with respect to the orientation of the tuberculum. The distal ends of the cranial ribs are often expanded and squared instead of tapering to a point (Madsen, 1976; Dong et al., 1983).

Using these criteria, the largest, longest, most robust preserved ribs — 4-10, 4-11, 4-12 and 4-15/4-16 — undoubtedly originated from the cranial end of the thorax of *Acrocanthosaurus* and probably correlate with the fifth and sixth dorsal vertebrae. Ribs 4-12 and 4-15/4-16 have expanded, flattened, and rectangular distal ends (Fig. 28E).

In the three cranial ribs that preserve the proximal end, the capitular-tubercular web is not greatly pronounced, resulting in prominent tubercula. The capitula make weakly acute angles to the tuberculum and proximal end of the shaft (Table 3; Figs. 28A, B). 4-12 and 4-15/4-16 are placed as the fifth ribs, and 4-10 and 4-11 as the sixth ribs.

All other preserved ribs are smaller in size and, where the proximal ends are preserved, have prominent capitular-tubercular laminae and less pronounced tubercula. Ribs 2-18, 2-19, 2-24, 2-39, 2-40, and 2-41 were found in sequence; all but 2-18
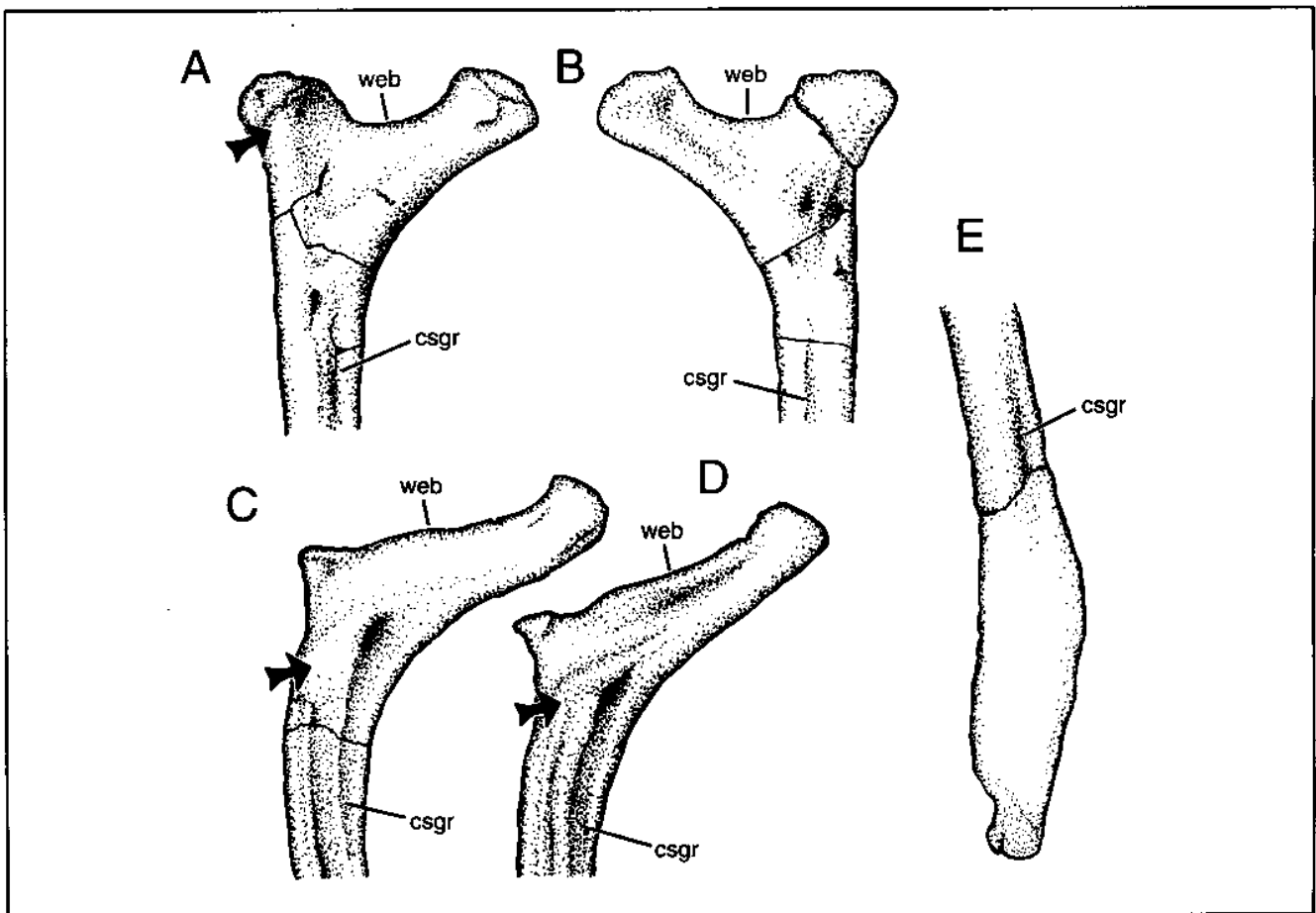
Figure 28. Dorsal ribs of *Acrocanthosaurus*, SMU 74646. Proximal end of sixth dorsal rib, 4-11, in (A) cranial and (B) caudal views. Proximal ends of (C) second, A1-11/2C-9, and (D) third, A1-5/2C-2, dorsal ribs in cranial view. (E) Distal end of fifth dorsal rib, 4-12. Arrows indicate proximal extent of intercostal ridge.

and 2-41 bear matching pathologies (see below). They are attributed to the seventh through eleventh ribs of one side.

Paleopathological research of theropods is largely unpublished, although numerous examples exist (Gilmore, 1920; Molnar and Farlow, 1990; Currie and Zhao, 1993; Rothschild et al., 1997; D. Tanke, personal communication, 1997; personal observation). Rib pathologies, particularly rehealed fractures and breaks, are relatively common in carnosaurs (Rothschild and Martin, 1993), although they have thus far been documented more thoroughly in hadrosaurs and centrosaurine neoceratopsids (Rothschild and Tanke, 1992). The most common pathology in the ribs of SMU 74646 are non-displaced, healed fractures. These are evident in A1-5/ 2C-2, 2-19, 2-24, 2-39, and 2-40 (Fig. 29). 2-19 and 2-24 both display double pathologies, within a few centimeters of each other, towards the distal end of the rib (Figs. 29A, C). These two ribs lay immediately adjacent to each other in the ground

(Fig. 4). The sequential taphonomic positions, coupled with the coincidence of pathologies in the sequence of ribs 2-19, 2-24, 2-39, and 2-40 indicates that the ribs were fractured together in simultaneous incidents during the life of the animal, as in a similarly injured specimen of *Allosaurus* (Laws, 1997). The more proximal of the bulbous healed fractures on 2-19 bears a groove, leading into and out of a tunnel, that parallels the axis of the rib (Fig. 29D). The opening is very small, just under 3 mm wide at the proximal end, and extends a distance of 45 mm. The groove is only slightly offset from a costal groove, and probably represents bone overgrowth of costal vessels and nerves during the healing of the fracture.

A second type of pathology is visible on the large rib, 4-10. Here, at mid-shaft, the proximal and distal portions expand suddenly and are separated by a narrow gap that circumscribes the entire rib (Fig. 29E). This is characteristic
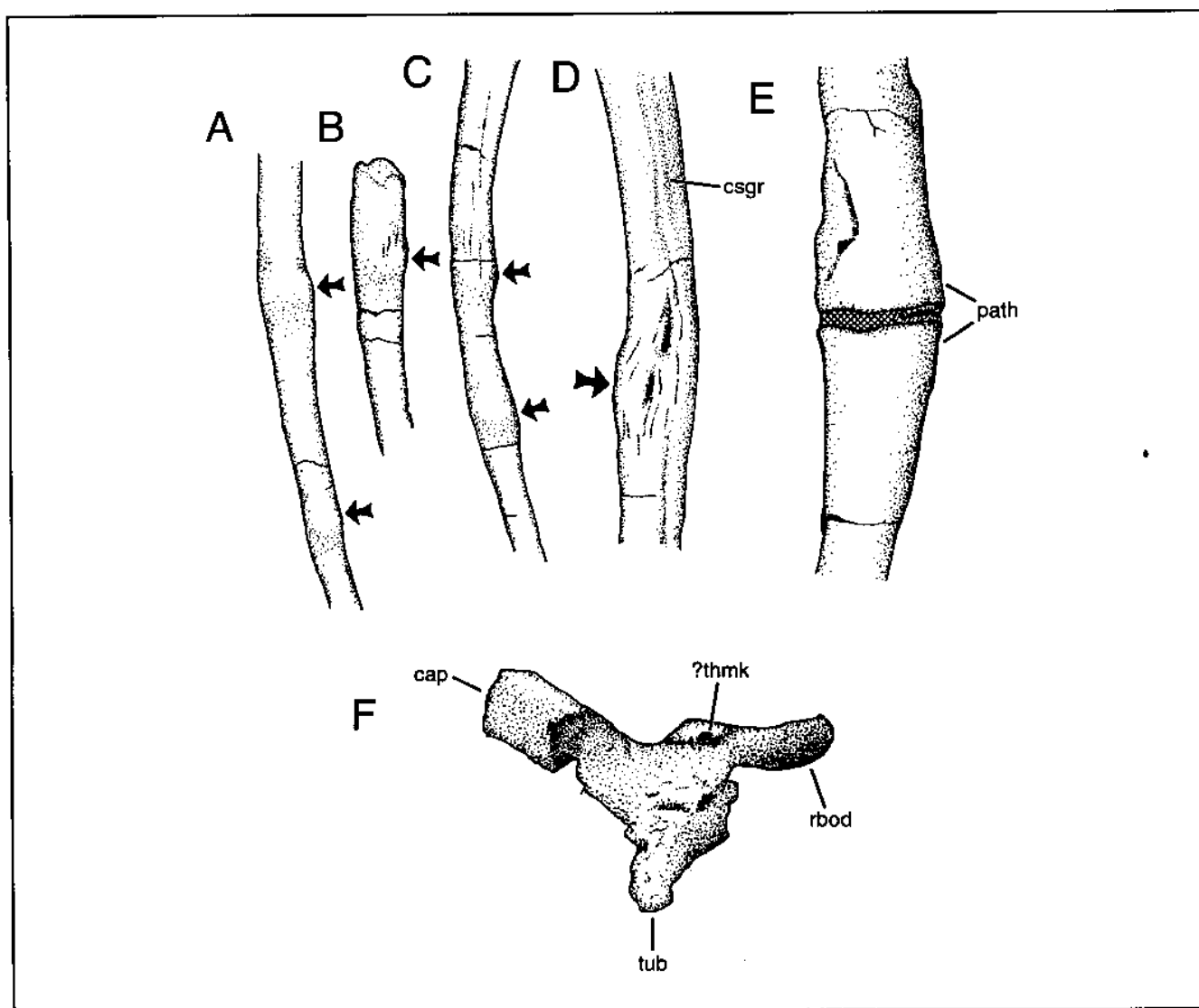
Figure 29. Dorsal rib pathologies of *Acrocanthosaurus*, SMU 74646. Mid-shafts of (A) eighth rib, 2-19, (B) eighth rib, 2-23, and (C) ninth rib, 2-24. (D) Opposite side of (A), showing tunnel where bone overgrew costal vessels. Arrows indicate healed fractures. (E) Pseudarthrosis of sixth dorsal rib, 4-10. (F) Pathologic proximal end of thirteenth dorsal rib, 2-43, in proximal view. Cross-hatching represents matrix. Not to scale.

of a pseudoarthrosis ("false joint"), formed at a non-rejoined but non-displaced fracture, although in this specimen, it appears that the expanded ends did eventually reunite, as there is cancellous bone visible between them in the gap at one point.

A final rib pathology occurs on the head of 2-43. In this specimen, the base and body of the tuberculum are disfigured and inflated (Fig. 29F). When viewed ventrally, looking up the axis of the rib shaft, there is a definite oblique lineation at the base of the mass that represents a line of fracture. Like the pathology of the caudal vertebra, there is a small, blind pit on the dorsal surface of this rib, just above the line of fracture, though it is somewhat less smooth-walled than the one on the caudal neural spine. As before, this may represent a healed bite mark.

GASTRALIA: Numerous fragments and partial gastralia are preserved in SMU 74646 in their life sequences. The presence of gastralia is ubiquitous among the Theropoda, but they have been described in detail only for *Poekilopleuron* (Deslongchamps, 1838), *Allosaurus* (Gilmore, 1920), and *Albertosaurus* (*Gorgosaurus*) *libratus* (Lambe, 1917) and noted in numerous other taxa. Only one gastralium has been previously reported in *Acrocanthosaurus* (Stovall and Langston, 1950:716).

Most gastralia that have been described in detail (e.g., Lambe, 1917) consist medially of two overlapping elements. However, the medial portion of the gastralia preserved in SMU 74646 consist of single, V-shaped elements. It is possible that these represent a fusion of two overlapping pieces, but no clear sutures are visible between the pieces. The only means of placing the region of origin of a gastralium is by the angle of divarication between the two main branches, although length can also be used when the elements are complete (Lambe, 1917). The caudal gastralia tend to have more acute angles of divarication than their cranial counterparts.

Only two gastralia, 1-6 and 3-6 (Fig. 30A), can be identified as belonging to the cranial end of the cuirass. Specimen 1-6 has a medial divarication angle of 133°; 3-6 has an angle of 123°. The medial V is not as flattened in 3-6 as in 1-6. The distal portions of the limbs of 3-6 are contorted, the result of diagenetic plastic deformation because there are no breaks or healed fractures on the shafts. The distal end of one limb, the only one preserved, does not taper to a flattened, narrow point as in most gastralia; instead, the end is inflated and expanded and has a rough and pitted surface (Fig. 30B). An isolated fragment of bone, 3-37, is somewhat smaller and flatter than 3-6, but the distal end is similarly inflated and squared off, and may belong to a similar gastralium. This implies that
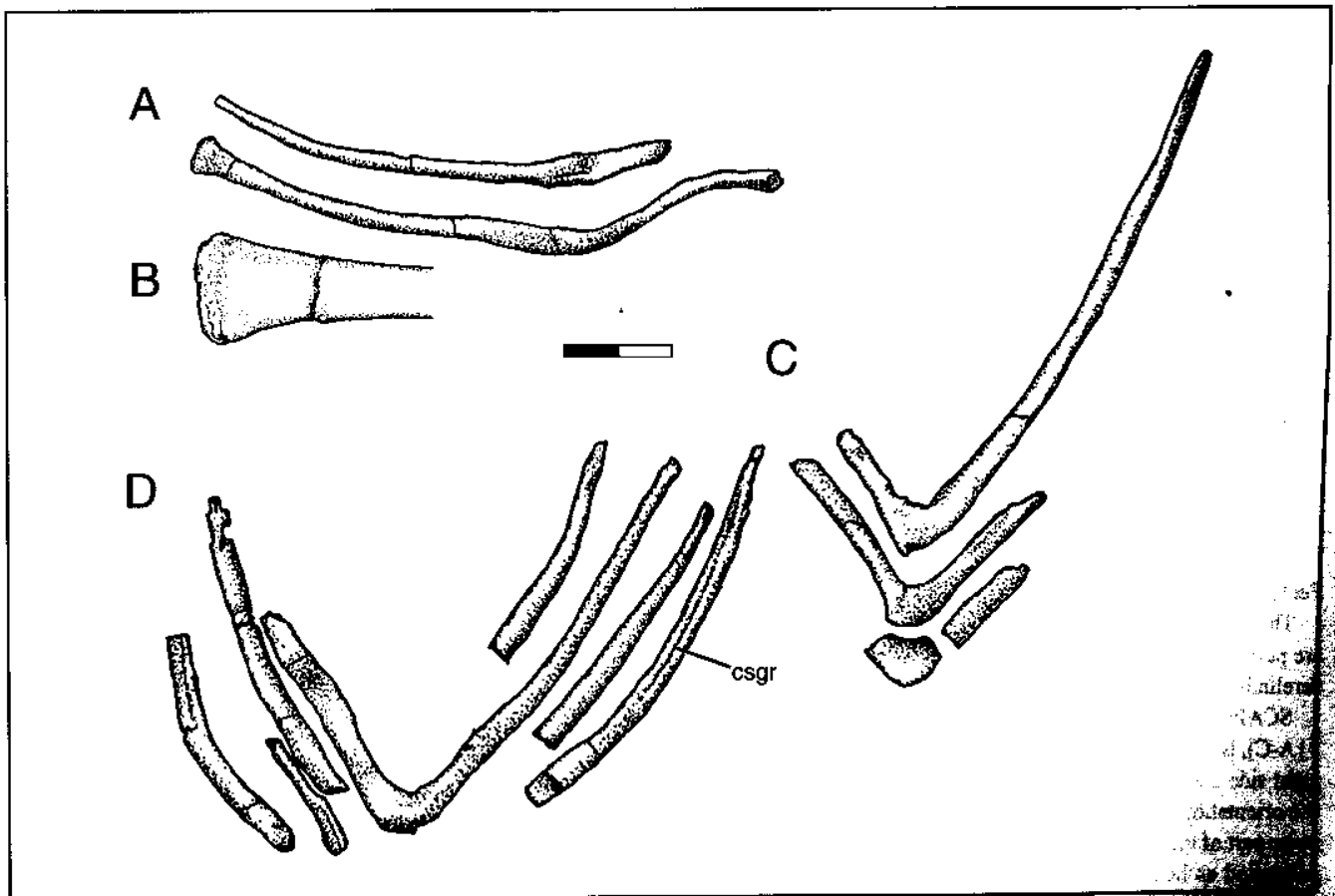
Figure 30. Gastralia of *Acrocanthosaurus*, SMU 74646. (A) Cranial gastralia: 1-6 (top) and 3-6 (bottom). (B) Close-up of showing expanded "head." (C) Caudal sequence of gastralia, as preserved. (D) Caudal sequence of gastralia, as pres numbers, see text. Scale bar = 10 cm.

the terminal end of these gastralia articulated with another element or elements. In all known theropods, the gastralia cuirass is composed not only of the medial, V-shaped elements, but of straighter lateral elements that overlap the distal ends of the V-shaped elements as well, and it is most probable that the peculiar distal ends 3-6 and 3-37 represent points of articulation with the lateral gastralium elements. If so, this kind of "condylar" distal articulation is unique among known theropod gastralia. It is also possible that these represent pseudarthrotic, pathologic gastralia, similar to some discussed in a specimen of *Allosaurus* by Laws (1997), but because the elements of SMU 74646 were not found in articulation, this cannot be confirmed.

The rest of the preserved gastralia of SMU 74646 display more acute divarication angles than the more cranial of the cuirass. These gastralia were found in two natural series, although their precise placements, either in the cuirass or to each other, cannot be made more specifically.

In one series (Fig. 30C), the most proximal of these is a fragmentary gastralium in two pieces, specimen 2B-8. Only the median V and a piece of one branch are preserved. The median juncture has an angle of 90°. The next element, 2B-7, is a single piece consisting of the medial union and subequal portions of both branches. The branches form a 77° angle. The last gastralium of this series, 2B-6, consists of the medial union, a small portion of one branch, and an almost complete opposing branch that measures 487 mm. Its median angle is 79°. The only fairly complete gastralium of the second sequence, 2-13, consists of a median juncture with an angle of 80° (Fig. 30D).

None of the aforementioned elements or preserved gastralium-like fragments can be definitively shown to be pieces of clavicles or a furcula. True furculae are definitively known in at least one allosauroid, and evidence for their presence in *Allosaurus* is strongly supported (Chure and Madsen, 1996); possession of a furcula is considered a synapomorphy of the Neotetanurae by Sereno et al. (1996), so their presence in *Acrocanthosaurus* would be expected. Criteria for diagnosing allosauroid furculae provided by Chure and Madsen (1996) are subject to individual variation, thus rendering difficult recognition of potential furcula fragments in SMU 74646.

Appendicular Skeleton

Pectoral Girdle and Forelimb

The only preserved pectoral girdle elements in SMU 74646 are portions of both scapulae. No elements pertaining to the forelimb could be discerned.

SCAPULAE: The proximal end of a scapula, 4-28 (Figs. 31A-C), is virtually intact and can be identified as that of the right side based on the curvature of its blade coupled with the orientation of the glenoid fossa and acromial process. A large part of the distal end of a scapular blade (2C-7) can be identified as belonging to the left side because its dorsal margin bears the terminal end of a narrow, longitudinal trough as well as a large degree of longitudinal scarring, presumably for the M. levator scapulae (Figs. 31D-F), that inserts on the

medial side of the craniodorsal margin of the scapular blade (Bakker et al., 1992; Currie and Zhao, 1993).

The proximal end, 4-28, measures 288 mm in its longest proximodistal dimension and is 276 mm tall from the highest portion of the acromial process to the caudal process of the glenoid. The acromial process is the dominant feature of the bone (Fig. 31A), rising sharply and abruptly from the proximal end of the scapular blade. In lateral view (Fig. 31A), there is a small foramen, approximately equidistant from both the apex of the acromial process and the glenoid. Its small size and unrefinished surface texture indicates that it is a nutrient foramen similar to one described in *Piatnitzkysaurus* by Britt (1993:189).

The craniodorsal margin of the acromial process is much thinner than the rest of the process, and this region is indented slightly on the lateral surface (Fig. 31A). This region, the subacromial depression (*sensu* Currie and Zhao, 1993), is probably associated with the origin of the deltoideus musculature (Bakker et al., 1992). The acromial process reaches its maximum height approximately midway across its span, and slopes downwards towards the coracoid articulation. This indicates that *Acrocanthosaurus* possessed a pronounced notch between the scapula and the coracoid.

The coracoid articular surface is a large, triangular facet on the proximal margin of the scapula, broadly expanded on the ventral end (Fig. 31B). The articular surface is more or less perpendicular to the blade, unlike the situation in tyrannosaurids (Walker, 1964). The facet is somewhat concave; this is similar to the notch mentioned in *Edmarka* by Bakker et al. (1992:14), into which a short process of the coracoid fits to assist in immobilizing the joint between these elements.

The portion of the blade of the left scapula measures 508 mm long, 100 mm wide at the distal end (which is broken), and 95 mm wide at the narrowest preserved place. The preserved portion of the distal end expands only slightly (Fig. 31D); if a distal expansion was present in *Acrocanthosaurus*, then it was either minimal or very abrupt. Its absence would indicate that the suprascapular cartilage was poorly developed and that the Mm. rhomboideus were likewise reduced (Bakker et al., 1992).

Pelvic Girdle and Hindlimb

SMU 74646 preserves both ischia and both pubes. The pubes and ischia display no signs of having been fused either with each other or with the ilia, as noted by Stovall and Langston (1950:717), though fusion of the pubes, when present in other theropods, is an ontogenetic feature (e.g., Stovall and Langston, 1950). Only portions of the hindlimb were recovered, including both femora and a partial metatarsal.

PUBES: Both pubes are represented in SMU 74646. The right pubis, 2-1, measures 956 mm. It lacks much of the proximal end as well as some of the pubic boot. The left pubis, 2-2/2-3, is less complete, lacking all of the proximal end, but has a more complete pubic boot than 2-1 (Figs. 32A-C). The preserved portion of the left pubis is 849 mm long.

The shafts of both pubes possess prominent, thin ridges of bone, the bases of the medial symphysis that begin proxi-

mally on the caudoventral edge of the pubis, but rapidly curve inwards, so that the majority runs along the medial side (Fig. 32C). The crest terminates by grading into the pubic boot. Though broken along most of their length, the distal ends of the laminae on both pubes, just above the pubic boots, do not possess broken edges, and thus were not coossified at this point, creating a pubic foramen, that is visible in the holotype and paratype specimens.

In theropods that possess an obturator foramen instead of an obturator notch, the foramen pierces a proximal extension of the same lamina that, distally, forms the pubic symphysis. Although the proximal ends of the pubes are lacking in all described specimens of *Acrocanthosaurus*, 2-1 from SMU 74646 is sufficiently complete to demonstrate that this lamina grades into the shaft of the pubis well below the proximal articular surface (Figs. 32B, C). Thus, it possessed an obturator notch instead of an obturator foramen.

In cranial view (Fig. 32B), the pubis is initially roughly vertical and then, just distal to the proximal articular surfaces, curves abruptly medially. Below this point, the shaft is gently concave laterally. At the point at which the shaft curves medially, there is, on the lateral surface of both pubes, a slightly pronounced and moderately rugose eminence. Bonaparte (1986) diagnoses this region in *Piatnitzkysaurus* as an ambiens process for the attachment of the M. ambiens (= M. rectus femoris, in part), but Gregory and Camp (1918) place the origin of this muscle much more proximally in *Ornitholestes*, at a point where it overlaps the pubic peduncle of the ilium and the iliac process of the pubis, the arrangement seen in both the crocodilian *Alligator* and the avian *Struthio*. Gregory and Camp (1918) and Colbert (1989) note that much of the pubic surface in theropods served as the attachment site for the M. puboischiofemoralis externus, so the eminence in *Acrocanthosaurus* and other theropods may be associated with this muscle.
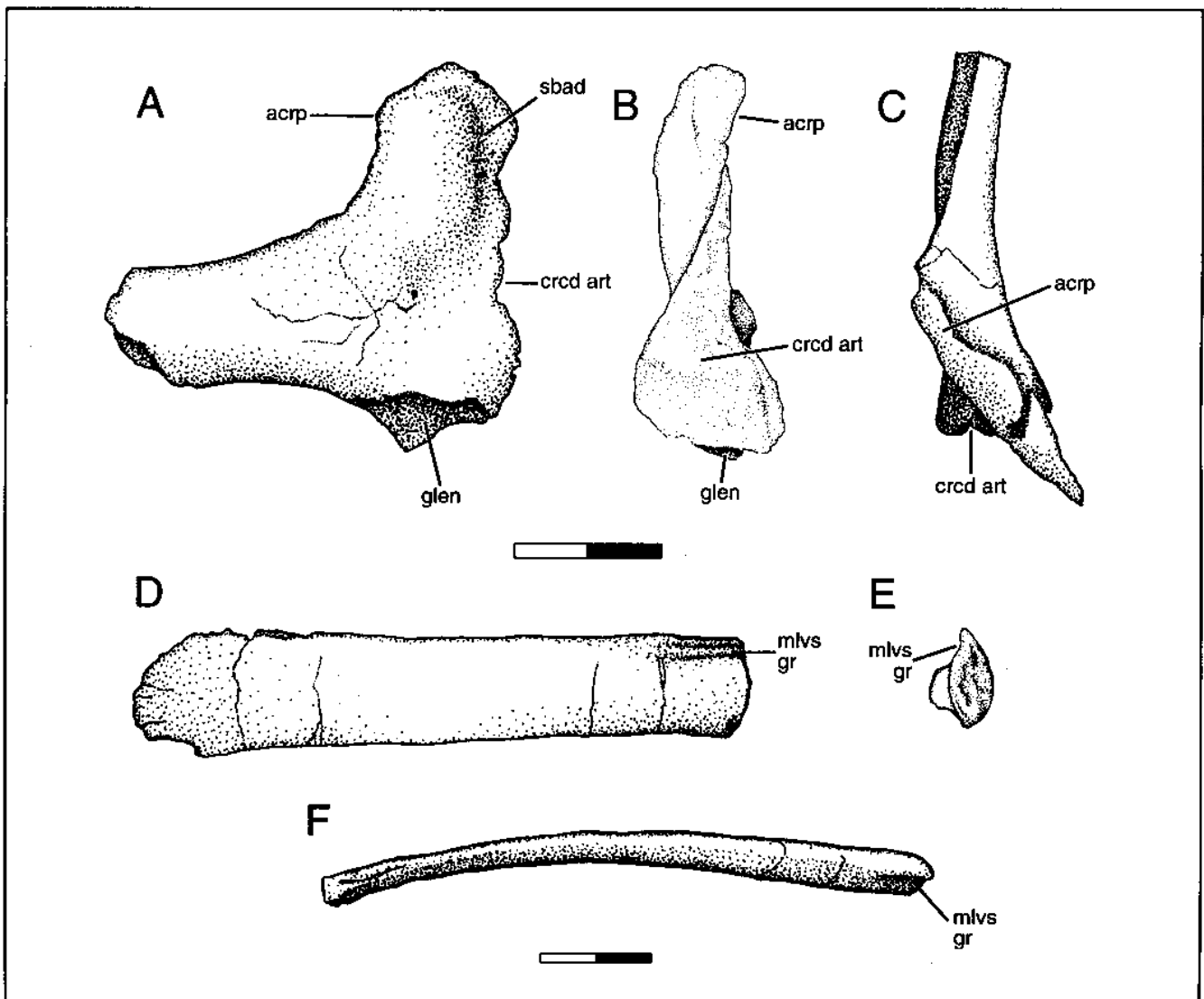
Figure 31. Scapulae of *Acrocanthosaurus*, SMU 74646. Proximal end of right scapula, 4-28, in (A) lateral, (B) proximal, and (C) dorsal views. Distal end of left scapula, 2C-7, in (D) medial, (E) proximal, and (F) dorsal views. Scale bars = 10 cm.

In lateral view (Fig. 32A), the shafts of the pubes of *Acrocanthosaurus* are gently curved cranially. The pubic boot is large and expanded both cranially and caudally. The caudal projection is set off from the rest of the pubis by its abrupt mediolateral compression, especially visible on the lateral face. The cranial projection, in contrast, initially retains the thickness of the shaft and then thins gradually while

Figure 32. Pelvic girdle elements of *Acrocanthosaurus*, SMU 74646. Left pubis, 2-2/2-3, in (A) lateral, (B) cranial, and (C) medial views. Right ischium, 2B-1, in (D) lateral, (E) caudal, and (F) medial views. Cross-hatching represents matrix. Scale bar = 10 cm.

curving cranially towards the distal end. The boot of the left pubis of SMU 74646 is 340 mm long, but lacks the distal ends of both cranial and caudal expansions. The ratio of length of the boot to the length of the pubis (assuming the length of the right pubis to be close to life) shows the boot to be roughly 36% the length of the pubis as a whole; were it complete, the percentage may approach 50%.

Holtz (1994) describes the morphology of the pubic boot in ventral view as a narrow triangle with the apex directed caudally; the shape is confirmed by the holotype and paratype specimens, but the apex is directed cranially, not caudally.

ISCHIA: Portions of both ischia are preserved in SMU 74646 (Figs. 32D-F). The right ischium, by far the more complete of the two, lacks only the obturator process and a small piece of the caudal end of the boot. The left is represented by a fragment of the shaft lacking both proximal and distal extremities. The right ischium, here denoted 2B-1, measures 844 mm in its longest proximodistal dimension and 287 mm in the widest dimension across the pubic and iliac processes. The preserved portion of the distal boot measures 186 mm. In its narrowest craniocaudal dimension, just below the origin of the obturator process, the shaft measures only 48 mm. The shaft fragment of the left ischium is 586 mm long. Both the proximal and distal ends of the ischium are mediolaterally compressed, but the portion of the shaft between the obturator process and the distal expansion is more rounded and slightly compressed craniocaudally. The ischium 2B-1 is 88% the length of the most complete pubis (2-1); the small quantity missing from the proximal end of the pubis would only lower this ratio by a few percentage points.

The proximal end of the ischium is bifurcate, possessing clearly demarked pubic and iliac processes (Figs. 32D, F) that diverge from the shaft at approximately equal angles. Both processes are approximately equally robust: the iliac process is 118 mm at its narrowest; the pubic process is 103 mm. The pubic process is rectangular in lateral view, but the iliac process is more triangular. The articular surface of the iliac process is longer than wide and is kidney-shaped, with a distinct notch on the medial surface.

There is a longitudinal, ovoid fossa on the dorsocaudal surface of 2B-1 (Figs. 32D, E) that extends from the base of the iliac peduncle a short way onto the shaft, terminating across from the proximal end of the obturator process. On the lateral surface, this depression is bounded by a thick, low ridge. Though it is not mentioned, it is present in the holotype as well (Stovall and Langston, 1950:plate 3, fig. 5). The fossa and ridge are undocumented in other theropods and may be an autapomorphy of *Acrocanthosaurus*. Beneath the fossa, on the caudal surface, there is a roughened area that was labeled by Molnar et al. (1990) as the attachment site of the M. ischiocaudalis. This muscle is not known to originate this far proximally on the ischium in any other animal; instead, it originates at the extreme distal end of the ischium in the salamander *Necturus* (Walker and Homberger, 1992), the crocodilian *Alligator* (Gregory and Camp, 1918; Galton, 1969), and, ostensibly, some dinosaurs (Gregory and Camp 1918; Galton, 1969; Norman, 1986). The region distal to the fossa in
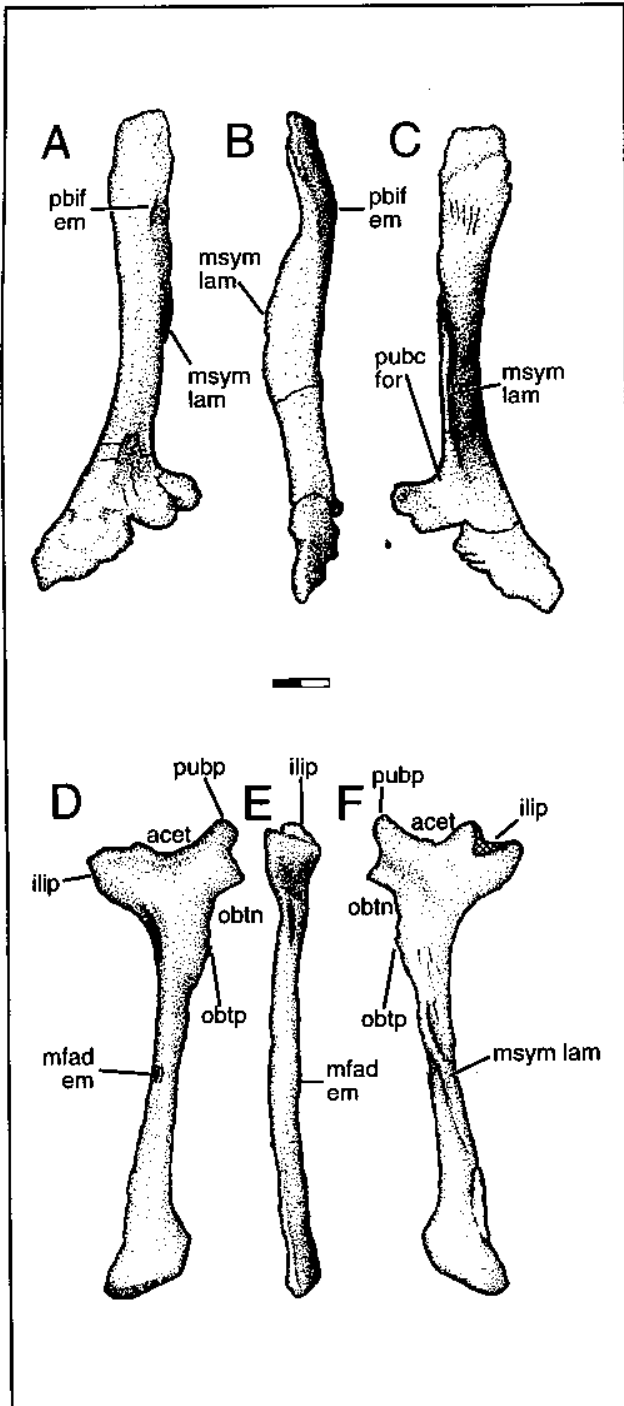
Acrocanthosaurus has also been interpreted as for the M. flexor tibialis internus (= M. semimembranosus; Gregory and Camp, 1918; Stromer, 1931; Bonaparte et al., 1990) and the M. ischiotrochantericus (Colbert, 1989:103). While it is unclear with which muscle the rough region on the ischium of *Acrocanthosaurus* was associated, it was almost certainly not the M. ischiocaudalis.

The obturator process is broken in both ischia of SMU 74646, but it is more complete in the holotype, OMNH 8-0-S8. Both agree with each other in a lack of an osseous connection between the obturator process and the iliac process, creating an obturator notch. The distal end of the process is unknown in any specimen of *Acrocanthosaurus*.

The shaft of 2B-1 is gently sigmoid in lateral view (Fig. 32D), and there is a gentle medial curve approximately on-fourth of the way below the proximal expansion (Fig. 32E); below this, the shaft is virtually straight. Contrary to Currie and Zhao (1993:2069), *Acrocanthosaurus* does not possess a well-developed crest on the dorsocaudal surface. A narrow, proximodistally ovoid, slightly elevated, rugose region present on the right lateral surface of 2B-1 (Figs. 32D, E) is in a position that is probably homologous to the crest and marks the attachment of the femoral adductor musculature (Currie and Zhao, 1993).

Both 2B-1 and 1-5 possess long, thin, broken ridges of bone, the symphysial laminae, along their craniomedial and medial edges. In the more complete ischium 2B-1, this ridge begins just beneath the obturator process, runs along the craniomedial surface for a short distance, then abruptly curves inwards and persists along the medial surface until it grades into the rough, weathered medial surface of the distal boot (Fig. 32F).

Acrocanthosaurus possesses a roughly triangular, modestly mediolaterally flattened distal ischial expansion. Its caudal end is pointed; the cranial projection is broken. The distal surface of the boot is rugose in *Acrocanthosaurus*. The medial surface of the proximal end of the ischial boot in 1-5 is heavily striated, with lines raking approximately parallel to the trend of the shaft. This argues against a coossification of the ischia distally, but implies a close appression of the ischial boots.

FEMORA: Both femora are well-preserved. The right femur, herein designated 2B-1J, is virtually complete, lacking only the distal end of the caput and the medial condyle (Fig. 33). It measures 1090 mm in length. At mid-length, the shaft is slightly wider mediolaterally than craniocaudally and has a circumference of 388 mm. Following Anderson et al. (1985), this implies a mass of the individual represented in SMU
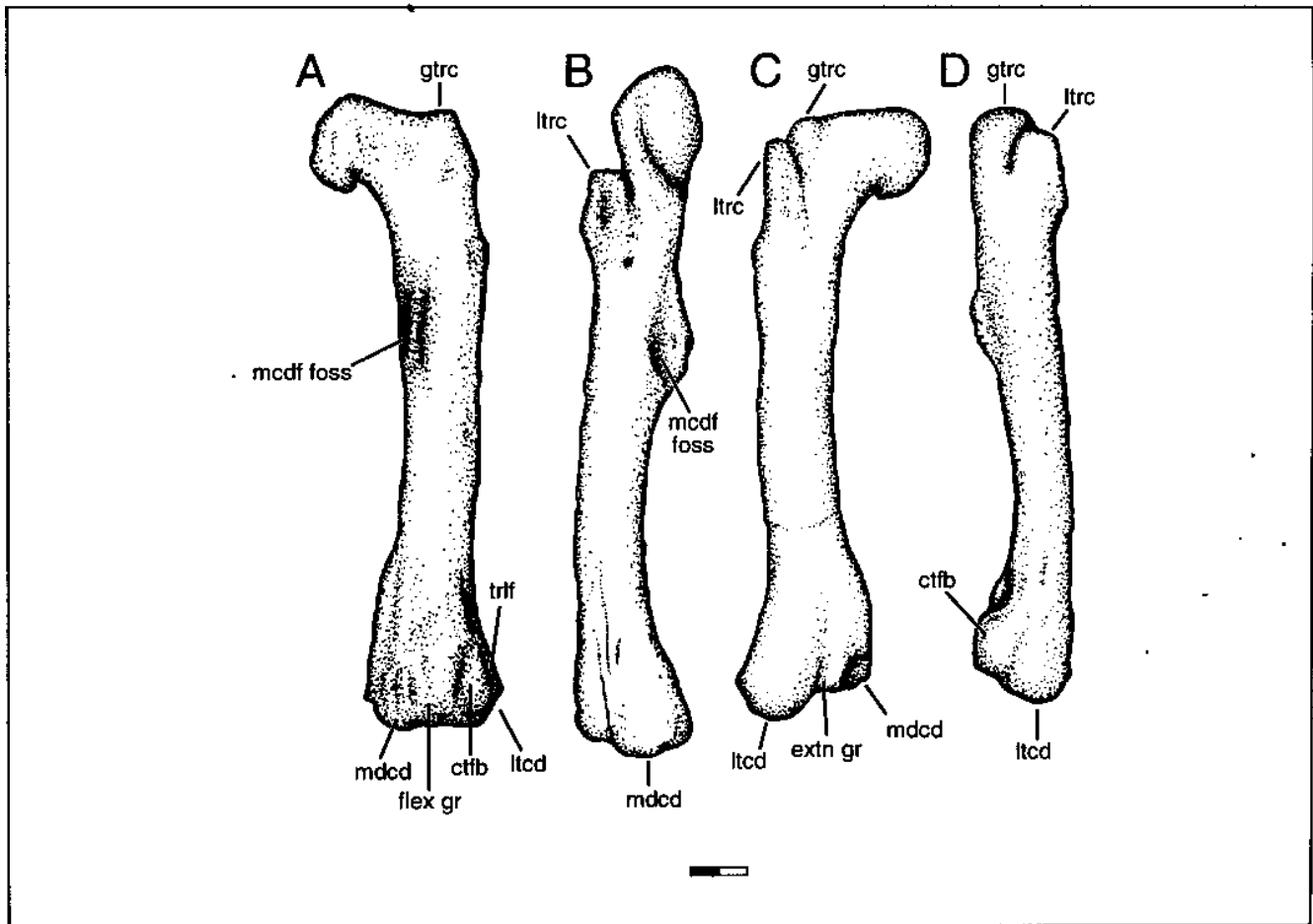
Figure 33. Right femur of *Acrocanthosaurus*, SMU 74646 2B-1J, in (A) caudal, (B) medial, (C) cranial, and (D) lateral views. Scale bar = 10 cm.

74646 of 1869 kg, just under 2 metric tons. Gatesy and Middleton (1997) note that *Acrocanthosaurus* possesses a longer femur compared to other hindlimb elements than any other theropod, but it should be noted that their femoral measurement was based on the estimate, which is probably too long, of Stovall and Langston (1950) from an incomplete femur. The left femur, designated 2B-2J, lacks the entire femoral head and the bulk of the greater and lesser trochanters, but has a complete distal end. It is 1051 mm long.

The caput projects from the shaft at an almost 90° angle (Figs. 33A, C). The condyle is slightly longer dorsoventrally than it is mediolaterally (Fig. 33B). In dorsal view, the caput is contiguous with the neck and greater trochanter (Fig. 34A). The proximal surface of this assembly is rugose and measures 288 mm, which is much longer than wide. As noted by Currie and Zhao (1993), this shape would have caused the leg to describe an outwardly bowed arc during locomotion. In caudal view, the proximal margin of the caput and greater trochanter assembly slopes somewhat ventrolaterally.

The lesser trochanter is separated from the greater trochanter by a deep but narrow intertrochanteric fossa. The process measures 62 mm. The lesser trochanter is rectangular in shape, tapering only slightly distally. It is concave on its inner (medial) surface and attains an elevation just shy of confluence with the proximal margin of the greater trochanter (Figs. 33C, D). Stovall and Langston (1950) describe, on the femur of the *Acrocanthosaurus* paratype OMNH 8-0-S8, a

Figure 34. (A) Proximal view of right femur of *Acrocanthosaurus*, SMU 74646 2B-1J. (B) Distal view of left femur, SMU 74646 2B-2J.

small flange projecting laterally from the distal end of the lesser trochanter. No such additional process is visible on 2B-1J; its significance on the paratype is unclear.

There is a small nutrient foramen on the medial surface of the femur, below the intertrochanteric fossa, approximately at the level of the proximal extent of the fourth trochanter (Fig. 33B). The fourth trochanter is a pronounced, thick, rugose ridge on the mediocaudal surface of the shaft (Figs. 33A, B, D). It measures 208 mm in length. Its distal-most extent occurs just above the mid-shaft point of the femur as a whole; it does not reach the level of the base of the lesser trochanter proximally. The medial surface of the ridge is concave, and is probably the insertion site for the M. caudofemoralis longus (Currie and Zhao, 1993).

Between the distal end of the fourth trochanter and the distal condyles, the femoral shaft is gently curved medially (Fig. 33C) and cranially (Fig. 33D). On the caudal surface of the shaft, proximal to the lateral condyle and crista tibiofibularis, there is an elongate, narrow fossa that opens laterally. This fossa is bounded medially by a low ridge and leads distally into the trochlea fibularis (Fig. 33A).

The distal end of 2B-2J is 248 mm wide. The distal condyles are well developed. In caudal view, the medial condyle is longer proximodistally but narrower mediolaterally than the lateral condyle, which is bulbous. The medial condyle also protrudes much further caudally than does the lateral condyle, though not as far as the crista tibiofibularis (Fig. 34B). The crista tibiofibularis is a tall, mediolaterally narrow, rectangular shelf that has a marked lateral deflection (Fig. 34B). Its medial surface is gently concave.

The extensor groove (= intercondylar sulcus, in part) on the cranial surface of the femur is moderately deep and U-shaped in distal view (Fig. 34B). The flexor (= intercondylar, in part) groove on the caudal surface is deep and contains a low longitudinal ridge between the medial condyle and the crista tibiofibularis. This ridge has been associated with the origin of the cruciate ligamenture (Currie and Zhao, 1993).

METATARSALS: Only one partial metatarsal (1.2WST) is preserved in SMU 74646 (Fig. 35). It is a distal end measuring 218 mm long and 97 mm wide. Comparison with the metatarsals of other theropods indicates that 1.2WST is the distal end of the left metatarsal II. It is wider (97 mm) than tall (80 mm). It is clearly not the end of metatarsal IV because of the broad, quadrangular (though not square) shape (Molnar et al., 1990). The distal articular surface is angled laterally from the axis of the shaft. The higher end of the articular surface is on the lateral side of the metatarsal; thus, 1.2WST must belong to the left foot.

In distal view, the ginglymus of 1.2WST is divided into two condyles by a deep notch on the caudal side (Figs. 35C, E). The notch has a ventral and cranial orientation. The notch is not centered, and the subrectangular lateral condyle is much larger than the triangular lateral one. This is identical to that noted in metatarsal II of the *Acrocanthosaurus* paratype OMNH 8-0-S9 (Stovall and Langston,1950:720). The lateral and medial collateral ligament fossae are deep and consist of large, gently sloping depressions that contain centrally-placed, steep-walled, blind, ovoid pits.
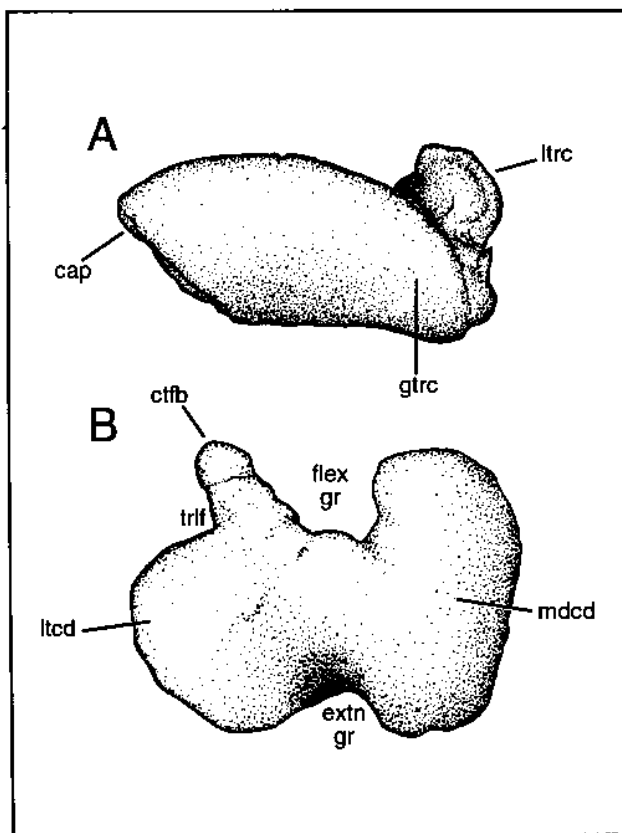
COMPARATIVE, PALEOBIOGEOGRAPHIC, AND PHYLOGENETIC ANALYSES

Comparison with Other Theropods

The palatine of *Acrocanthosaurus* most closely resembles that of *Allosaurus* (Madsen, 1976:plate 10, fig. A, B); the tetraradiate morphology is derived with respect to the rectangular palatine of *Syntarsus* (Raath, 1977). The large palatine pneumatic recess and associated foramina are likewise derived features; they are absent in *Allosaurus*, but present in *Sinraptor* (Currie and Zhao, 1993) and *Tyrannosaurus* (Molnar, 1991); a fossa without invasive foramina is also present in *Deinonychus* (Ostrom, 1969), so it appears that invasion of the palatine occurred at least twice: once in the allosauroid lineage and again in the Maniraptora. The presence in *Acrocanthosaurus* of the dorsoventral expansion of the jugal process (= lacrimal process of Sereno et al., 1996) agrees with the diagnostic condition of the Allosauroidea (Sereno et al., 1996).

The ectopterygoid of *Acrocanthosaurus* has a shallower ectopterygoid flange than *Allosaurus* (Madsen, 1976:plate 10C) and *Sinraptor* (Currie and Zhao, 1993:fig. 10A). The subtemporal fenestra of *Acrocanthosaurus* has parallel lateral and medial boundaries because it lacks the eminence of the ectopterygoid flange seen in *Allosaurus* (Madsen, 1976:plate 10D). Lateral invasion of the jugal process by the

ectopterygoid pneumatic recess is given as a diagnostic character of the Neotetanurae by Sereno et al. (1996), a criterion met by *Acrocanthosaurus*. However, the recess in *Acrocanthosaurus* is neither divided into multiple smaller fossae by bony laminae as in *Tyrannosaurus* (Molnar, 1991) nor bulbous and inflated like that of *Deinonychus* (Ostrom, 1969).

The jugal of *Acrocanthosaurus* differs from those of *Allosaurus* (Madsen, 1976), *Torvosaurus* (Britt, 1991), *Edmarka* (Bakker et al., 1992) and tyrannosaurids (Bakker et al., 1988; Molnar, 1991) by lacking a pronounced lobe beneath the orbit. Possession of a jugal pneumatic recess differentiates *Acrocanthosaurus* from *Allosaurus* because the latter lacks sizable foramina or other indications that the interior is hollow. Medial jugal foramina such as the one on the jugal of *Acrocanthosaurus* are also known in *Monolophosaurus* (Zhao and Currie, 1993), *Sinraptor* (Currie and Zhao, 1993), and *Tyrannosaurus* (Molnar, 1991), and again appear to have been independently evolved at least twice. The presence of pneumatic excavations of the jugal is cited by Sereno et al. (1994, 1996) as a trait diagnostic of the Tetanurae, although it is lacking in *Torvosaurus* (Britt, 1991) and *Edmarka* (Bakker et al., 1992).

The surangular shelf in *Acrocanthosaurus* is relatively much larger than that of *Allosaurus*; likewise, it possesses a pronounced knob undocumented in other theropod taxa. The adductor fossa of *Acrocanthosaurus* is much broader
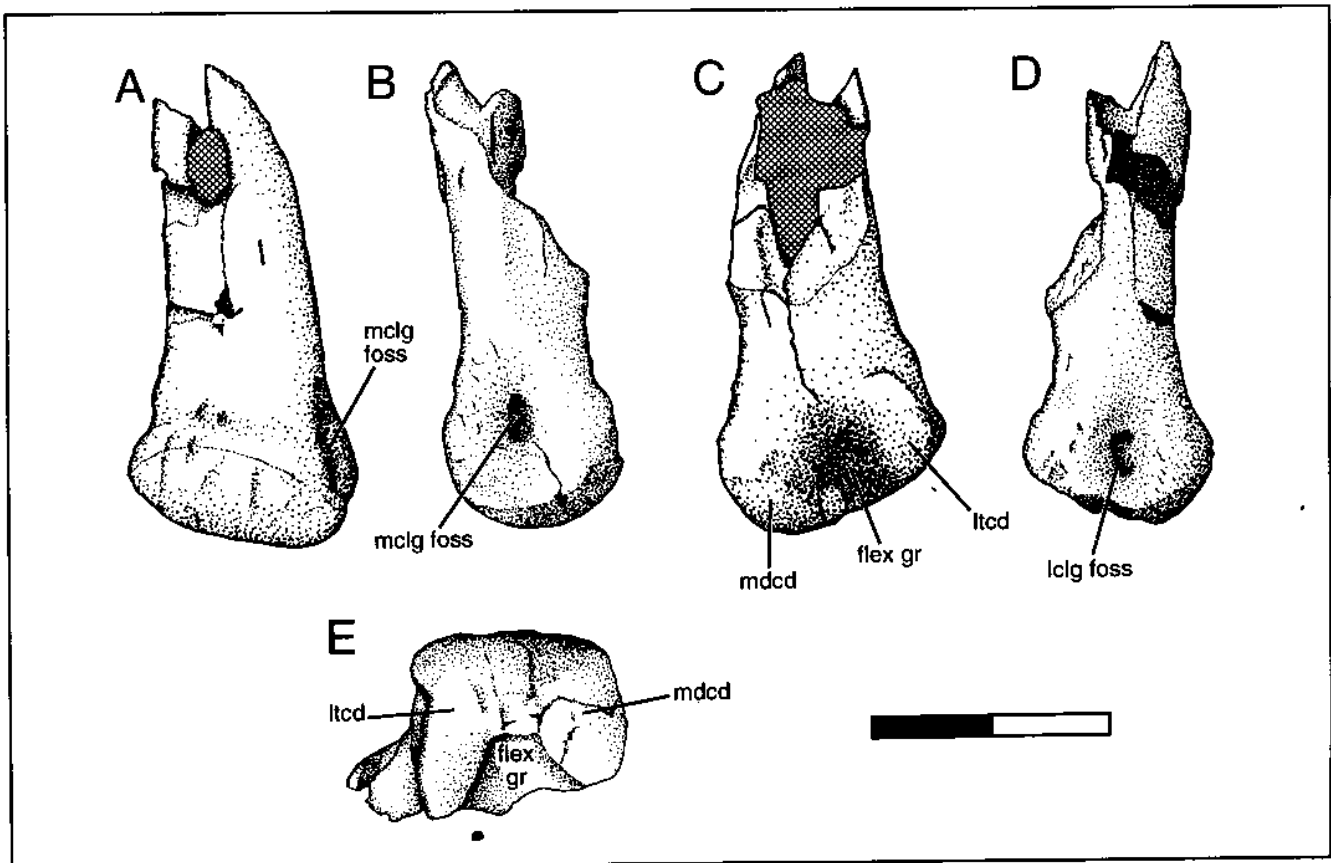
Figure 35. Distal end of left metatarsal II of *Acrocanthosaurus*, SMU 74646 1-2WST, in (A) cranial, (B) medial, (C) caudal, (D) lateral, and (E) distal views. Cross-hatching represents matrix. Scale bar = 10 cm.

mediolaterally and more inflated than that of *Allosaurus*, indicating it had a more powerful bite. The articular of *Acrocanthosaurus* retains a long retroarticular process, unlike the abbreviated processes of *Allosaurus* (Currie and Zhao, 1993) or *Tyrannosaurus* (Molnar et al., 1990).

Teeth of the small Late Cretaceous theropod *Richardoestesia* possess apical denticulation, but these teeth differ from that of *Acrocanthosaurus* because their rostral carinae are much less extensive (Currie et al., 1990). Teeth attributed to the primitive tyrannosaurid *Alectrosaurus* from Asia and the Cedar Mountain Formation of Utah are also reported to have this trait (J. Kirkland, personal communication, 1996), but these teeth are all much smaller than *Acrocanthosaurus*.

All preserved cervical and cranial dorsal vertebral centra are strongly opisthocoelous in *Acrocanthosaurus*, as in *Torvosaurus* (Britt, 1991), *Spinosaurus maroccanus* and *Sigilmassasaurus* (Russell, 1996), *Eustreptospondylus* (Walker, 1964) and allosauroids. Gauthier (1986) and Rauhut (1995) caution that cervical opisthocoely may be a size-dependent homoplasy among large theropods, but the cervical centra of large tyrannosaurids are only slightly opisthocoelous (Osborn, 1906; Carpenter, 1992), whereas the cervicals of the very small theropods *Compsognathus* (Ostrom, 1978) and *Mononykus* (Perle et al., 1994) are opisthocoelous. Cervical opisthocoely appears to be predominant in, but not necessarily diagnostic of, theropods more advanced than the Ceratosauria but more primitive than the Coelurosauria.

The presence of a groove offsetting the cranial ball from the rest of the cervical centrum is shared by *Acrocanthosaurus*, *Torvosaurus*, and some specimens of *Allosaurus* (Britt, 1991). Sereno et al. (1996) state that *Acrocanthosaurus* shares with *Carcharodontosaurus* reniform caudal articular facets on the cervical vertebrae, but a cervical vertebra from Morocco referred to the latter by Russell (1996) has a much more circular caudal articular cup, so this feature may be restricted to only a few cervical vertebrae. There are no hyposphenous articulations between the cervicals of *Acrocanthosaurus* as in tyrannosaurids (Molnar et al., 1990). The cervicals of *Acrocanthosaurus* lack large, laterally-projecting diapophyses as in *Carcharodontosaurus* (Sereno et al., 1996) and ventral processes (=hypapophyses) like those of maniraptoriforms (Gauthier, 1986; Holtz, 1996a) and *Sigilmassasaurus* (Russell, 1996).

The axial neural spine of *Acrocanthosaurus* is much taller with respect to the centrum, and much more reduced distally than all other theropods (Fig. 36). The presence of a keel on the ventral margin of the axis in *Acrocanthosaurus* is unusual among allosauroids because an axial keel has been lost in *Allosaurus* (Gilmore, 1920) and *Chilantaisaurus* (Hu, 1964). The central placement of the pleurocoelous fossa on the axial centrum of *Acrocanthosaurus* contrasts with the disparate, cranial and caudally placed dual fossae seen in *Sinraptor* (Currie and Zhao, 1993). The axial centrum is unlike that of the "megalosaurid" "Brontoraptor" (Siegwarth et al., in press) because the caudal cup is not angled from the vertical. The greatly reduced distal expansion on the axial neural spine of *Acrocanthosaurus* is an autapomorphic reversal of the diagnostic expansion of the Tetanurae (Gauthier, 1986).

Britt (1993) finds the camellate interior of *Acrocanthosaurus* cervical vertebrae to be more similar to that of tyrannosaurid, avian, and numerous other coelurosaurian theropods than to any other theropod taxa; in contrast, *Piatnitzkysaurus*, *Allosaurus*, and *Sinraptor* all possess much simpler camerate interiors. Camellate structure therefore appears to have evolved twice within the Theropoda. The large, planar postzygapophyseal facets of *Acrocanthosaurus* differ from the coelurosaurian condition in which the facets are bent to form to facets that are set at angles to each other. *Acrocanthosaurus* and *Saurophaganax* (Chure, 1996) mimic maniraptoriform theropods (Gauthier, 1986; Russell and Dong, 1993b) in possessing large epipophyses on the cranial cervical vertebrae.

At least five, possibly six (see above), dorsal vertebrae are opisthocoelous in *Acrocanthosaurus*. Opisthocoely also occurs in the first two dorsals of *Sinraptor* (Currie and Zhao, 1993), the third or fourth of *Piatnitzkysaurus* (Bonaparte, 1986) and *Allosaurus* (Madsen, 1976), and the fifth of *Monolophosaurus* (Zhao and Currie, 1993); the larger number may be autapomorphic for a group within the Allosauroidea.

Both placement and morphology of the elongate neural spines of *Acrocanthosaurus* differentiate the taxon from *Spinosaurus* (Stromer, 1915), *Metriacanthosaurus* (Walker, 1964), *Baryonyx* (Charig and Milner, 1990), and vertebrae attributed to the tooth genus *Altispinax* (Huene, 1926; = ?*Acrocanthosaurus altispinax* [Paul, 1988] and *Becklespinax* [Olshevsky, 1991]) (Fig. 37). Whereas spine elevations are constant across the presacral column in *Acrocanthosaurus*, they vary in *Spinosaurus* (Stromer, 1915; Russell, 1996). *Baryonyx* is similar to *Spinosaurus*, although the spines are not nearly as high (Charig and Milner, 1990). Both *Spinosaurus* and *Baryonyx* cervical neural spines lack rugose, expanded summits and cranial and caudal processes seen in *Acrocanthosaurus*. The dorsal neural spines of *Spinosaurus* are laterally compressed, with craniocaudally expanded bases (Stromer, 1915), unlike those of *Acrocanthosaurus*. Presacral vertebrae of both *Metriacanthosaurus* (Huene, 1926; Walker, 1964) and *Altispinax* (Huene, 1926) include dorsals that possess tall, mediolaterally thick, rectangular spines, but these lack the pronounced interspinous ligament attachment sites and strongly backturned and dorsally angled diapophyses of *Acrocanthosaurus*. *Altispinax* also apparently lacked the pronounced pleurocoelous fossae and foramina of *Acrocanthosaurus*, and is certainly not congeneric with the latter as asserted by Paul (1988).

Acrocanthosaurus shares with *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993), and tyrannosaurids (Molnar et al., 1990) hyposphene-hypantrum accessory articulations on the mid- and caudal dorsal vertebrae. In the latter taxa, the hypantral facets are oriented at right angles to the planar prezygapophyseal facets, but in *Acrocanthosaurus*, the prezygapophyseal facets are arched and grade more smoothly into the hypantral facets. Slight cranial inclinations of the caudal dorsal vertebral spines are figured for the tenth through thirteenth dorsals of *Sinraptor* (Currie and Zhao, 1993:figs. 17A-C) and for the fourteenth dorsal of *Allosaurus* (Madsen, 1976:plate 23, fig. B), but these are much less manifest than in *Acrocanthosaurus*.

Sereno et al. (1996) cite the presence of rudimentary caudal pleurocoels as a diagnostic trait of the Carcharodontosauridae, including *Acrocanthosaurus* but excluding *Allosaurus* and sinraptorids. In *Carcharodontosaurus* itself, as well as *Bahariasaurus*, the most proximal caudals apparently have well-developed pleurocoelous foramina (Stromer, 1931; Rauhut, 1995). Possible pleurocoelous fossae also occur in proximal caudals of *Herrerasaurus* (Novas, 1993), *Torvosaurus* (Britt, 1991), and oviraptorosaurians (Barsbold et al., 1990) Hu (1964) mentions "pits" in the proximal caudals of *Chilantaisaurus maortuensis*, and "Brontoraptor" possesses a pleurocoelous fossa on the first caudal vertebra (Siegwarth et al., in press), so the trait appears to have evolved

multiple times in the Theropoda. *Acrocanthosaurus* caudals lack infraprezygapophyseal foramina like those seen in *Carcharodontosaurus* (Stromer, 1931).

The cervical rib heads of *Acrocanthosaurus* are invaded by several deep fossae as in *Sinraptor* (Currie and Zhao, 1993) and *Allosaurus* (Madsen, 1976). The aliform processes at the bases of the shafts on many cervical ribs of *Acrocanthosaurus* are unknown in *Allosaurus*, but are present in *Sinraptor* (Currie and Zhao, 1993); large alae are reported for *Carnotaurus* (Bonaparte et al., 1990). Fusion of the ribs to the cervical vertebrae, absent in *Acrocanthosaurus*, is a diagnostic trait of the Coelurosauria (Gauthier, 1986), though absent in the therizinosauroid *Alxasaurus* (Russell and Dong,
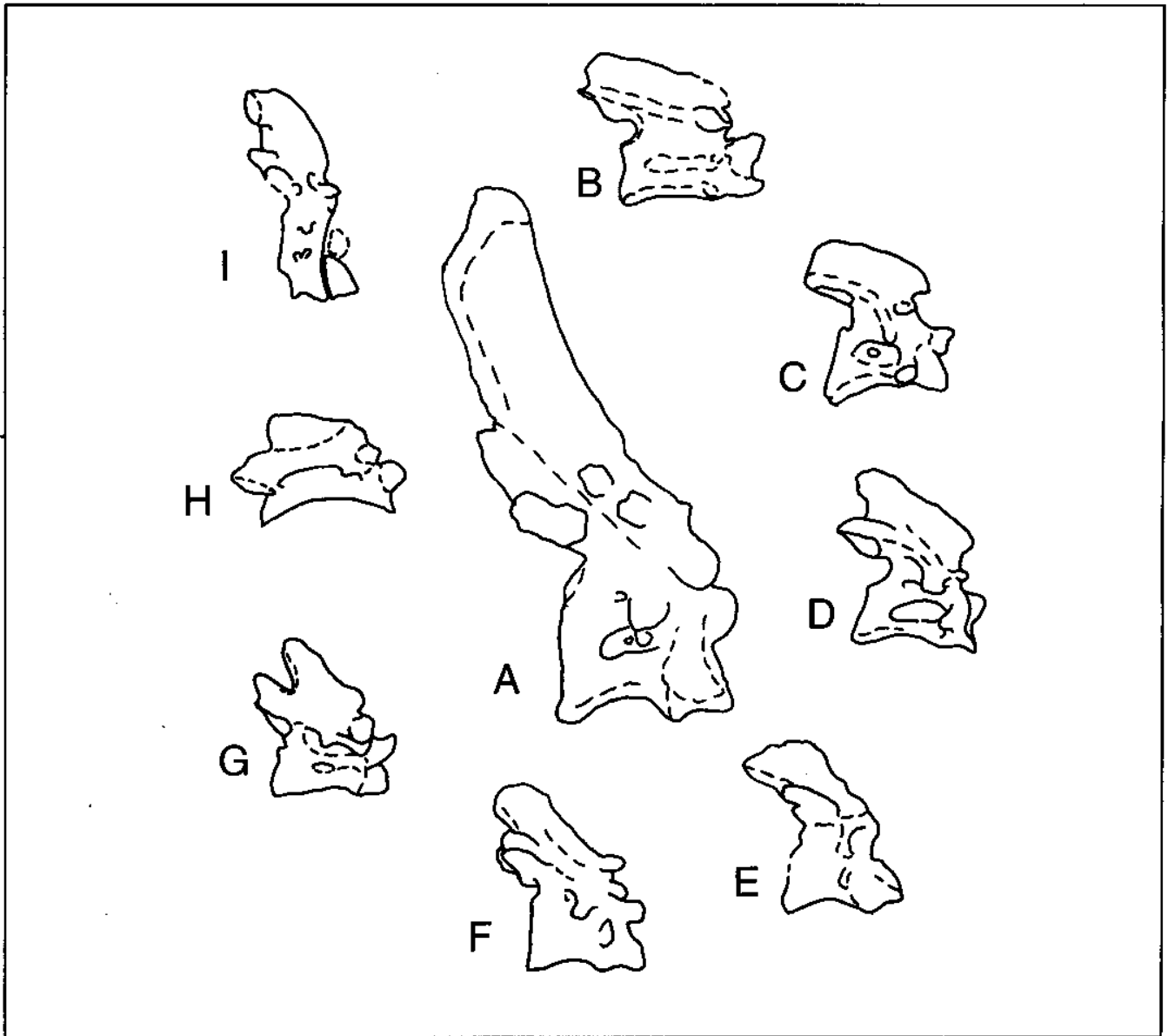
Figure 36. Comparisons of theropod axes in right lateral view. (A) *Acrocanthosaurus*, SMU 74646 3B-1. (B) *Herrerasaurus*, PVSJ 407 (reversed from Sereno and Novas, 1993). (C) *Ceratosaurus*, USNM 4735 (reversed from Gilmore, 1920). (D) "Brontoraptor," TATE 1012 (reversed from Siegwarth et al., in press). (E) *Sinraptor*, IVPP 10600 (from Currie and Zhao, 1993). (F) *Allosaurus*, UUVP 6000 (reversed from Madsen, 1976). (G) *Deinonychus*, YPM 5204 (reversed from Ostrom, 1969). (H) *Gallimimus*, GI DPS 100/11 (reversed from Osmólska et al., 1972). (I) *Tyrannosaurus*, AMNH 5866 (from Osborn, 1906).

1993a). Cranial processes on the cervical ribs are found in most theropods but are shorter in the allosauroids *Acrocanthosaurus*, *Sinraptor* (Currie and Zhao, 1993), *Monolophosaurus* (Zhao and Currie, 1993), *Allosaurus* (Madsen, 1976), and the tyrannosaurid *Albertosaurus* (*Gorgosaurus*) *libratus* (Lambe, 1917) than in primitive forms. Those of *Acrocanthosaurus* are more similar to the shorter processes of allosauroids than to those of ceratosaurians. Bakker et al. (1992) claim that the dorsal ribs of the "megalosaurid" *Edmarka* are unusual

among theropods because the cranial intercostal ridge does not perpetuate onto the tuberculum. The condition in the preserved ribs of SMU 74646 is variable: this ridge strongly bolsters the tuberculum in some ribs, weakly in others, and in the remainder, the ridge terminates well below the tuberculum (Fig. 28A, C, D).

Of theropods for which the gastralia have been described in detail, only *Acrocanthosaurus*, *Allosaurus* (Gilmore, 1920), and the "megalosaurid" *Poekilopleuron* (Deslongchamps,
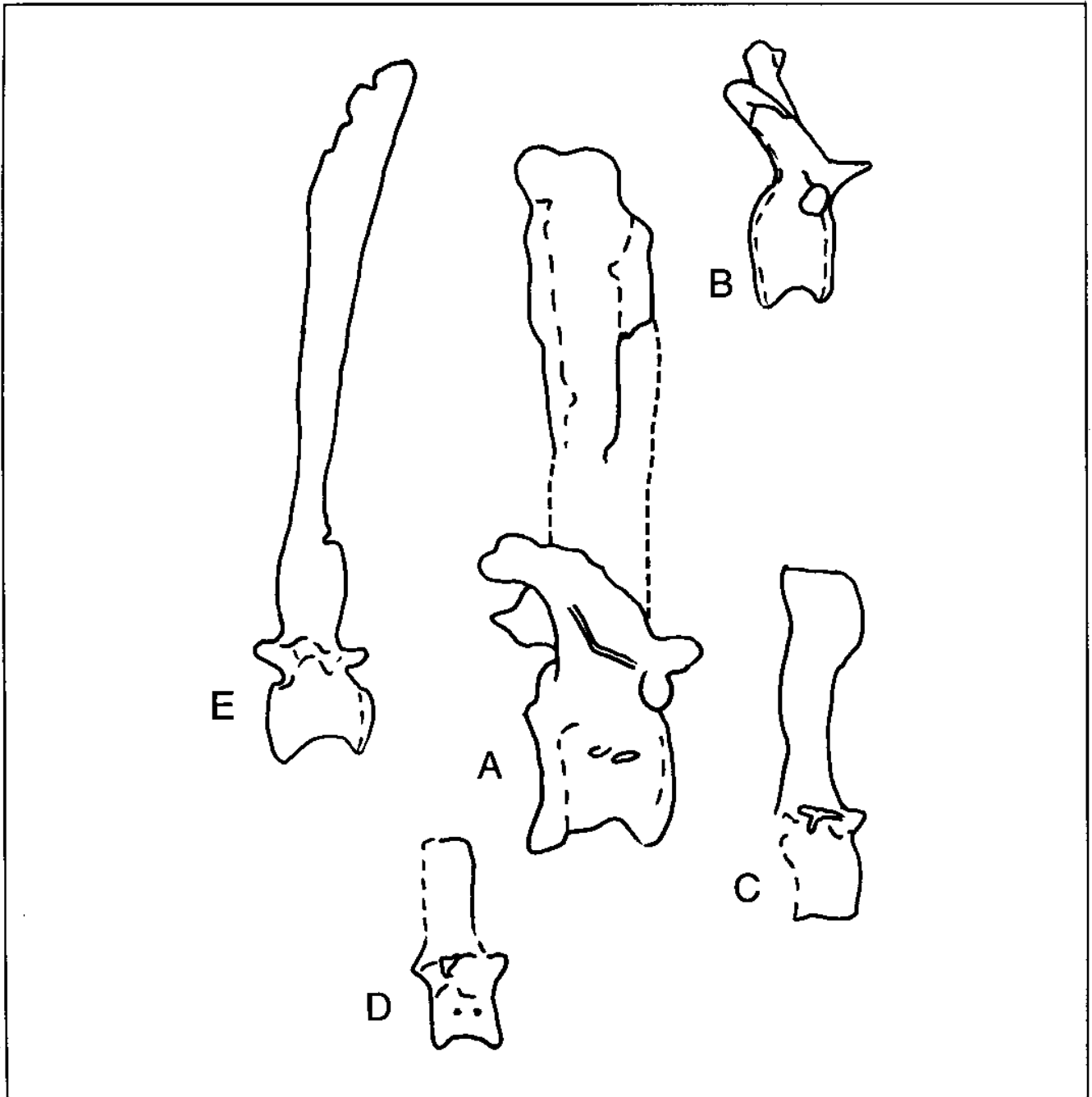
Figure 37. Comparisons of dorsal vertebrae of theropods with elongate neural spines in right lateral view. (A) Composite mid-dorsal based on isolated neural spine SMU 74646 2A-3 and ninth dorsal vertebra SMU 74646 A1-2-14 of *Acrocanthosaurus*. Spine height is a minimum estimate based on isolated neural spine of OMNH 8-0-S9. (B) Sixth dorsal of *Allosaurus*, UUVP 6000 (reversed from Madsen, 1976). (C) Unspecified dorsal vertebra of *Altispinax*, BMNH R1828 (reversed from Owen, 1855). (D) Unspecified dorsal vertebra of *Metriacanthosaurus*, OUM J12144 (reversed from Huene, 1926). (E) Unspecified dorsal vertebra of *Spinosaurus*, IPHG number unknown (from Stromer, 1915).

1838) possess gastralia that consist of a single element along the midline; *Albertosaurus (Gorgosaurus) libratus* (Lambe, 1917) and other theropod gastralia consist of two elements that overlap at the midline.

The presence of a deep notch between the acromial process of the scapula and the coracoid in *Acrocanthosaurus* also occurs in *Allosaurus* (Gilmore, 1920), *Piatnitzkysaurus* (Bonaparte, 1986), and possibly *Sinraptor* (Currie and Zhao, 1993); all theropods in which a notch is known fall into the Allosauroidea (*contra* Bakker et al., 1992).

Acrocanthosaurus possesses a pubic foramen (≠ pubic foramen of Gilmore [1920] or Walker [1964], which is the obturator foramen), as in *Sinraptor* (Currie and Zhao, 1993),

Yangchuanosaurus (Dong et al., 1983), *Metriacanthosaurus* (Huene, 1926b), and *Allosaurus* (Madsen, 1976), but not *Torvosaurus* (Britt, 1991; *contra* Currie and Zhao, 1993) or *Carcharodontosaurus* (Rauhut, 1995). Moderate cranial curvature of the pubic shaft, also present in *Carcharodontosaurus* (Rauhut, 1995) and *Allosaurus* (Gilmore, 1920; Madsen, 1976), is more derived than the strongly downturned pubes of primitive theropods such as *Herrerasaurus* (Novas, 1993) and *Coelophysis* (Colbert, 1989) and the relatively straight pubic shafts of *Eustreptospondylus* (Walker, 1964), *Torvosaurus* (Galton and Jensen, 1979), *Afrovenator* (Sereno et al., 1994), and *Szechuanosaurus zigongensis* (Gao, 1993) (Fig. 38).
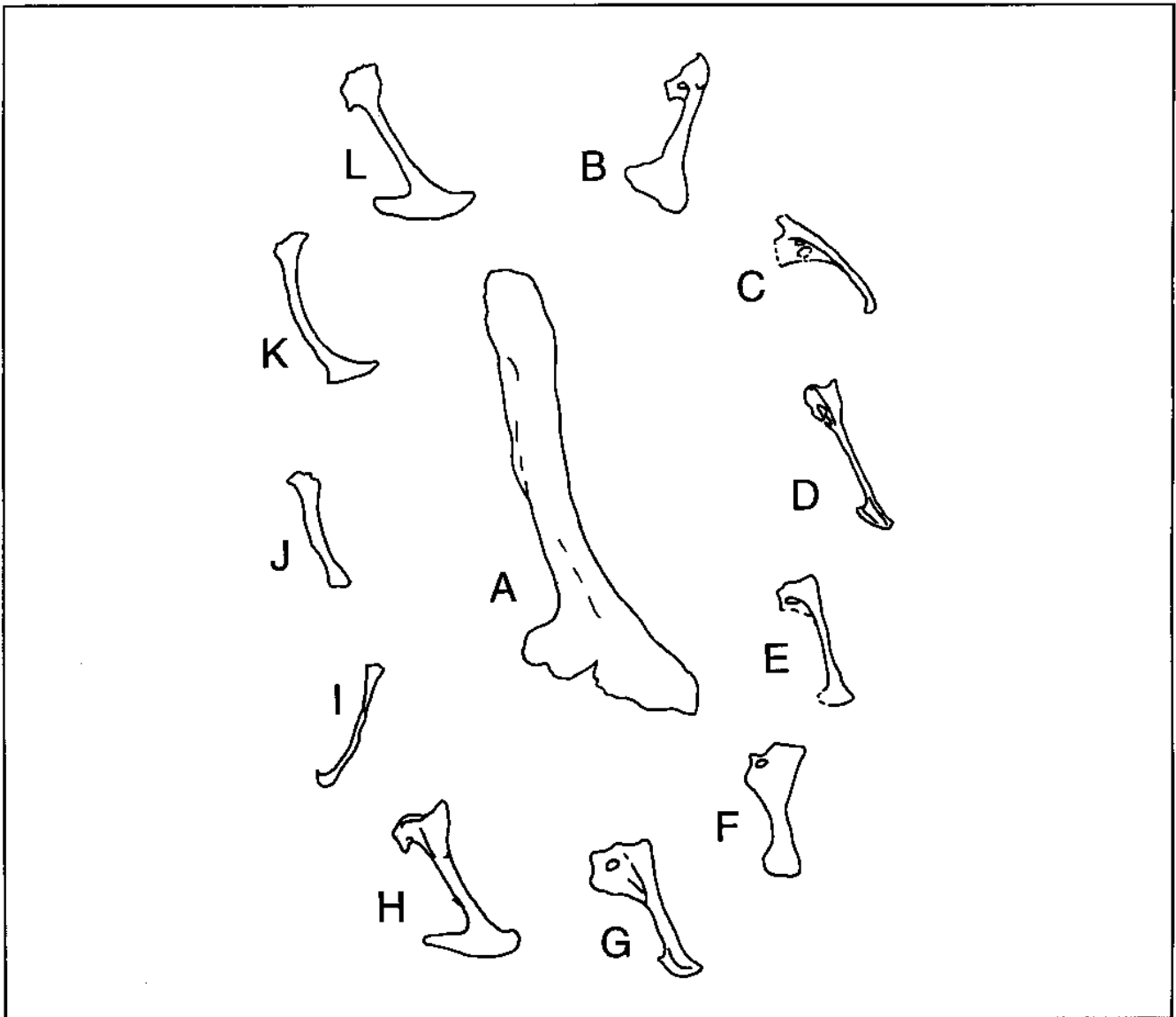
Figure 38. Comparisons of theropod pubes in right lateral view. (A) Right pubis of *Acrocanthosaurus*, SMU 74646 2-2/2-3. (B) Right pubis of *Herrerasaurus*, PVSJ 373 (from Novas, 1993). (C) Left pubis of *Syntarsus*, QG/1 (reversed from Raath, 1977). (D) Left pubis of *Sinraptor*, IVPP 10600 (reversed from Currie and Zhao, 1993). (E) Left pubis of *Piatnitzkysaurus*, PVL 4073 (reversed from Bonaparte, 1986). (F) Left pubis of *Edmarka*, CPS 1010 (reversed from Bakker et al., 1992). (G) Right pubis of *Torvosaurus*, BYU 2014 (from Galton and Jensen, 1979). (H) Left pubis of *Allosaurus*, UUVP 6000 (reversed from Madsen, 1976). (I) Right pubis of *Archaeopteryx*, JM "Eichstätt Specimen" (from Wellnhofer, 1974). (J) Left pubis of *Carcharodontosaurus*, IPHG number unknown (reversed from Rauhut, 1995). (K) Right pubis of *Ingenia*, GI 100/30 (from Barsbold et al., 1990). (L) Right pubis of *Albertosaurus (Gorgosaurus)*, NMC 2120 (from Lambe, 1917).

Possessing a pubic boot at least 30% of the pubic length is considered a synapomorphy of the Carcharodontosauridae by Sereno et al. (1996), although no complete pubis of *Carcharodontosaurus* has been documented. *Allosaurus* has a boot:pubis ratio of 56% (Gilmore, 1920; Madsen, 1976). Percentages much greater than 30% are also obtained for *Herrerasaurus* (Novas, 1993), *Neovenator* (Hutt et al., 1996), and *Albertosaurus* (*Gorgosaurus*) *libratus* (Lambe, 1917:62); values within a few percent of 30% are obtained for *Piatnitzkysaurus* (restored; Bonaparte, 1986), *Edmarka* (Bakker et al. 1992), *Szechuanosaurus zigongensis* (Gao, 1993), *Gasosaurus* (Dong and Tang, 1985), "Brontoraptor" (Siegwarth et al., in press), and *Compsognathus* (Ostrom, 1978); thus, the feature, as defined by Sereno et al. (1996), has arisen several times in the Theropoda. The triangular shape, in distal view, of the pubic boot shared by *Acrocanthosaurus* and *Allosaurus* (Holtz, 1994) is derived with re-

spect to the T-shape in sinraptorids, *Torvosaurus*, and *Metriacanthosaurus* (Currie and Zhao, 1993).

Acrocanthosaurus does not meet the ischial character state of the Coelurosauria, in which the ischium is $\leq 2/3$ the pubic length (Gauthier, 1986; Holtz, 1994). In lateral view, the ischium of *Acrocanthosaurus* is straight, similar to those of *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993), and *Yangchuanosaurus* (Dong et al., 1983); it lacks a marked ventral curvature like *Coelophysis* (Colbert, 1989) and *Dilophosaurus* (Welles, 1984) and does not curve strongly medially as in *Herrerasaurus* (Novas, 1993). It is much more gracile than that of *Metriacanthosaurus* (Walker, 1964). The presence of an obturator process for attachment of the M. puboischiofemoralis externus (Currie and Zhao, 1993), instead of an obturator lamina contiguous with the iliac process, is diagnostic of the Tetanurae, and its proximal placement on the shaft, as in *Acrocanthosaurus*, is diagnostic of all
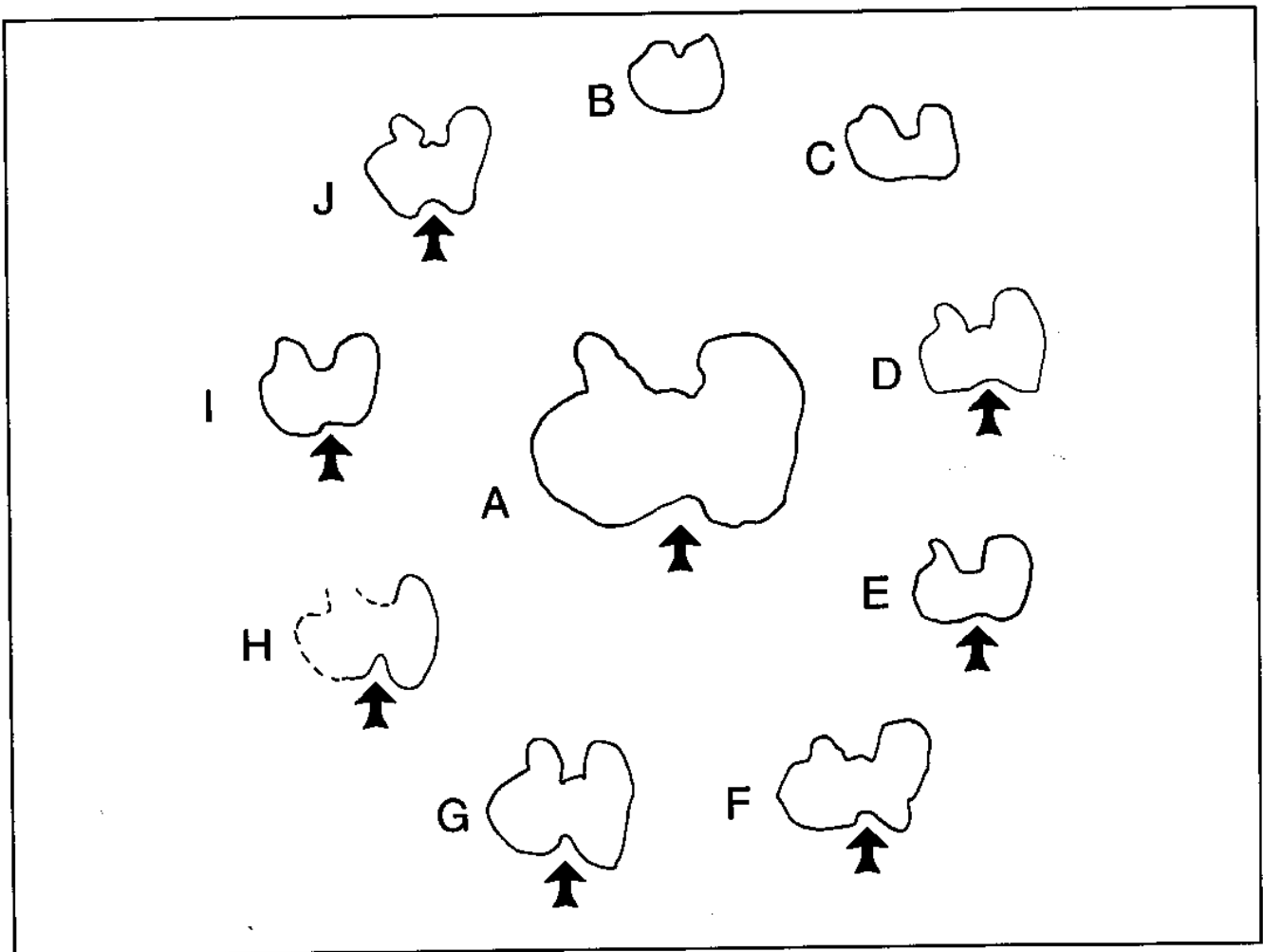
Figure 39. Comparisons of the distal ends of theropod femora in distal view. (A) Left femur of *Acrocanthosaurus*, SMU 74646 2B-2J. (B) Right femur of *Herrerasaurus*, PVSJ 373 (reversed from Novas, 1993). (C) Left femur of *Dilophosaurus*, UCMP 37302 (from Welles, 1984). (D) Left femur of *Megalosaurus*, J13506 (reversed from Huene, 1926). (E) Right femur of *Eustreptospondylus*, OUM 13558 (reversed from Huene, 1926). (F) Left femur of *Sinraptor*, IVPP 10600 (from Currie and Zhao, 1993). (G) Left femur of *Allosaurus*, USNM 4734 (from Gilmore, 1920). (H) Right femur of *Carcharodontosaurus*, IPHG number unknown (reversed from Stromer, 1931). (I) Right femur of *Deinonychus*, ?MCZ 4371 (reversed from Paul, 1988). (J) Left femur of *Albertosaurus*, specimen unknown (from G..Paul, personal communication, 1997). Arrows indicate extensor grooves.

tetanurans more primitive than the Maniraptoriformes (Holtz, 1996a). A distal expansion of the ischium with both caudal and cranial projections as in *Acrocanthosaurus* is a feature seen elsewhere in the Allosauroidea only in *Neovenator*.

The 90° angle between the femoral caput and shaft in *Acrocanthosaurus* is unlike the obtuse angle seen in *Carcharodontosaurus* (Stromer, 1931:fig. 14a). The caput is confluent with the greater trochanter, as in all theropods more primitive than the Maniraptoriformes (Holtz, 1994, 1996a). The morphology of the lesser trochanter in *Acrocanthosaurus* is shared by all allosauroids in being proximally placed (a tetanurine character [Gauthier, 1986]) and not confluent with the greater trochanter (a synapomorphy of the Maniraptoriformes [Holtz, 1996b]).

The ridge for the cruciate ligaments in the flexor groove of the femur of *Acrocanthosaurus* is also known in *Sinraptor* (Currie and Zhao, 1993), *Allosaurus* (Madsen, 1976), *Megalosaurus* (Owen, 1856), and "Brontoraptor," (Siegwarth et al., in press) but is absent in *Eustreptospondylus* and *Carcharodontosaurus* (Stromer, 1931). The deep but narrow extensor groove on the distal femur of *Acrocanthosaurus*, considered diagnostic of the Carnosauria by Molnar et al. (1990) is derived with respect to *Herrerasaurus* (Novas, 1993), ceratosaurians (Molnar et al., 1990), primitive tetanurans such as *Eustreptospondyulus* (Huene, 1926b), *Megalosaurus* (Owen, 1856; Huene, 1926b) and "Brontoraptor" (Siegwarth et al., in press), and all coelurosaurians except *Gallimimus* (Molnar et al., 1990) and tyrannosaurids (Fig. 39).

Cladistic Analysis

A matrix of 48 cranial, 35 axial, and 62 appendicular characters was assembled using traits previously shown to be potentially useful in cladistic analyses of theropods (Gauthier, 1986; Holtz, 1994; Sereno et al., 1994, 1996), and 15 new ones were added. Character state definitions and the matrix are given in Appendices 2 and 3.

Because of the large quantity of missing data from the matrix, more than 1000 equally parsimonious trees (tree length = 467), all with a low consistency index (C.I. = 0.49, R.I. = 0.56), were produced in the first (unrestricted) analysis. These still merit discussion because some consistent and noteworthy features can be seen: a random sample of the allosauroid and immediate outgroup taxa from three of these trees are presented in Figure 40. *Acrocanthosaurus* invariably occurs with other taxa previously included in the Allosauroidea (*Allosaurus, Neovenator, Chilantaisaurus, Saurophaganax, Carcharodontosaurus*, and *Giganotosaurus*), thus indicating that similarities between *Acrocanthosaurus* and tyrannosaurids noted by Bakker et al. (1988) and Britt (1993) are most parsimoniously interpreted as convergent. Specifically, *Acrocanthosaurus* and *Neovenator* frequently occur as closest sister taxa (Figs. 40A, B); *Chilantaisaurus* sometimes occurs in a clade including the former two (Fig. 40B). *Carcharodontosaurus* and *Giganotosaurus* usually pair in a clade (Figs. 40B, C) that also occasionally includes *Chilantaisaurus* (Fig. 40A). *Allosaurus* usually occurs as the immediate outgroup taxon to the aforementioned

allosauroids; the Sinraptoridae (*Sinraptor* + *Yangchuanosaurus*) usually occurs one node further out. A strict consensus tree of the allosauroid taxa produces a giant polytomy and is uninformative.

A second, more restricted analysis was performed, minus all inadequately described taxa. *Herrerasaurus* was retained as the outgroup to all other theropods. Based on the first analysis, the Ceratosauria was removed. To assess the claim of Holtz (1994) that tyrannosaurids are closer to coelurosaurian than allosauroid taxa, the basal coelurosaurian *Ornitholestes* and the highly derived maniraptoriform *Archaeopteryx* were retained in the matrix. Next, all characters with indeterminate states for fewer than two-thirds of the represented taxa were eliminated as uninformative. The resultant 73 characters and matrix are presented in Appendices 2 and 3. The results of the second analysis produced two equally parsimonious trees (tree length = 139, C.I. = 0.71, R.I. = 0.56), differing only in the placement of *Monolophosaurus* relative to the Tyrannosauridae, *Ornitholestes* and *Archaeopteryx* (Fig. 41). The results of this analysis support the conclusion of Sereno et al. (1996) that the closest (well-known) theropod to *Acrocanthosaurus* is *Carcharodontosaurus*, forming the monophyletic clade Carcharodontosauridae. *Allosaurus* is one step removed. One node further out includes the Sinraptoridae (*Sinraptor* + *Yangchuanosaurus*). This node is the Allosauroidea (Currie and Zhao, 1993) and has the same structure (except the exclusion of *Giganotosaurus*) as the Allosauroidea diagnosed by Sereno et al. (1996) using cranial characteristics.

Paleobiogeography

Prior to the occurrence of *Acrocanthosaurus* in the late Aptian (~ 113 Ma), allosauroids are represented in North America by *Saurophaganax* and the unnamed Dinosaur National Monument theropod (Chure and Madsen, 1996) as well as by *Allosaurus* itself, all from the Kimmeridgian-Tithonian Morrison Formation of the western United States. A tibia from the Upper Jurassic of Tanzania called ?*Allosaurus tendagurensis* (Janensch, 1925) represents the group in the Tendaguru fauna. The presence of allosauroids in Asia in the late Middle-early Late (*Sinraptor, Yangchuanosaurus*) and Late (*Szechuanosaurus*) Jurassic (Fig. 42A) and *Piatnitzkysaurus* in the Middle Jurassic of Argentina indicates that allosauroids had attained a wide geographic distribution by Morrison time. Thus, there is a hiatus of approximately 34 million years between *Acrocanthosaurus* and its nearest temporal precursor in North America, during which time the presence of allosauroids in North America has not been documented.

Following Morrison time, allosauroids are poorly represented globally. A possible allosauroid astragalus was reported from the poorly constrained (?Valanginian-?Aptian) Strzelecki Formation of Australia (Molnar et al., 1981, 1985). Fragmentary remains of a possible allosauroid have also been reported from the Valanginian of France (Pérez-Moreno et al., 1993). *Neovenator*, a possible allosaurid, was recovered from poorly constrained (?Barremian-?Aptian) strata of the Isle of

A

Afrovenator
Sinraptor
Yangchuanosaurus
Metriacanthosaurus
Allosaurus
Acrocanthosaurus
Neovenator
Chilantaisaurus
Carcharodontosaurus
Giganotosaurus
Saurophaganax
Gasosaurus

A: (119[0])
B: —
C: 7[0], 16[1], 24[1], 25[1], 31[1], 32[1], (33[4]), 40[1], 49[1], (65[1]),(128[1]), 137[1], 138[0]
D: 2[4], 11[1], 38[0], 50[1]
E: 93[1], 106[2], 111[2], 113[0]
F: (2[3]), 22[1], 23[1], (26[2]),27[1], 28[0], 47[1], 76[1], 78[0], (109[2]), 112[1], 135[1]
G: 19[0], 57[1], 66[2]
H: 121[2]
I: —
J: 2[1], 8[1]

B

Afrovenator
Sinraptor
Yangchuanosaurus
Allosaurus
Acrocanthosaurus
Neovenator
Chilantaisaurus
Carcharodontosaurus
Giganotosaurus
Saurophaganax
Gasosaurus
Metriacanthosaurus

A: (110[2]), (119[1])
B: (55[0])
C: 7[0], 16[1], 24[1], 25[1], 31[1], 32[1], (33[4]), 40[1], 49[1], (65[1]), 66[1], (128[1]), 137[1], 138[0]
D: 2[4], 11[1], 38[0], 50[1], 121[1]
E: 93[1], 108[2], 111[2]
F: 2[3], 22[1], 23[1], (26[2]), 27[1], 28[0], 47[1], 76[1], 78[0], (109[2]), 112[1], 113[0], 135[1]
G: 57[1], 66[2], (121[2])
H: 19[0]
I: 119[2]
J: 2[1], 8[1]

C

Afrovenator
Sinraptor
Yangchuanosaurus
Allosaurus
Acrocanthosaurus
Chilantaisaurus
Neovenator
Carcharodontosaurus
Giganotosaurus
Saurophaganax
Gasosaurus
Metriacanthosaurus

A: (110[2]), (119[1])
B: —
C: 7[0], 16[1], 24[1], 25[1], 31[1], 32[1], (33[4]), 40[1], 49[1], (65[1]), (128[1]), 137[1], 138[0]
D: 2[4], 11[1], 38[0], 50[1]
E: 93[1], 106[2], 111[2], 113[0]
F: (2[3]), 22[1], 23[1], (26[2]), 27[1], 28[0], 47[1], 76[1], 78[0], (109[2]), 112[1], 135[1]
G: 19[0], 57[1], 66[2]
H: 121[2]
I: —
J: 2[1], 8[1]

Figure 40. Random selection of the allosauroid taxa and immediate outgroups from 3 equally parsimonious trees from first 100 trees generated in the unrestricted analysis of phylogenetic relationships of *Acrocanthosaurus*. (A) Tree 150, (B) tree 492, and (C) tree 966. Synapomorphies uniting clades given in table below cladogram: first number is character, number in brackets indicates character state (both listed in Appendices 2 and 3). States given in parentheses include additional character states at less inclusive nodes. Dash indicates that node is supported only by equivocal character states.

Wight, England (Hutt et al., 1996). The large, apparent allosauroid *Chilantaisaurus* occurs in the Aptian-Albian Dshuigou Formation of Inner Mongolia, China (Hu, 1964; Molnar et al., 1990). Thus, although remaining unknown in North America between Morrison time and the late Aptian, allosauroids appear to retain a virtual global distribution throughout the Early Cretaceous (Fig. 42B).

Carcharodontosaurus was originally described from the Albian or Cenomanian Baharije Formation of Egypt (Stromer, 1931); the genus has subsequently been noted from the Cenomanian Kem Kem beds of Morocco (Sereno et al., 1996). Sereno et al. (1996) place the South American *Giganotosaurus* in the Carcharodontosauridae, although the sole published description (Coria and Salgado, 1995) is insufficient to warrant inclusion in the present analysis. *Giganotosaurus* occurs in the Albian or Cenomanian Río Limay Formation of Argentina. Occuring in the Cenomanian, and possibly Albian, *Carcharodontosaurus* and *Giganotosaurus* are younger than the late Aptian *Acrocanthosaurus*. Thus, their common ancestor must have been present by the late Aptian.

Rifting began between North America and Africa in the Middle Jurassic (Scotese, 1993; Smith et al., 1994), so the ancestral North Atlantic ocean made a direct terrestrial migration of carcharodontosaurid taxa from North America (*Acrocanthosaurus*) to Africa (*Carcharodontosaurus*) during the Early Cretaceous impossible. Tectonic support for the severance of a land bridge between North and South America during this time is ambiguous: Anderson and Schmidt (1983) propose that faunal exchange could have occurred across the Chortis microplate throughout the Cretaceous, particularly in the Cenomanian-Maastrichtian, but Pindell and Barrett (1990) found that the Chortis block was not situated far enough south to have served

A

Herrerasaurus
Megalosaurus
Piatnitzkysaurus
Sinraptor
Yangchuanosaurus
Allosaurus
Acrocanthosaurus
Carcharodontosaurus
Monolophosaurus
Ornitholestes
Archaeopteryx
Tyrannosauridae

A: (2[1]), 18[0], 53[1], (61[1]), 65[1], (66[1]), (115[9])
B: (52[2]), 55[2], 62[1], 90[0], 109[1], 123[1]
C: 7[0], 10[1], 24[1], 34[0], 66[1], 78[0], 99[0], (110[2]), 115[0]
D: 2[4], 64[0], 119[1]
E: 22[1], 28[0], 108[2], 109[2], 111[2], 113[0], 116[0]
F: 57[1]

B

Herrerasaurus
Megalosaurus
Piatnitzkysaurus
Sinraptor
Yangchuanosaurus
Allosaurus
Acrocanthosaurus
Carcharodontosaurus
Monolophosaurus
Ornitholestes
Archaeopteryx
Tyrannosauridae

A: (52[2]), 55[2], (62[1]), 65[1], 66[1], 90[0], 109[1], 123[1]
B: 10[1], 24[1], 34[0], 68[1], 78[0], 99[0], (110[2]), 115[0], 116[0]
C: 2[4], 64[0], 119[1]
D: 22[1], 28[0], 108[2], 109[2], 111[2], 113[0]
E: 57[1]

Figure 41. Two equally most parsimonious trees generated in restricted analysis of phylogenetic relationships of *Acrocanthosaurus*. Note that the position of *Acrocanthosaurus* is stable in both trees. Synapomorphies uniting clades given in table below cladogram: first number is character, number in brackets indicates character state (both listed in Appendices 2 and 3). States given in parentheses include additional character states at less inclusive nodes.

as this bridge and that North and South America were separated by the Valanginian (see also Parrish, 1993). Paleocoastline maps of Smith et al. (1994) indicate that seaways separated North and South America since the Middle Jurassic. Scotese (1993) places the termination of North and South American terrestrial connections in the Early Cretaceous.

To account for the phylogenetic closeness of *Acrocanthosaurus* to *Carcharodontosaurus* on continental landmasses that were separate during the Aptian-Cenomanian, and given that *Acrocanthosaurus* is the older of the two taxa, at least two explanations are possible. First, a common allosauroid ancestor of both taxa migrated from North America to Africa (or vice-versa) prior to the separation of those two continents in the Middle Jurassic. This scenario is considered

unlikely, because this ancestor would have to be closer to *Acrocanthosaurus* and *Carcharodontosaurus* than to *Allosaurus* and other Middle and Late Jurassic allosauroids and is currently unknown from any fauna. Alternatively, the common ancestral taxon migrated from North to South America prior to the separation of these two landmasses and then proceeded from South America into Africa.

Additional explanations must be considered if *Giganotosaurus* and *Carcharodontosaurus* stem from a closer common ancestor than either share with *Acrocanthosaurus* and that originated in North America:

1. The common ancestor originated in North America and undertook two separate migrations: one into Africa and one into South America.
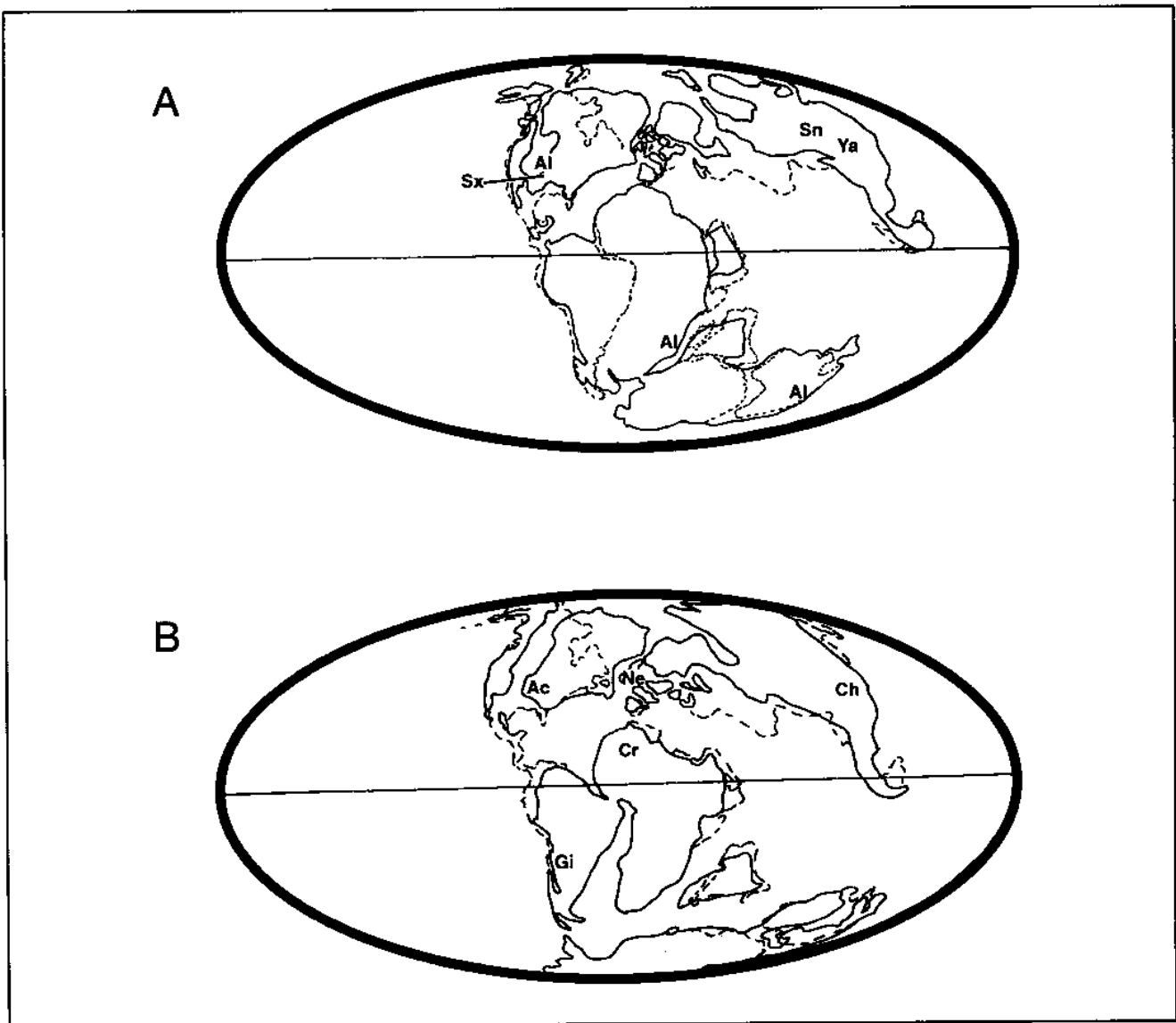
Figure 42. Distributions of allosauroids in the (A) Late Jurassic – early Early Cretaceous (map of continental paleopositions in Tithonian after Smith et al., 1994), and (B) late Early Cretaceous (map of continental paleopositions in Albian after Smith et al., 1994). Ac = *Acrocanthosaurus*, Al = *Allosaurus*, Ch = *Chilantaisaurus*, Cr = *Carcharodontosaurus*, Gi = *Giganotosaurus*, Ne = *Neovenator*, Sn = *Sinraptor*, Sx = *Saurophaganax*, Ya = *Yangchuanosaurus*. Dark lines on both maps indicate paleocoastlines; dashed lines indicate present-day coastlines.

2. The common, ancestral taxon spread from North into South America before the severance of those two continents, giving rise to *Giganotosaurus*, and from there into Africa, producing *Carcharodontosaurus*.

3. The ancestral taxon had a Gondwanan origin and produced the *Carcharodontosaurus-Giganotosaurus* lineage prior to migration into North America, where it produced *Acrocanthosaurus*. This explanation is broader in scope than the two aforementioned because it takes into account the African and Australian purported allosauroid specimens. Smith et al. (1994) find that North America was separated from both Africa and South America since the Callovian (though the similarities of the Kimmeridgian-Tithonian Morrison and Tendaguru faunas seem to imply a more recent connection between North America and Africa), so the possibility that the ancestral taxon is closer to a Gondwanan allosauroid than a Laurasian one is viable.

4. The ancestral taxon had a global distribution and produced *Acrocanthosaurus* in North America and the *Carcharodontosaurus-Giganotosaurus* clade on Gondwana in independent radiations.

At present, none of these explanations is more parsimonious than any other. Still more paleobiogeographic pathways can be considered when the European *Neovenator* and the Asian *Chilantaisaurus* are factored in, including a northern distribution route through Europe. (D. Chure [personal communication, 1997] notes that the original description of the braincase of *Chilantaisaurus* is inaccurate, and the material is probably not allosauroid.)

It is clear that the trend begun in the Middle Jurassic of allosauroids to dominate the niche of large carnivore continued through the Early Cretaceous. Bakker et al. (1990:14) postulated an unspecified "biotic disturbance" and later a "massive dinosaur extinction" (Bakker, 1996:48) at the Jurassic-Cretaceous boundary, at least in North America. The Jurassic-Cretaceous boundary lacks an internationally accepted definition (Remane, 1991; Gradstein et al., 1994, 1995) and is marked globally by a pronounced provincialism of numerous invertebrate taxa induced by the Purbeckian regression (Remane, 1991). Magnetostratigraphic (Ogg et al., 1991) and invertebrate biostratigraphic (Gradstein et al., 1994, 1995) markers are frequently used to place the boundary. Stegosaurids and "megalosaurid" and torvosauroid theropods are not found in North America in the Early Cretaceous, but they are found in the Early Cretaceous of other continents; allosauroid theropods are likewise unaffected given their continued dominance in Early Cretaceous faunas globally. Thus, the "massive dinosaur extinction" at the Jurassic-Cretaceous boundary cited by Bakker (1996) may be more artifactual than real. Only around the beginning of the Late Cretaceous (late Albian-early Cenomanian) do allosauroids seem to become extinct, with the niches of large carnivore being taken over in Laurasia by tyrannosaurids and in Gondwana by abelisauroids, both of which have their earliest occurrences in the Albian or Cenomanian (Bonaparte et al., 1990; Cifelli et al., 1997).

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APPENDIX 1: LIST OF ABBREVIATIONS

Institutional Abbreviations

AMNH = American Museum of Natural History, New York City
BMNH = British Museum of Natural History, London
BYU = Brigham Young University, Provo
CPS = Wyoming-Colorado Paleontographical Society, University of Colorado, Boulder
FWMSH = Fort Worth Museum of Science and History, Fort Worth
GI = Geological Institute, Academy of Sciences of the Mongolian People's Republic, Ulan Bator
IPHG = Institut für Paläontologie, Humbolt Museum, Berlin (collections destroyed)
IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
JM = Jura Museum, Eichstätt
MCZ = Museum of Comparative Zoology, Harvard University, Boston
NMC = National Museum of Canada, Ottawa
OMNH = Oklahoma Museum of Natural History, Norman (formerly MUO)
OUM = Oxford University Museum, Oxford
PVL = Paleontologia de Vertebrados de la Fundación Miguel Lillo, Argentina
PVSJ = Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan
QG = Queen Victoria Museum, Salisbury
SMU = Southern Methodist University, Dallas
TATE = Tate Geological Museum, Casper
UCMP = University of California Museum of Paleontology, Berkeley
USNM = United States National Museum, Smithsonian Institution, Washington, D.C.
UUVP = University of Utah Vertebrate Paleontology Collections, Salt Lake City
YPM = Peabody Museum, Yale University, New Haven

Anatomical Abbreviations

4trc = fourth trochanter
acet = acetabulum
acrp = acromion process
add fos = adductor fossa
alfp = aliform process
ang = angular
axin = axial intercentrum
cap = capitulum/caput
caud art = caudal articular surface
chvf = facet for chevron articulation
crcd art = articular surface for coracoid
cmp = cranial process
crpd foss = cranial peduncular fossa
csgr = costal groove
ctfb = crista tibiofibularis
ctn for = foramen for chorda tympani nerve
diap = diapophysis
dist art = distal articular surface
dorp = dorsal process of articular
ect art = articular surface for ectopterygoid
ecfl = ectopterygoid flange
ectr = ectopterygoid recess
epip = epipophysis
extn gr = extensor groove
flex gr = flexor groove
for = foramen/foramina
foss = fossa
frag = fragment
glen = glenoid
gtrc = greater trochanter
hol = hole/hollow

Anatomical Abbreviations (continued)

idpf = infradiapophyseal fossa/foramen
iprd for = infraprediapophyseal foramen
iptd for = infrapostdiapophyseal foramen
ilip = iliac process
inch = internal narial choana
insp lig = insertion site for interspinous ligamenture
intf = infratemporal fenestra
jugp = jugal process
kn = knob
lclg foss = lateral collateral ligament fossa
lgle = lateral glenoid
ltcd = lateral condyle
ltrc = lesser trochanter
max art = articular surface for maxillary
maxp = maxillary process
mcdf foss = fossa for insertion of M. caudofemoralis
mclg foss = medial collateral ligament fossa
mdcd = medial condyle
medp = medial process
medp = medial process
mfad emin = eminence for insertion of femoral adductor musculature
mgle = medial glenoid
mjug for = medial jugal foramen
mlvs gr = groove for insertion of M. levator scapulae
msym lam = medial symphysial lamina
nsp = neural spine
nutr for = nutrient foramen
obtn = obturator notch
obtp = obturator process
odon = odontoid
orb = orbit
palt fen = palatine fenestra
para = parapophysis
path = pathology
pbif emin = eminence for insertion of ?M. puboischiofemoralis
plpr = palatine pneumatic recess
plrc for = pleurocoelous foramen
plrc foss = pleurocoelous fossa
pock = pocket
posp = postorbital process
posz = postzygapophysis
prat = prearticular
prez = prezygapophysis
prox art = proximal articular surface
ptep = pterygoid process
pubc for = space for pubic foramen
pubp = pubic process
qdjp = quadratojugal process
ram = ramus
rbod = body of rib
retp = retroarticular process
sbad = subacromial depression
sbtf = subtemporal fenestra
scrb = sacral rib
sp = spine
sur = surangular
thmk = ?tooth mark
tran for = transverse foramen
trvp = transverse process
tub = tuberculum
vfor = vertebral foramen
vmpt = vomeropterygoid process
web = capitular-tubercular web

APPENDIX 2: CHARACTER STATES

To determine the states of the characteristics below for each taxon, the resources listed below were consulted. Taxa marked with an asterisk (*) were retained in the more exclusive analysis described in the text.

Herrerasaurus: ischigualastensis: Brinkman and Sues (1987), Novas (1989, 1993), Sereno (1993), Sereno and Novas (1993)

Non-abelisauroid Ceratosauria: Gilmore (1920), Camp (1936), Raath (1977), Welles (1984), Colbert (1989), Rowe (1989), Rowe and Gauthier (1990)

Abelisauroidea: Bonaparte and Novas (1985), Bonaparte et al. (1990), Chatterjee and Rudra (1996)

Torvosaurus tanneri: Galton and Jensen (1979), Britt (1991)

Afrovenator abakensis: Sereno et al. (1994)

Megalosaurus bucklandii: Owen (1855, 1856), Philips (1871), Huene (1926), Waldman (1974), Molnar et al. (1990)

Poekilopleuron bucklandii: Deslongchamps (1838)

Edmarka rex: Bakker et al. (1992), Siegwarth et al. (in press)

"Brontoraptor:" Siegwarth et al. (in press)

Eustreptospondylus oxoniensis: Philips (1871), Huene (1926, 1932), Walker (1964); Molnar et al. (1990)

Piatnitzkysaurus floresi: Bonaparte (1986)

Sinraptor dongi: Currie and Zhao (1993)

Yangchuanosaurus shangyuensis and *Y. magnus*: Dong et al. (1983), Currie and Zhao (1993)

Gasosaurus constructus: Dong and Tang (1985), Molnar et al. (1990)

Szechuanosaurus campi: Dong et al. (1983), Gao (1993)

Metriacanthosaurus parkeri: Huene (1926), Walker (1964)

Cryolophosaurus ellioti: Hammer and Hickerson (1993)

Allosaurus fragilis: Gilmore (1920), Madsen (1976), Molnar et al. (1990)

Acrocanthosaurus atokensis: Stovall and Langston (1950)

Chilantaisaurus maortuensis: Hu (1964), Molnar et al. (1990)

Saurophaganax maximus: Chure (1996)

Monolophosaurus jiangi: Zhao and Currie (1993)

Neovenator salerii: Hutt et al. (1996)

Carcharodontosaurus saharicus: Stromer (1931), Rauhut (1995), Sereno et al. (1995)

Giganotosaurus carolinii: Coria and Salgado (1995)

Sigilmassasaurus brevicollis: Russell (1996)

Baryonyx walkeri: Charig and Milner (1986, 1990)

Ornitholestes hermanii: Osborn (1903, 1916)

Compsognathus longipes: Bidar et al. (1972), Ostrom (1978)

Dromaeosauridae: Colbert and Russell (1969), Ostrom (1969, 1976), Sues (1978), Barsbold (1983), Kirkland et al. (1993), Currie (1995)

Ornithomimosauria: Parks (1928b), Osmólska et al. (1972), Russell (1972), Barsbold and Osmólska (1990), Pérez-Moreno et al. (1994)

Troodontidae: Barsbold (1976, 1983), Barsbold et al. (1987), Osmólska and Barsbold (1990), Currie and Peng (1993), Russell and Dong (1993b)

*Tyrannosauridae: Osborn (1906, 1916), Lambe (1917), Russell (1970), Maleev (1974), Bakker et al. (1988), Molnar et al. (1990), Molnar (1991), Carpenter (1992), Holtz (1994)

Oviraptorosauria: Barsbold (1976, 1983), Barsbold et al. (1990), Smith (1992)

Therizinosauroidea: Barsbold (1976), Barsbold and Perle (1980), Paul (1984), Russell and Dong (1993a), Clark et al. (1994)

Archaeopteryx lithographica and *A. bavarica*: de Beer (1954), Ostrom (1976), Wellnhofer (1974, 1993), Elzanowski and Wellnhofer (1996)

In addition, the following references were consulted for the listed character states:

Characters 2, 4, 10, 12, 13, 14, 33, 34, 35: Witmer (1997)

Characters 57, 60, 61, 65, 69, 71, 80: Britt (1993)

Appendix 2 *(continued)*

Characters marked with an asterisk (*) are those retained for the second (restricted) analysis described in the text.

*(1) Sides of rostrum (maxillae): 0 = Angle towards each other rostrally; premaxillary symphysis parabolic; 1 = Subparallel; premaxillary symphysis U-shaped

Holtz (1994) cited "premaxillary symphysis U-shaped," as a trait diagnostic of the Avetheropoda; Holtz (personal communication, 1997) elucidated that the character was intended to describe the shape of the snout as a whole, not just the premaxillae. This distinction is necessary because some theropods (e.g., oviraptorosaurs) possess inflated premaxillae that do not also describe the angulation of the maxillae to each other.

*(2) State of additional openings within the antorbital fossa rostral to the internal antorbital fenestra: 0 = None; 1 = Promaxillary fenestra and recess only; 2 = Promaxillary and maxillary fenestrae and recesses present; 3 = Promaxillary, maxillary, and excavatio pneumatica present; 4 = Promaxillary, maxillary, excavatio pneumatica, and additional openings present

The problems surrounding the variable nomenclature of openings in the antorbital fossa rostral to the internal antorbital fenestra were detailed by Witmer (1997). Sereno et al. (1996) cite "promaxillary recess extends into maxilla ascending (= anterior) ramus" as a characteristic of the Neotetanurae. As noted by Witmer (1997), by definition, the promaxillary recess (or series of recesses) invades the ascending ramus of the maxilla whenever present and seems to be characteristic of all theropods except *Herrerasaurus*. The presence of a maxillary fenestra (= accessory or subsidiary antorbital fenestra) was used by both Gauthier (1986) and Sereno et al. (1996) as diagnostic of the Tetanurae; a large and round fenestra was cited as a more restrictive characteristic within the unnamed Node 6 of Holtz (1994). However, as noted by Witmer (1997), the term "maxillary fenestra" has been applied to openings that are not the maxillary fenestra *sensu stricto*, thus rendering previous uses of this characteristic dubious. The maxillary fenestra is an opening rostral to the antorbital fenestra within the antorbital fossa. It is differentiable from the promaxillary fenestra; in particular, Witmer (1997) notes that the slit in the antorbital fossa, rostral to the internal antorbital fenestra, in the Ceratosauria is most likely homologous with the promaxillary fenestra and not the maxillary fenestra. Currie and Zhao (1993) cite the presence of more than two openings into the maxillary sinus as diagnostic of the Sinraptoridae, but it is unclear to what extent the numerous smaller openings to which they refer are homologous with, for example, the excavatio pneumatica of Witmer (1997). Although it is conceivable, no confirmed reports exist of theropods that possess a maxillary but no promaxillary fenestra; therefore, those that possess a fenestra that more closely matches the morphology and location of the maxillary fenestra *sensu stricto* are coded as having both a maxillary and promaxillary fenestrae.

*(3) Maxillary tooth row: 0 = Extends caudally to point beneath orbit; 1 = Completely antorbital

This character has been used in numerous analyses (Gauthier, 1986 [Tetanurae]; Currie and Zhao, 1993 [Allosauroidea]; Holtz, 1994 [Tetanurae]; Sereno et al., 1996 [Tetanurae]). An apparent corollary of this is that the jugal process of the maxilla is shortened, and, as a consequence, its articular surface on the jugal is restricted to the rostral end of that element.

*(4) Nasal participates in antorbital fossa: 0 = None or slightly; 1 = Broadly

This character was cited by Sereno et al. (1996) for the Allosauroidea.

*(5) Prefrontal: 0 = Large; 1 = Reduced; 2 = Absent

Presence or absence of the prefrontal bone was used by Gauthier (1986) as a trait of the Maniraptora (= Maniraptoriformes *per* Holtz [1996a]). Absence of the bone, as used here, includes the apparent condition in many derived theropods in which this bone is seamlessly fused to the frontal.

(6) Prefrontal-frontal articulation peg-in-socket: 0 = No; 1 = Yes

This trait was cited by Sereno et al. (1996) for the Tetanurae.

*(7) Ventral extent of postorbital substantially above ventral margin of orbit: 0 = Yes; 1 = No; postorbital process of jugal still tall; 2= No; postorbital process of jugal reduced or absent

This trait refers to whether or not the ventral ramus of the postorbital bone extends as far down as the ventral limit of the orbit. In many cases, it terminates well above this level, where it contacts the postorbital process of the jugal. In other cases, however, either the ventral ramus continues ventrally along the rostral margin of the postorbital process of the jugal or the postorbital ramus of the jugal is greatly reduced or lost entirely, and the postorbital forms the entirety of the bar separating the orbit from the lateral temporal fenestra. Because these are different conditions, this character is expanded here to encompass all possible states. It was originally used by Currie and Zhao (1993) as diagnostic of the Allosauroidea.

*(8) Postorbital-lacrimal contact: 0 = Absent; 1 = Present

In taxa that have lost the prefrontal bone, two morphologies exist to form the dorsal margin of the orbit: either the lacrimal and postorbital processes are expanded to form the roof of the orbit, or the frontal intrudes between the two. As originally used by Sereno et al. (1996) for the Carcharodontosauridae, the postorbital-lacrimal contact was viewed either as "broad" or "small." However, as used here, it is either present or absent; the extent of any contact is not distinguished.

*(9) Suborbital flange on postorbital: 0 = Absent; 1 = Small; 2 = Large

This condition described the presence, on the rostral margin of the postorbital, of a rostrally-projecting eminence that partially divides the orbit into dorsal and ventral parts (though never closing it off entirely). The resultant shape of the orbit has been described as "keyhole-shaped" by numerous authors. The presence of a large process was cited as diagnostic of the Carcharodontosauridae by Sereno et al. (1996).

*(10) Lacrimal pneumatic recess: 0 = Absent; 1 = Present

Although the lacrimal normally houses part of the antorbital fossa (Witmer, 1997), the lacrimal pneumatic recess is, more specifically, one or more excavations (fossa with or without foramina) in the dorsal elbow of the lacrimal, frequently within a lacrimal horn. This is not to be confused with the nasolacrimal canal, which is also located in this region, usually ventral to the pneumatic recess (Witmer, 1997). The presence of the recess was considered useful in diagnosing the Tetanurae by Sereno et al. (1996).

(11) Lacrimal horn height above skull roof: 0 = Nonexistent; 1 = Low; 2 = High

Expansion of the lacrimal dorsally to form a small horn was considered characteristic of the Sinraptoridae by Currie and Zhao (1993); larger horns are formed in other taxa.

*(12) Jugal pneumatic (jugal pneumatic recess present): 0 = No; 1 = Yes

Pneumaticity of the jugal was cited as a diagnostic trait of the Tetanurae by Sereno et al. (1996). Pneumaticity is represented at the surface nominally by the presence of a jugal pneumatic recess, an opening that sits within the caudoventral corner of the antorbital fossa. It leads caudally into the body of the jugal. Its presence was considered diagnostic of the Allosauroidea by Currie and Zhao (1993).

(13) Medial jugal foramen: 0 = Absent; 1 = Present

*(14) Jugal expressed on rim of external antorbital fenestra: 0 = No; 1 = Yes

Holtz (1994) considered the presence of the jugal on the rim of the antorbital fenestra as a characteristic of the Maniraptoriformes.

(15) Length of upper prong of quadratojugal process of jugal with respect to the lower prong: 0 = Subequal; 1 = Upper prong markedly shorter; 2 = Upper prong markedly longer

Virtually all theropods possess a caudally bifurcate jugal, the prongs of which interdigitate with the rostral process of the

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quadratojugal. The length of the upper prong with respect to the lower prong vary between taxa; a shorter upper prong was considered diagnostic of the Allosauroidea by Currie and Zhao (1993).

(16) Quadrate short, with head near level of mid-orbit: 0 = No; 1 = Yes

This state was cited by Sereno et al. (1996) as characteristic of the Allosauroidea.

(17) Fenestration of the quadrate and quadratojugal: 0 = None; 1 = Quadrate-quadratojugal fenestra present; 2 = Quadrate fenestra present

Many theropods possess a small opening in the vicinity of the quadrate and quadratojugal, although terminology applied to this opening has not been consistent. As used here, a quadrate-quadratojugal fenestra is one that is bounded laterally by the quadratojugal and medially by the quadrate; in contrast, an opening that is restricted to the quadrate is a quadrate fenestra. Currie and Zhao (1993) cite the presence of a quadrate-quadratojugal fenestra with an associated sinus as diagnostic of the Allosauroidea.

*(18) Expanded, circular orbit: 0 = Absent; 1 = Present

This trait, noted by Holtz (1994) for the Coelurosauria, separates those theropods with primitive tear-drop, ovoid-, or cartouche-shaped, longer dorsoventrally than rostrocaudally, orbits from those with subcircular orbits, which tend to be larger with respect to the skull as a whole.

(19) Supraoccipital forms part of foramen magnum: 0 = No; 1 = Yes

Molnar et al. (1990) note that, among some members of their Carnosauria, the supraoccipital sends a small, rectangular process ventrally, interceding between the exoccipitals, to form the roof of the foramen magnum.

(20) Parasphenoid capsule: 0 = Not bulbous; 1 = Bulbous

Cited by Holtz (1994) as diagnostic of the Bullatosauria.

(21) Braincase box: 0 = Not open caudally; tubera modestly pronounced; 1 = Open caudally; tubera pronounced and widely separated (basituberal web reduced)

Currie and Zhao (1993) cite "braincase box [has] opened up caudally between tubera, which are no longer pedunculate" as a feature of the Allosauroidea. At issue here is the status of the basal tubera. In primitive Theropoda, the basisphenoid and basioccipital (see character 22) forms a ventral projection rostroventral to the occipital condyle and which walls the basisphenoid recess caudally. This projection normally possesses two slight ventral expansions on either side (the basal tubera) that serve as attachment sites for the M. rectus capitis (= M. longus colli) and M. longissimus dorsi (= M. iliocostalis cervicis capitis) (Bakker et al., 1992). Normally, the tubera are modest expansions, but in many theropods, the basituberal web between them is reduced, resulting in elongate tubera. In these taxa, the tubera also tend to migrate laterally, increasing the width between them, resulting in the openness referred to by Currie and Zhao (1993).

*(22) Basioccipital participation in the basal tubera: 0 = Participates; 1 = Does not participate

Sereno et al. (1996) use the exclusion of the basioccipital from the basal tubera as a diagnostic feature of the Allosauroidea. Lacking basioccipital participation, the basal tubera are formed exclusively by the basisphenoid.

(23) Basisphenoid recess: 0 = No additional foramina; 1 = Small foramina; 2 = Large (pneumatic?) foramina

Pneumaticity of the basisphenoid recess is indicated by the presence, within the larger cavity, of further fossae and/or foramina leading dorsally into the braincase. This trait was considered diagnostic of the Allosauroidea by Currie and Zhao (1993). While theropods primitively lack any additional openings in this recess, Bakker et al. (1988) describe a variety of openings in some more advanced taxa. Very small, usually paired, foramina occur in a few taxa, while larger, more irregular foramina occur in some tyrannosaurids.

*(24) Paroccipital processes strongly downturned: 0 = No; 1 = Yes

Paul (1988) and Currie and Zhao (1993) cite this trait as diagnostic of the Allosauroidea.

(25) Caudoventral limit of exoccipital-opisthotic contacts basisphenoid but separated from basal tubera by notch: 0 = No; 1 = Yes

Currie and Zhao (1993) describe the presence of this notch as characteristic of the Allosauroidea.

(26) Separation of ophthalmic nerve from trigeminal before exiting trigeminal foramen: 0 = Absent; 1 = Incipient; 2 = Complete

Primitively, cranial nerve V (trigeminal) is undivided as it passes through the subcircular trigeminal foramen between the prootic and laterosphenoid. Currie and Zhao (1993) note that, in the Allosauroidea, the trigeminal foramen is partially closed off by a constriction (the incipient condition), which implies that the ophthalmic nerve had begun to separate from the trigeminal prior to its egress through the foramen. This constriction of the trigeminal foramen is thus evidence of this separation. In some later theropods (e.g., tyrannosaurids [Molnar, 1991], the ophthalmic nerve passes through a completely separate foramen from the rest of the trigeminal nerve.

(27) Pneumatic openings associated with internal carotid artery canal: 0 = Absent; 1 = Present

The term "internal carotid artery canal" refers to a deep foramen at the contact of the laterosphenoid and basisphenoid (as described by Molnar [199J] in *Tyrannosaurus rex*). This foramen is overlain by a groove in the laterosphenoid (Molnar, 1991). This trait was cited by Sereno et al. (1996).

*(28) Basipterygoid processes: 0 = Long; 1 = Short

Sereno et al. (1996) use this trait to differentiate the roughly spherical dimensions of the processes in allosauroids from the longer, primitive processes that have cylindrical dimensions.

(29) Palatine morphology: 0 = Subrectangular or trapezoidal; 1 = Tetraradiate; 2 = Triradiate (jugal process absent)

The primitive palatine morphology is a relatively simple subrectangular sheet of bone. In more advanced forms, presumably, the various margins of the sheet are recessed to form a starkly tetraradiate bone. In still more advanced theropods, however, the jugal process of the palatine is lost, resulting in a triradiate element.

(30) Subsidiary palatal fenestra: 0 = Absent; 1 = Present

The reduction in size of the palatine process of the pterygoid coupled with the depression of the lamina that connects the ascending and jugal processes and the reduction of the caudal lamina of the medial process of the palatine form the subsidiary palatal fenestra on the roof of the palate, which Gauthier (1986) considered synapomorphic of the Coelurosauria.

(31) Palatines meet medially: 0 = No; 1 = Yes

Absence of medial contact of the palatines was cited by Rowe and Gauthier (1990) for the Ceratosauria.

(32) Jugal process of palatine expanded distally: 0 = No; 1 = Yes

Sereno et al. (1996) describe the distal end of the jugal process as expanded for the Allosauroidea.

*(33) Palatine pneumatic recess: 0 = None; 1 = Small fossa only; 2 = Small foramen only; 3= Large fossa only; 4 = Large fossa with ≥ 1 foramina

The palatine pneumatic recess is housed on the medial side of the palatine, at the confluence of the vomeropterygoid, maxillary, and jugal processes. Witmer (1997) voiced reservations about the phylogenetic utility of this trait when coded simply as "present" or "absent," but coding for the various conditions seen in theropod taxa can elucidate phylogenetic relationships.

*(34) Ectopterygoid pneumatic recess morphology: 0 = Elongate; 1 = Subcircular

In theropods primitively, the ectopterygoid pneumatic recess is a rostrocaudally elongate, dorsoventrally short opening spanning the ectopterygoid and pterygoid flanges of the ectopterygoid. However, in some derived taxa, the ectopterygoid is inflated dorsoventrally, making the recess much more circular in shape.

(35) Ectopterygoid pneumatic recess extends deeply into jugal process: 0 = No; 1 = Yes

Sereno et al. (1996) cite this as a characteristic of the Neotetanurae.

(36) Rostral end of dentary squared and expanded: 0 = No; 1 = Yes

Sereno et al. (1996) note that the slope of the rostral end of the dentary in the Carcharodontosauridae is more vertical than in other

Appendix 2 *(continued)*

taxa. The square shape is enhanced by a small ventral projection on the rostroventral margin of the dentary.

(37) Dorsoventral height of the surangular: 0 = < 2x the maximum dorsoventral height of the angular; 1 = ≥ 2x the maximum dorsoventral height of the angular

Sereno et al. (1996) diagnose increase in depth of the surangular with respect to the angular as an autapomorphy of the Neotetanurae. They cite this specifically as the cause of reduction in size of the external mandibular fenestra, but the fenestra may remain unchanged while the bones bordering it are increased in dimension. This is an important difference because, even within the Neotetanurae, there is variability in the size of the external mandibular fenestra that has potential phylogenetic significance (see character 38).

(38) External mandibular fenestra: 0 = Large; 1 = Reduced

Madsen (1976) and Currie and Zhao (1993) note that the external mandibular fenestra of *Allosaurus* is smaller relative to the size of the mandible as a whole than in most other theropods.

*(39) Caudal surangular foramen: 0 = Small; 1 = Large

Holtz (1994) noted that the presence of an enlarged surangular foramen was characteristic of theropods in his unnamed Node 16, including ornithomimosaurians, tyrannosaurids, and troodontids.

(40) Splenial with notched rostral margin of internal mandibular fenestra: 0 = Absent; 1 = Present

Sereno et al. (1996) find as an autapomorphy of the Neotetanurae that the splenial contributes to the rostral end of the fenestra. In particular, the splenial ceases to be a simple sheet of bone and become triradiate as the fenestra incises the rostrodorsal margin of the bone.

(41) Ridge dividing mandibular glenoid: 0 = Pronounced; 1 = Reduced

In most theropods, the medial and lateral portions of the mandibular glenoid are separated by a distinct, obliquely-oriented ridge that fits into a corresponding groove between the condyles of the quadrate. Reduction of the ridge would enhance mediolateral motion at the craniomandibular joint.

(42) Articular pneumatic: 0 = No; 1 = Yes

Pneumaticity of the articular is evidenced by expansion of the foramen for the chorda tympani nerve caudal to the medial glenoid and was noted by Molnar (1991) in *Tyrannosaurus rex*.

(43) Retroarticular process of articular: 0 = Absent; 1 = Short; 2 = Long

(44) Broad retroarticular surface of articular facing caudally: 0 = No; 1 = Yes

Initially noted as an autapomorphy of the Neotetanurae by Sereno et al. (1996), this analysis clarifies the trait somewhat by adding the term "broad" to the diagnosis. Without such clarification, the trait is meaningless because, by definition, any three-dimensional object will have a surface, even if only an edge, that faces caudally. However, the intention of Sereno et al. (1996) was undoubtedly to note that in primitive theropods, the articular has only a simple edge that faces caudally, while a much broader, flat surface faces rostromedially. More advanced theropods, particularly those with short or absent retroarticular processes, present a broad, planar face directly caudally or caudoventrally.

(45) Denticulation of tooth carinae contiguous over tip: 0 = Absent; 1 = Present

(46) Premaxillary teeth asymmetrical in cross-section: 0 = No; 1 = Yes, due to migration of rostral carina, tooth remains laterally compressed; 2 = Yes, tooth inflated and D-shaped in cross-section

Asymmetry in cross-section of premaxillary tooth crowns has been most frequently noted in the Tyrannosauridae (as D-shaped), but Holtz (1994) finds it more broadly distributed, characteristic of the Avetheropoda. However, some theropod taxa possess premaxillary teeth that, although not inflated on one side, display asymmetry effected by migration of the rostral carina away from a position antipolar to the mesial carina. The conditions are differentiated here.

*(47) Number of teeth in the premaxilla: 0 = ≤ 4; 1 = 5; 2 = > 5

Theropods primitively possess 4 teeth in the premaxilla. The presence of 5 premaxillary teeth is usually considered a diagnostic trait of the Allosauridae.

(48) Enlarged, fang-like tooth in dentary that inserts into a notch between the premaxilla and maxilla: 0 = Absent; 1 = Present

The absence of this enlarged tooth was cited as a diagnostic character of the Tetanurae by Gauthier (1986).

(49) Atlantal neurapophysis morphology in lateral view: 0 = Not triangular; 1 = Triangular

Currie and Zhao (1993) describe a triangular (in lateral view) atlantal neurapophysis as an autapomorphy of the Allosauroidea that contrasts with the primitive morphology in which there is a subrectangular, elongate, caudally-directed process at the top.

(50) Angular relation of ventral margin of axial intercentrum to ventral margin of axis: 0 = Subparallel; 1 = Tilted strongly dorsally

Currie and Zhao (1993) noted that a strong upward tilt of the axial intercentrum with respect to the axial centrum was characteristic of the Sinraptoridae.

(51) Ventral keel on axis: 0 = Absent; 1 = Present

Currie and Zhao (1993) find that the presence of a ventral keel on the axis is a synapomorphy of the Allosauroidea.

*(52) Axial epipophyses: 0 = None; 1 = Small; 2 = Large

Gauthier (1986) used the presence of large axial epipophyses as a diagnostic trait of the Maniraptora (= Maniraptoriformes *per* Holtz, 1996b).

*(53) Distal end of axial neural spine: 0 = Not expanded; 1 = Expanded

Expansion of the distal end of the neural spine (especially, but not exclusively, laterally) beyond the more proximal portions of the spine, forming a "spine table," was considered a diagnostic trait of the Tetanurae by Gauthier (1986) and Sereno et al. (1996).

(54) Axial neural spine reduced cranially: 0 = No; 1 = Yes

Currie and Zhao (1993) use the reduction of the axial neural spine as a trait of the Allosauroidea. Neural spine reduction occurs independent of the presence or absence of a "spine table" (see character 53). This refers to the lack of any expansion of the spine that extends cranial to the prezygapophyses.

*(55) Cervical vertebrae: 0 = Not opisthocoelous; 1 = Weakly opisthocoelous; 2 = Strongly opisthocoelous

*(56) Cervical vertebral cranial facets reniform (= kidney-shaped): 0 = No; 1 = Yes

Gauthier (1986) noted that the cranial articular facet of the cervical vertebrae in members of the Coelurosauria are indented below the vertebral foramen, giving the facet a kidney-shape. This condition presages full heterocoely seen in Aves and is different from the state described in character 57 (see below).

*(57) Caudal cup of cervical vertebrae reniform (= kidney-shaped) and ≥ 20% wider than tall: 0 = No; 1 = Yes

Sereno et al. (1996) believed that lateral expansion and dorsoventral compression of the caudal articular facet of the cervical vertebrae, coupled with indentation of the facet beneath the vertebral foramen (giving the face a kidney-shape) was diagnostic of the Carcharodontosauridae. Though numerous theropods are characterized by having centrum facets that are indented below the vertebral foramen, the facets are typically otherwise subcircular In carcharodontosaurids, the centrum face is at least 20% wider mediolaterally than tall dorsoventrally, giving the diagnostic reniform shape.

*(58) Number of pleurocoelous fossae in postaxial cervical vertebrae: 0 = None; 1 = One; 2 = Two

Rowe and Gauthier (1990) and Holtz (1994) both cite the presence of "two pairs of pleurocoels" on the post-axial cervical vertebrae to be diagnostic of the Ceratosauria. However, neither stated specifically whether this referred to the number of fossae, foramina, or both. Investigation of the literature reveals that the ceratosaurian condition is multiple fossae, which may or may not include foramina. Across the Theropoda, the number of fossae present seems to be more diagnostic than the number of foramina within them, so this diagnosis focuses only on the fossae.

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(59) Cervical vertebral transverse processes: 0 = Ventral and lateral projection; 1 = Predominately lateral projection

Primitively, theropods have short transverse processes with a small degree of lateral projection, but some more advanced theropods have greatly enlarged transverse processes that have a more lateral than ventrolateral orientation.

(60) Cervical prezygapophyseal morphology: 0 = Planar; 1 = Flexed

Gauthier (1986) described the morphology of the prezygapophyses on the cervical vertebrae of the Coelurosauria as "flexed" in reference to the fact that the facets are smoothly curved such that the smaller medial portion faces medially while the larger lateral portion faces dorsally. Holtz (1994) considered this character more restrictive and diagnostic of the Maniraptoriformes.

*(61) Post-axial cervical pleurocoel: 0 = Absent; 1 = Fossa only; 2 = Fossa with one foramen; 3 = Fossa with > 1 foramina (dividing laminae present); 9 = Not applicable

*(62) Interior of cervical vertebrae type: 0 = No interior spaces (apneumatic); 1 = Simple (camerate); 2 = Complex (camellate)

Britt (1993) suggests that camerate and camellate vertebrae types develop exclusively of each other, and one is not necessarily directly derived from the other.

(63) Ventral processes (= hypapophyses) on caudal cervical and cranial dorsal vertebrae: 0 = Absent; 1 = Present on cranial dorsals only; 2 = Present on caudal cervicals and cranial dorsals

The presence of ventral processes on vertebrae from the cervicothoracic region, as attachments for a powerful M. longus colli ventralis, was considered a diagnostic trait of the Maniraptora (= Maniraptoriformes *per* Holtz, 1996b).

*(64) 10th presacral vertebra incorporated into dorsal region: 0 = No; 1 = Yes

Currie and Zhao (1993) consider the inclusion of the 10th presacral vertebra into the dorsal region, as determined by associated rib morphology, a diagnostic trait of the Allosauroidea. As pointed out by Welles (1984), transition between cervical and dorsal vertebrae is difficult to determine when ribs are not directly associated with the vertebrae, and instead used the position of the parapophysis on the vertebra to determine the position of the element.

*(65) Cranial dorsal vertebrae opisthocoelous: 0 = No; 1 = Yes

*(66) Dorsal vertebral pleurocoel: 0 = None; 1 = Pronounced on cranial dorsals; 2 = Pronounced on all dorsals

Holtz (1994) cited the presence of a pleurocoel on the dorsal vertebrae to be an autapomorphy of the Tetanurae. However, as in character 58, no specification was provided as to what constitutes a pleurocoel. In this analysis, the nature of the pleurocoel is elucidated: fossae refer to relatively shallow, usually broad indentations that do not penetrate deeply to the interior of the centrum; foramina are deep, usually restrictive in size, and do invade the interior of the bone.

(67) Dorsal vertebral parapophyses reduced in lateral extent: 0 = No; 1 = Yes

In the Ceratosauria, the parapophyses project far laterally, upwards of one-half the length of the transverse process. As noted by Currie and Zhao (1993), the parapophyses of the Allosauroidea are shorter.

*(68) Caudal dorsal vertebral neural spines inclined cranially: 0 = No; 1 = Yes

In primitive theropods, the neural spines of the caudal dorsal vertebrae are unremarkable in that they are either vertical or inclined slightly caudally with respect to the horizontal axis of the centrum. However, in many allosauroids, the neural spines of the caudal dorsals have a tendency to incline cranially to varying degrees.

*(69) Presacral vertebral column reduced in length with respect to femoral length: 0 = No; 1 = Yes

Holtz (1994) perceived that, in the Tetanurae, the presacral vertebral column was reduced in length with respect to the femur. This likely is, at least in part, accomplished by the shortening of each

cervical vertebral centrum, which are very long in the Ceratosauria, as well as the relative decrease in length of the femur with respect to the lower hindlimb elements among the Tetanurae (q.v. Gatesy and Middleton, 1997).

*(70) Sacral vertebrae pleurocoelous: 0 = No; 1 = Yes

Possession of either or both pleurocoelous fossae and foramina constitutes "pleurocoelous" in this trait.

(71) Synsacrum: 0 = Absent; 1 = Present

Rowe and Gauthier (1990) use the presence of a synsacrum as an synapomorphy of the members of the Ceratosauria, with a convergence in the Ornithurae.

*(72) Pleurocoels of the proximal caudal vertebrae: 0 = Absent; 1 = Fossa only; 2 = Fossa with foramina

Sereno et al. (1996) cite the existence of pleurocoels on the proximal caudal vertebrae as a diagnostic trait of the Carcharodontosauridae. However, as before (characters 58 and 66), the use of the term "pleurocoel" does not differentiate between fossae and/or foramina. Distinction is made in this analysis.

(73) Ventral groove (= double ventral keel) on proximal caudals: 0 = Absent; 1 = Present

Rowe and Gauthier (1990) propose that the presence of the groove may be a definitive feature of the Ceratosauria. In contrast, many other theropods possess a groove only on more distal caudals.

(74) Subsidiary foramina in proximal and distal excavations of caudal vertebral neural spines: 0 = Absent; 1 = Present

(75) Paired cranial and caudal processes at chevron bases: 0 = Absent; 1 = Present

Sereno et al. (1996) find the presence of paired processes to be a synapomorphy uniting members of the Tetanurae.

(76) L-shape in distal chevrons: 0 = Absent; 1 = Present

The presence of this character was given as diagnostic of the Neotetanurae by Sereno et al. (1996).

(77) Transition point pronunciation: 0 = Graded; 1 = Pronounced

Gauthier (1986) emphasized the idea that the Tetanurae differ from primitive theropods in that the point at which the transverse processes and neural spines disappear and prezygapophyses become significantly elongate occurs abruptly, over a short sequence of vertebrae, whereas it occurs over a longer succession of several vertebrae in more primitive theropods.

*(78) Number of caudal vertebrae with transverse processes (= transition point close to base of tail): 0 = > 15; 1 = ≤ 15

Gauthier (1986) cited the position of the transition point (see character 77) in the Maniraptora (= Maniraptoriformes *per* Holtz, 1996b) close to the base of the tail (circa caudal 15), but Holtz (1994) and Sereno et al. (1996) find this state occurs, less restrictively, among the Coelurosauria.

(79) Cervical rib relation to centra in adults: 0 = Not fused; 1 = Fused

Fusion of the ribs to the centra was cited by Gauthier (1986) as diagnostic of the Coelurosauria.

(80) Cranial processes on cervical ribs: 0 = Short or absent; 1 = Elongate

The term "elongate," as used here, refers specifically to processes that protrude beyond the cranial facet of the cervical centrum to which it articulates.

(81) Pneumatic excavations on cervical rib heads: 0 = Absent; 1 = Present

(82) Aliform process at base of cranial cervical rib shafts: 0 = Absent; 1 = Present

(83) Medial element of gastralia composed of: 0 = Single element; 1 = Two overlapping elements

*(84) Pronounced notch separating acromial process of scapula and coracoid: 0 = Absent; 1 = Present

*(85) Elongate scapular blade set off from glenoid and acromial process: 0 = Grades smoothly; 1 = Abrupt transition

Currie and Zhao (1993) find that the sudden transition from dorsoventrally tall acromial process to dorsoventrally narrow scapular blade is an autapomorphy of the Allosauroidea. Stated another

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way, the caudal margin of the acromial process is closer to perpendicular to the dorsal margin of the scapular blade in allosauroids than in other theropods, where the caudal margin of the acromion slopes much less steeply, and over a craniocaudally longer distance, into the dorsal margin of the blade.

(86) Scapular blade strap-like: 0 = No; 1 = Yes

Gauthier (1986) uses the strap-like (= dorsoventrally narrow and with roughly parallel dorsal and ventral margins) morphology of the scapular blade as a diagnostic characteristic of the Tetanurae.

(87) Mid-shaft expansion on scapular blade: 0 = Absent; 1 = Present

(88) Distal end of scapula possesses: 0 = Large expansion; 1 = Slight or no expansion

Currie and Zhao (1993) note that the lack of any distal expansion of the scapular blade is characteristic of the Sinraptoridae. A "large" expansion is one that is subequal in width to the proximal end of the scapula.

*(89) Coracoid caudoventral (= acrocoracoid) process placement with respect to glenoid diameter: 0 = ≈ Same level; 1 = Protrudes markedly caudoventral to the glenoid

The caudoventral margin of the coracoid, cranioventral to the glenoid, is primitively roughly contiguous with the glenoid itself. Some theropods develop a longer process of the coracoid in front of the glenoid that projects caudoventrally beyond the level of the glenoid. Gauthier (1986) introduced this character as one diagnostic of the Tetanurae; it was subsequently cited by Holtz (1994) for the Avetheropoda and Sereno et al. (1996) for the Neotetanurae. Once developed, the caudoventral process of the coracoid becomes much longer with respect to the glenoid diameter in the Coelurosauria than in more primitive theropods (Sereno et al., 1996).

*(90) Coracoid morphology in lateral view: 0 = Not rectangular; 1 = Subrectangular

Gauthier (1986) notes that the cranioventral margin of the coracoid forms a distinct arc in lateral view in primitive theropods, but members of the Maniraptora (= Maniraptoriformes *per* Holtz, 1996b) have a much straighter cranioventral margin, that gives the coracoid overall (excepting the caudoventral process; see character 89) a subrectangular morphology.

(91) Furcula: 0 = Absent; 1 = Present

The presence of coossified clavicles to form a furcula was considered diagnostic of the Coelurosauria by Gauthier (1986) but of the less-restrictive Neotetanurae by Sereno et al. (1996).

(92) Ossified sternal plates fused in adults: 0 = No; 1 = Yes; 9 = Not applicable

Of those theropods that possess ossified sternal plates, Gauthier (1986) considered the fusion of the paired plates into a single sternum autapomorphic for the Coelurosauria.

*(93) Humerus morphology in cranial view: 0 = Straight; 1 = Sigmoid

*(94) Ulna bowed strongly caudally: 0 = No; 1 = Yes

Both Gauthier (1986) and Holtz (1994) cite the caudal curvature of the ulna to be a synapomorphy of theropods within the Maniraptora (= Maniraptoriformes *per* Holtz [1996b]). This contrasts with the primitive condition in which the ulna is straight.

*(95) Ratio of manus length:length of radius + humerus: 0 = < 2/3; 1 = ≥ 2/3

Gauthier (1986) notes that, in members of the Tetanurae, the maximum length of the manus was at least 2/3 the cumulative lengths of the humerus and radius, providing larger mani than those possessed by primitive theropods.

(96) Articular facets on conjoined distal carpals 1 and 2 (= "semilunate" carpal): 0 = None or proximal only (not true "semilunate" carpal); 1 = Proximal and distal facets (true "semilunate" carpal)

The Maniraptora (= Maniraptoriformes *per* Holtz [1996b]) possess a large, half-moon-shaped carpal element that allowed for enhanced flexibility of the wrist. Ostrom (1974) and Gauthier (1986)

decided that this element was homologous with the primitive, unfaceted radiale, but Tarsitano (1991) and Padian (1997) both conclude that the element instead is a maniraptoriform neomorph arising from the fusion of the first and second distal carpals. The three facets developed include one proximal facet for a proximal carpal (the radiale), and two distal facets for metacarpals I and II. In contrast to Gauthier, Sereno et al. (1994) find that the development of the proximal facet, for the radiale, to be present in a much broader spectrum of theropods, the Tetanurae.

*(97) Proximal ends of metacarpal I closely appressed to metacarpal II for at least half the length of metacarpal II: 0 = No; 1 = Yes

While the proximal ends of metacarpals I and II in primitive theropods (and theropod outgroups) overlap, Gauthier (1986) found that, in the Tetanurae, they are in close contact over a much larger area: at least half the length of metacarpal II. Holtz (1994) found this trait to characterize a more restrictive group, the Avetheropoda. The state presumes that the digits of a tridactyl theropod manus are I, II, and III, as opposed to II, III, and IV, which may be incorrect (Tarsitano and Hecht, 1980; Thulborn and Hamley, 1982; Hinchliffe and Hecht, 1984; Thulborn, 1993). All subsequent manus characters used in this analysis view the tridactyl theropod manus as retaining digits I, II, and III, which is supported by the manus digital formula of *Herrerasaurus* (Sereno, 1993).

*(98) Ratio of metacarpal I length:metacarpal II length: 0 = > 1/3; 1 = ≤ 1/3

Holtz (1994) cites the reduction in length of the first metacarpal, so that it is less than or equal to 1/3 the length of the second, as an autapomorphy of the Maniraptora (= Maniraptoriformes *per* Holtz [1996b]).

*(99) Metacarpal III long and slender: 0 = No; 1 = Yes

This characteristic was used by both Gauthier (1986) and Holtz (1994) for the Maniraptora (= Maniraptoriformes *per* Holtz [1996b]). Sereno et al. (1996) quantify the adjective "long" by citing that the shaft diameter of metacarpal III must be ≤ 50% of the diameter of the shaft of metacarpal II; they find this a diagnostic trait of the Tetanurae.

*(100) Metacarpal IV: 0 = Retained; 1 = Lost

Gauthier (1986) cited the absence of manual digit IV as a diagnostic trait of the Tetanurae.

*(101) Ratio of forelimb length:presacral vertebral column; manus length with respect to pes length: 0 = < 75%; pes greater; 1 = ≥ 75%; manus and pes subequal

According to Gauthier (1986), members of the Maniraptora (= Maniraptoriformes *per* Holtz, 1996b) share a greatly elongate forelimb (≥ 75% of the length of the entire presacral vertebral column). As a corollary to this, the manus is subequal in length to the pes.

*(102) Hook-like, ventrally-oriented process on cranioventral margin of ilium, forming preacetabular notch: 0 = Absent; 1 = Present

*(103) Pronounced ridge on lateral side of ilium:

The primitive theropod ilium is unadorned laterally, but in several more derived theropods, a ridge develops on the lateral side, originating above the acetabulum, that divides the lateral surface of the iliac blade into pre- and postacetabular fossae.

*(104) Caudodorsal margin of ilium morphology in lateral view: 0 = Subvertical; 1 = Angled caudoventrally

In the Saurischia, primitively, the entire dorsal margin of the ilium lies roughly along the same more or less horizontal line. As noted by Gauthier (1986) and Holtz (1994) in the Maniraptora (= Maniraptoriformes *per* Holtz [1996b]), the caudodorsal margin the ilium angles caudoventrally, while the craniodorsal margin remains roughly horizontal.

*(105) Iliac blades contact dorsally: 0 = No; 1 = Yes

Contact of both iliac blades along a sagittal plane was considered a diagnostic characteristic of the unnamed Node 16 of Holtz (1994).

(106) Pubic peduncle of ilium twice as long craniocaudally as mediolaterally: 0 = No; 1 = Yes

This was initially diagnosed by Sereno et al. (1996) for the Neotetanurae.

(107) Iliac-ischial articulation much smaller than iliac-pubic articulation: 0 = No; 1 = Yes

Appendix 2 *(continued)*

Reduction of the pubic peduncle was noted by Sereno et al. (1996) for the Tetanurae.

*(108) Obturator opening on pubis: 0 = Foramen; 1 = Incipient Notch; 2 = Notch

Holtz (1994) found the complete loss of the obturator foramen to characterize the Avetheropoda, while Sereno et al. (1996) found it characterizes the Coelurosauria.

*(109) Morphology of pubes in lateral view: 0 = Curve caudally; 1 = Straight; 2 = Curve cranially; 3 = Retroverted

*(110) Distal opening on pubes: 0 = None; 1 = Pubic notch present; 2 = Pubic foramen present

The pubes of primitive theropods are fused medially for most of their length. However, the distal ends are unfused; thus, a notch that is open ventrally exists between them. In more derived theropods, the distal ends of the pubes are fused to each other. However, the medial symphysial laminae are reduced in some advanced forms, particularly proximal to the distal ends, where they diverge, creating a foramen bounded proximally by the conjoined laminae and distally by the distal fusion of the pubes.

*(111) Distal pubis (length): 0 = Not significantly expanded; 1 = Slightly expanded (= 30% pubis length); 2 = Greatly expanded (>> 30% pubis length)

Significant expansion of the distal ends of the pubes (no proportions given) are cited as autapomorphic for restricted groups of theropods (Tetanurae for Gauthier [1986] and for the Tetanurae Avetheropoda for Holtz [1994]). A pubic boot that is at least 30% the length of the entire pubis was considered an autapomorphy of the Carcharodontosauridae by Sereno et al. (1996).

(112) Conjoined pubic boots morphology in distal view: 0 = Not triangular; 1 = Triangular; 9 = Not applicable

Holtz (1994) united *Acrocanthosaurus* and *Allosaurus* in part with the synapomorphy of fused pubic boots that are triangular (with the apex of the triangle directed caudally) in distal view.

*(113) Cranial projection of pubic boot compared to the caudal projection: 0 = Large; 1 = Small or absent; 9 = Not applicable

Reduction of the cranial portion of the boot was cited as an autapomorphy of the Maniraptora by Gauthier (1986).

*(114) Obturator opening on ischium: 0 = None (unbroken lamina); 1 = Obturator foramen; obturator process absent; 2 = Obturator notch; obturator process present

Gauthier (1986) and Sereno et al. (1996) cite the presence of the coupled notch and process as diagnostic of the Tetanurae; Currie and Zhao (1993) found it diagnostic of the Allosauroidea.

*(115) Obturator process of ischium placement: 0 = Proximal; 1 = Distal; 9 = Not applicable

Migration of the obturator process towards the proximal end of the ischium was considered diagnostic of the Maniraptora (= Maniraptoriformes *per* Holtz [1996]) by Gauthier (1986).

*(116) Ischial obturator process morphology: 0 = Not triangular; 1 = Triangular; 9 = Not applicable

Primitively, the obturator process of the ischium had a quadrangular shape, but more derived theropods, the Coelurosauria (Sereno et al., 1996) reduced it to a triangular morphology.

*(117) Ratio of ischium length: length of pubis: 0 = > 2/3; 1 = ≤ 2/3

Whereas in most primitive theropods the ischium to be subequal in length to the pubis, in the Coelurosauria (Gauthier, 1986; Holtz, 1994) the length of the ischium is reduced to the point where it is ≤ 2/3 the length of the pubis.

*(118) Fusion of distal halves of ischia: 0 = Absent; 1 = Present

*(119) Significant distal ischial expansion: 0 = Absent; 1 = Present, but not boot-shaped; 2 = Present and boot-shaped

As with the pubic boot (see character 111), an ischial boot is defined as an expansion predominantly in the cranial and/or caudal directions whose axis is angled sharply from the long axis of the shaft.

(120) Pelvic girdle coossified in adults: 0 = No; 1 = Yes

Gauthier (1986) and Holtz (1994) noted that, in the Ceratosauria, the elements of the pelvic girdle become coossified in adults.

*(121) Angle of femoral caput to shaft in cranial or caudal view: 0 = << 90°; 1 = ≈ 90°; 2 = >> 90°

*(122) Mound-like greater trochanter: 0 = Absent; 1 = Present

In the Archosauria primitively, the greater trochanter and the femoral caput are confluent, and there is no real distinction between them save the rugosity on the trochanter developed along with muscle insertion. However, a synapomorphy uniting theropods in the Coelurosauria is the development of a distinct eminence at the greater trochanter, making it more distinct from the caput (Gauthier, 1986).

*(123) Deep notch separating greater from lesser trochanter: 0 = Absent; 1 = Present

The enlargement of a proximally-placed lesser trochanter was considered an autapomorphy of the Tetanurae by Gauthier (1986); correlative with this enlargement was the development of a highly distinct notch separating the lesser from the greater trochanter. However, a synapomorphy uniting many advanced theropods into the Maniraptora (= Maniraptoriformes *per* Holtz [1996b]) was the loss of this deep groove and the near-confluence of the lesser and greater trochanters.

*(124) Lesser trochanter placement: 0 = Distal; 1 = Proximal

The lesser trochanter can be situated in one of two positions: distal, defined as having both its origin and distal end situated well below the dorsal margin of the head, or proximal, defined as having its origins at the same level or above where the caput angles from the shaft.

*(125) Lesser trochanter morphology: 0 = Shelf; 1 = Non-aliform process; 2 = Aliform

In the Theropoda primitively, the lesser trochanter is a simple shelf of bone. Some slightly more advanced theropods elongate the trochanter somewhat to form a small process that is pointed at its distal end. Gauthier (1986) and Sereno et al. (1996) find that an aliform (= wing-shaped) process (one that is elongate, craniocaudally broad, and subrectangular in lateral view) is characteristic of the Tetanurae. As noted by Rowe and Gauthier (1990), a lesser trochanteric shelf is present in some members of the Ceratosauria, but its distribution is apparently broader than that, because the shelf is also present in *Herrerasaurus*.

*(126) Femoral fourth trochanter: 0 = Robust; 1 = Weak; 2 = Absent

Both Gauthier (1986) and Sereno et al. (1996) found that the fourth trochanter was weakly developed or entirely absent in the Coelurosauria.

(127) Extensor groove on femur: 0 = Absent; 1 = Shallow and mediolaterally broad; 2 = Deep and mediolaterally narrow

The extensor groove (= sulcus intercondylaris, in part) of the femur, located on the cranial side of the distal end of the femur, between the crista tibiofibularis and the bulge of the medial condyle, varies in the degree of its development within the Theropoda. It is completely absent primitively; somewhat more derived theropods possess a shallow groove. Further derived taxa possess a very deep and pronounced groove, as was noted by Molnar et al. (1990) as a feature of their Carnosauria.

(128) Ridge for cruciate ligaments in flexor groove: 0 = Absent; 1 = Present

In distal view, the flexor groove is primitively U-shaped, but in some derived taxa, it becomes more W-shaped due to the presence of a low ridge flooring the groove to which the cruciate ligaments attached.

(129) Sulcus at base of crista tibiofibularis: 0 = Absent; 1 = Present

Rowe and Gauthier (1990) noted that the members of the Ceratosauria are united by the presence of a pronounced sulcus on the ventrolateral side of the crista tibiofibularis.

(130) Incisura tibialis (= fibular fossa) occupies all of medial aspect of proximal end of tibia: 0 = No; 1 = Yes

Sereno et al. (1996) note that a synapomorphy uniting theropods into the Coelurosauria is an expansion of the incisura tibialis (for passage of a tendon of the M. tibialis cranialis [Baumel and Witmer, 1993]) on the medial side of the proximal end of the tibia (seen in

Appendix 2 *(continued)*

proximal view) to span the entire medial side. In less derived theropods, the incisure is present but more restricted, and occupies only a portion of the medial side.

(131) Crista fibularis: 0 = Absent; 1 = Present

Holtz (1994) found that the presence of a crista fibularis on the tibia for added bracing of the fibula was an autapomorphy of the Tetanurae.

(132) Distal end of tibia backs calcaneum: 0 = No; 1 = Yes; 9 = Not applicable (calcaneum lost)

In primitive theropods, the calcaneum articulates caudodorsally with the fibula exclusively, but Sereno et al. (1996) find that, in the Tetanurae, the calcaneum is backed in part by the tibia. This change is brought about in part due to the reduction in size of the distal end of the fibula, that was listed as a separate character by Sereno et al. (1996).

*(133) Astragalus and calcaneum fused to each other and to tibia: 0 = No; 1 = Yes

The formation of an astragalocalcaneum, plus fusion of this element to the distal end of the tibia, forming a functional tibiotarsus, was used by Rowe and Gauthier (1990) as an autapomorphy of the Ceratosauria (convergent with ornithurine birds).

(134) Distal end of fibula: 0 = Expanded (≥ 2x the craniocaudal width at midshaft); 1 = Reduced (≤ 2x the craniocaudal width at midshaft)

Sereno et al. (1996) cited the reduction in size of the distal end of the fibula as a trait of the Tetanurae.

*(135) Ratio of height of ascending process of astragalus:length of epipodium: 0 = < 1/6; 1 = 1/6 - 1/4; 2 = ≥ 1/4

Holtz (1994) twice cited the length of the ascending process of the astragalus as a phylogenetically meaningful characteristic: once, uniting his unnamed Node 6, in which the ascending process is > 1/6 the length of the epipodium, and again as an autapomorphy of the Coelurosauria, where the process attains a height > 1/4 that of the epipodium. The three possible states are combined here into one character with multiple states. Both Gauthier (1986) and Sereno et al. (1996) cite the increase in both height and width of the ascending process of the astragalus to be characteristic of the Tetanurae.

(136) Astragalar condyles oriented: 0 = Ventrally; 1 = Cranioventrally

As noted by Sereno et al. (1996), in the Tetanurae, the condyles have a marked cranioventral orientation.

(137) Horizontal groove across craniodorsal margin of astragalar condyles: 0 = Absent; 1 = Present

Both Holtz (1994) and Sereno et al. (1996) find that the presence of a distinct groove on the craniodorsal face of the astragalus is a diagnostic character of the Tetanurae.

(138) Metatarsal I more on caudal than medial side of metatarsal II: 0 = No; 1 = Yes; 9 = Not applicable (metatarsal I lost)

Gauthier (1986) found that the plesiomorphic position of metatarsal I in theropods was medial or slightly caudomedial to metatarsal II, but that the element had migrated to a strongly caudomedial or almost entirely caudal position with respect to its neighboring element in the Coelurosauria.

(139) Metatarsal I reduced with respect to other metatarsals: 0 = No; 1 = Yes

Gauthier (1986) found the reduction in length of metatarsal I to be a trait diagnostic of the Tetanurae.

*(140) Participation of metatarsals II and IV more strongly in ankle; metatarsal III pinched out proximally: 0 = Subequal to metatarsal III/no; 1 = >> metatarsal III/yes

The ankle joint of the Saurischia, primitively, involves primarily the distal tarsals and the proximal end of metatarsal III — the proximal ends of metatarsals II and IV are smaller than that of III in proximal view. However, the proximal end of metatarsal III is reduced somewhat, and pinched to varying degrees (see character 141) between II and IV, which, as a result, contribute to the ankle joint to a significantly larger degree. This was noted by both Gauthier (1986) and Sereno et al. (1996) as a characteristic of the Tetanurae.

*(141) Metatarsal III morphology in proximal view: 0 = Not hourglass-shaped; 1 = Hourglass-shaped; 2 = Barely or not visible (pinched out before reaching proximal end)

Sereno et al. (1996) note that a slight mediolateral compression of the proximal end of metatarsal III, giving that element an hourglass shape in proximal view, is characteristic of the Tetanurae. In still more derived theropods, metatarsal III is strongly reduced or entirely absent at the proximal end of the metatarsus — this is the arctometatarsalian condition described by Holtz (1994).

(142) Ratio of length of metatarsal V:length of metatarsal IV: 0 = ≥ 1/2; 1 = < 1/2

*(143) Metatarsus deeper craniocaudally than mediolaterally: 0 = No; 1 = Yes

Holtz (1994) considered the greater craniocaudal than mediolateral dimension of the metatarsus a diagnostic trait of the Arctometatarsalia.

(144) Tarsometatarsus: 0 = Absent; 1 = Present

Rowe and Gauthier (1990) cite the fusion of distal tarsals II and III to their respective metatarsals, forming a tarsometatarsus, to be characteristic of the Ceratosauria (convergent in ornithurine birds).

(145) Ratio of length of pedal digit I phalanges 1+2:length of pedal digit III phalanx: 0 = > 1; 1 = ≤ 1

The high degree of reduction of pedal digit I in the Neotetanurae, resulted in the combined lengths of the phalanx and ungual of digit I being roughly equal in length to the first phalanx of digit III (Sereno et al., 1996).

APPENDIX 3: PHYLOGENETIC DATA MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Herrerasaurus	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0
Ceratosauria	0	1,3	0	0	0	0	0,1	0	0	0,1	0,2	0	0	0,1	0	0	1	0	0	0
Abelisauroidea	0	1	0,1	1	2	0	0	1	2	0	0	0	0	1	0	0	0	0	?	0
Torvosaurus	?	1	?	?	?	?	?	?	0	1	?	0	0	?	1	0	?	?	?	?
Afrovenator	?	2	1	1	?	?	1	0	0	1	?	1	?	1	?	0	?	0	?	?
Megalosaurus	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Edmarka	?	?	1	?	?	?	1	?	?	?	?	1	0	?	1	?	?	?	?	?
Brontoraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eustreptospondylus	?	1	?	?	1	?	?	?	0	1	?	?	?	?	?	0	?	?	1	0
Piatnitzkysaurus	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinraptor	0	4	1	1	1	0	0	0	0	1	1	1	1	1	1	1	2	0	1	0
Yangchuanosaurus	?	4	1	1	1	1	0	0	0	1	1	?	?	1	?	1	?	0	?	?
Gasosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Szechuanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	1	?	?	?	1	0	1	1	2	?	?	0	?	1	?	0	?	?
Allosaurus	1	3	1	1	1	1	0	0	0	1	2	1	0	1	1	1	1	0	1	1
Acrocanthosaurus	?	?	?	?	?	?	?	0	?	1	?	1	1	1	?	?	?	0	0	?
Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?
Saurophaganax	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Monolophosaurus	1	1	1	1	1	1	?	1	0	1	0	2	1	?	1	1	1	1	0	0
Neovenator	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Carcharodontosaurus	0	1	1	1	1	?	0	1	1	1	0	1	?	1	1	?	?	0	?	?
Giganotosaurus	?	1	?	?	1	?	?	1	2	1	1	?	?	?	?	?	?	0	?	?
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baronyx	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Ornitholestes	?	2	1	1	2	0	1	0	0	?	0	?	?	0	?	1	?	1	?	?
Compsognathus	?	2	1	0	?	0	2	0	0	0	0	?	?	0	?	?	?	1	1	?
Dromaeosauridae	0	2	1	0	2	0	0	0	0	0,1	0,1	1	?	1	0,1	1	1	1	1	0
Ornithomimosauria	1	2	1	0	0	?	2	0	0	0	0,1	0	0	1	2	0	0	1	1	0
Troodontidae	1	2	1	0	2	0	2	0	0	0	0	0	0	1	2	?	?	1	1	0
Tyrannosauridae	1	2	1	0	1	0	0	0	0,2	1	0,1,2	1	1	1	1	1	1	0	1	0,1
Oviraptorosauria	1	2	1	0	2	0	1	0	0	0	0	0	0	0	?	1	?	1	?	?
Therizinosauroidea	1	0	1	0	1	?	1	0	0	0	0	0	0	1	2	1	1	1	1	0
Archaeopteryx	?	2	1	?	1	?	2	0	0	0	0	?	?	?	2	1	?	1	?	?

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Herrerasaurus	0	0	0	0	0	?	0	1	0	0	0	0	0	?	?	0	0	0	1	0
Ceratosauria	0	0	0	0	0	0	0	0,1	?	0	0	?	0	0	0	0	0	0	0	0
Abelisauroidea	0	0	?	0	0	?	?	1	?	?	?	?	?	?	?	0	1	0	1	0
Torvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Afrovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Megalosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Edmarka	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brontoraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eustreptospondylus	?	?	?	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Piatnitzkysaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinraptor	0	0	?	1	1	1	0	1	1	0	1	1	4	0	1	0	0	0	1	1
Yangchuanosaurus	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	0	?	0	1	?
Gasosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Szechuanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Allosaurus	0	1	1	1	1	2	1	0	1	0	1	1	2	0	1	0	0	1	1	1
Acrocanthosaurus	0	1	1	1	?	?	1	0	1	?	?	1	4	0	1	?	?	?	2	?
Chilantaisaurus	?	?	?	1	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Saurophaganax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Monolophosaurus	0	0	?	0	?	?	?	1	?	?	?	?	?	?	?	0	1	?	1	1
Neovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Carcharodontosaurus	?	?	?	1	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giganotosaurus	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baronyx	?	0	?	0	?	?	?	0	?	?	?	?	?	?	?	0	?	0	?	?
Ornitholestes	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Compsognathus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	1	?	0
Dromaeosauridae	0	0	?	0	0	2	0	1	1	1	?	0	3	1	1	0	?	0	1,2	1
Ornithomimosauria	1	0	?	0	0	2	0	1	1	1	?	?	0	?	?	0	1	1	0	0
Troodontidae	1	0	0	0	0	0	?	0	?	?	?	?	?	?	?	0	?	?	2	0
Tyrannosauridae	0	0	1,2	0	0	2	1	0	1,2	1	?	?	4	1	1	0	1	1	2	1
Oviraptorosauria	0	?	?	?	?	?	?	?	0	0	0	0	0	1	?	0	1	0	0	?
Therizinosauroidea	0	?	?	0	?	2	0	1	?	1	?	?	0	?	?	0	1	0	0	0
Archaeopteryx	?	0	?	0	?	1	?	1	2	?	?	0	3	1	0	0	0	1	?	0

Appendix 3 (continued)

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Herrerasaurus	?	0	1	0	?	?	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Ceratosauria	?	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	2	0	0
Abelisauroidea	0	0	1	?	?	?	0	0	0	0	1	2	0	0	2	0	0	1	0	0
Torvosaurus	?	?	?	?	?	0	0	0	0	?	?	?	?	?	2	0	0	1	0	0
Afrovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Megalosaurus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	0	0	1	0	0
Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Edmarka	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brontoraptor	?	?	?	?	?	?	?	?	0	0	1	1	0	0	?	?	?	?	?	?
Eustreptospondylus	?	?	?	?	?	?	?	?	?	?	?	?	0	2	?	?	1	?	?	
Piatnitzkysaurus	?	?	?	?	?	?	?	?	?	0	?	2	1	1	2	1	?	1	0	0
Sinraptor	0	0	1	1	?	1	0	0	1	1	0	2	?	1	2	0	0	1	0	0
Yangchuanosaurus	0	?	?	?	?	?	0	0	?	1	0	2	1	1	2	0	?	1	?	?
Gasosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Szechuanosaurus	?	?	?	?	0	2	?	?	?	?	0	2	1	1	?	?	?	1	?	?
Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Allosaurus	0	0	1	1	0	2	1	0	1	0	0	1	1	1	2	0	0	1	0	0
Acrocanthosaurus	1	0	2	1	1	?	?	?	?	0	1	2	1	1	2	0	1	1	0	0
Chilantaisaurus	?	?	?	?	0	?	?	?	?	?	0	?	?	1	?	?	?	?	?	?
Saurophaganax	?	?	?	?	?	?	?	?	1	?	?	?	?	?	2	?	?	2	?	?
Monolophosaurus	?	?	?	?	?	?	0	0	1	1	?	1	1	1	1	?	?	1	?	?
Neovenator	?	?	2	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Carcharodontosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	1	1	1	0
Giganotosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	1	1	0	0
Baronyx	?	?	?	?	?	0	2	0	?	?	?	2	0	1	2	?	?	?	?	0
Ornitholestes	?	?	?	?	?	2	0	0	?	?	?	?	?	?	1	?	?	1	?	?
Compsognathus	?	?	?	?	?	0	0	0	1	?	?	?	?	?	2	?	?	1	?	?
Dromaeosauridae	?	0	1	1	0	1	0	0	0	0	1	2	1	1	0	1	0	1	0	1
Ornithomimosauria	?	?	1	1	0	0,2	0,2	0	0	0	0	1	0	1	0	0	0	0,1	0	0
Troodontidae	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	1	?	0
Tyrannosauridae	0	1	0	1	0	2	0	0	?	0	?	1	0	1	1	0	0	1	0	0
Oviraptorosauria	?	0	1	?	?	?	0	0	?	?	?	?	?	?	0	?	?	1	?	?
Therizinosauroidea	0	1	1	0	1	?	0	0	?	?	?	?	?	?	0	?	?	1	?	?
Archaeopteryx	0	?	?	?	0	0	0	0	?	?	?	?	?	?	0	0	?	1	?	?

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Herrerasaurus	0	?	?	0	0	0	1	0	0	?	0	1	0	0	?	?	?	0	0	?
Ceratosauria	9	1	0	0	0	0	0	0	0	0	1	0,1	1	?	0	0	0	0	0	1
Abelisauroidea	2	?	0	0	0	2	1	0	1	0	1	0	?	0	0	?	?	?	0	0
Torvosaurus	1	1	0	?	1	2	1	0	1	?	?	1	1	0	1	?	?	1	0	?
Afrovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Megalosaurus	0	?	?	?	?	0	1	?	?	0	0	0	?	?	?	?	?	?	?	?
Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
Edmarka	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brontoraptor	?	?	?	?	?	?	?	?	?	1	0	1	0	?	1	?	?	0	?	?
Eustreptospondylus	0	1	0	1	1	0	?	?	?	0	?	0	?	?	?	?	?	0	?	?
Piatnitzkysaurus	1	1	1	1	1	1	1	?	?	?	0	?	?	?	?	?	?	?	?	?
Sinraptor	1	1	1	0	1	1	1	1	1	?	?	0	1	?	?	?	?	?	0	?
Yangchuanosaurus	1	?	0	0	1	?	1	?	1	?	?	?	?	?	?	?	?	1	0	0
Gasosaurus	?	?	?	?	0	0	?	?	?	0	0	?	?	?	?	?	?	?	?	?
Szechuanosaurus	?	?	0	0	0	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?
Metriacanthosaurus	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Allosaurus	1	1	1	1	1	1	1	1	1	0	0	0	1	?	1	1	1	0	0	0
Acrocanthosaurus	3	2	?	0	1	2	1	1	1	1	0	1	1	1	?	?	?	0	0	0
Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saurophaganax	0	?	?	?	1	0	?	?	?	?	?	?	?	?	0	0	?	?	?	?
Monolophosaurus	1	?	0	1	1	1	1	?	1	?	?	1	1	?	?	?	?	?	?	0
Neovenator	?	?	?	?	?	2	?	?	?	0	?	?	?	?	?	1	?	?	?	?
Carcharodontosaurus	1	?	?	?	0	?	?	?	?	?	?	2	0	?	0	?	?	0	0	?
Giganotosaurus	3	?	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Sigilmassasaurus	2	?	2	?	1	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?
Baronyx	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Ornitholestes	2	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	1	1	0	?
Compsognathus	?	?	0	0	0	0	?	?	1	?	?	0	?	?	?	?	0	1	0	?
Dromaeosauridae	2,3	1	2	0	0	2	0	0	1	1	0	0	1	0	0	0	1	1	0	0
Ornithomimosauria	0,2	2	0	0	0	0,2	1	0	1	1	0	0	?	?	0	0	1	1	0,1	0
Troodontidae	?	?	1	?	?	0	?	?	1	?	?	?	1	?	?	?	1	1	1	?
Tyrannosauridae	3	2	0	0	0	2	1	0	1	1	0	0	0	?	0	1	1	1	0	0
Oviraptorosauria	?	2	?	0	0	2	?	?	1	1	?	2	?	?	?	?	0	?	?	?
Therizinosauroidea	?	?	0	?	0	0	1	?	?	1	0	?	?	?	0	?	1	1	0	?
Archaeopteryx	?	?	?	1	0	2	?	?	1	?	?	?	?	?	?	0	1	1	?	?

Appendix 3 *(continued)*

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Herrerasaurus	?	?	?	0	1	1	0	1	0	0	?	?	0	0	0	0	0	0	0	0
Ceratosauria	0,1	0	?	0	0	0	0	0	0	0	0	?	0,1	0	0	0	0	0	0	1
Abelisauroidea	0	1	?	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Torvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	1	0	0	?
Afrovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	1
Megalosaurus	?	?	?	0	0	1	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Poekilopleuron	?	?	0	?	?	?	1	?	?	?	?	?	0	0	?	?	?	?	?	0
Edmarka	?	?	?	?	?	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Brontoraptor	?	?	?	1	0	1	1	?	0	0	?	?	?	?	?	?	?	?	?	?
Eustreptospondylus	?	?	?	?	?	1	0	?	?	?	?	?	0	?	?	?	?	?	?	?
Piatnitzkysaurus	?	?	?	1	1	1	0	1	?	0	?	?	1	0	?	?	?	?	?	?
Sinraptor	1	1	1	?	1	1	0	1	?	?	?	1	?	?	?	?	?	0	0	?
Yangchuanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gasosaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Szechuanosaurus	?	?	?	?	?	1	0	1	?	0	?	?	0	0	0	0	?	0	0	0
Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Allosaurus	1	0	1	1	1	1	0	1	1	0	1	0	1	0	1	?	1	0	0	1
Acrocanthosaurus	1	1	0	1	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?
Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Saurophaganax	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Monolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neovenator	?	?	?	?	?	1	0	1	?	0	?	?	?	?	?	?	?	?	?	?
Carcharodontosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giganotosaurus	?	?	?	?	?	1	0	?	?	0	?	?	?	?	?	?	?	?	?	?
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baronyx	?	?	?	?	?	1	?	1	1	?	?	?	1	?	1	?	?	?	?	?
Ornitholestes	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	1	1	1	1
Compsognathus	?	?	1	1	1	1	0	1	0	0	?	?	0	0	1	?	?	0	0	1
Dromaeosauridae	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Ornithomimosauria	1	?	1	0	0	1	0	1	1	0	?	0	0	0	1	0	1	0	0	1
Troodontidae	?	?	1	0	0	1	0	?	1	1	0	?	1	1	1	1	1	1	1	1
Tyrannosauridae	1	?	1	0	1	1	0	1	0	1	?	1	0	0	1	0	1	0	1	1
Oviraptorosauria	?	?	?	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1
Therizinosauroidea	?	?	?	0	1	1	0	1	1	1	?	?	0	0	1	1	1	1	0	1
Archaeopteryx	1	?	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Herrerasaurus	0	0	0	0	0	0	1	0	0	1	2	9	0	0	9	9	0	1	0	0
Ceratosauria	0	0,1	0	0	0	0	0	0	0,1	0	0,1	0,9	1,9	0	9	9	0	1	1	1
Abelisauroidea	0	1	0	0	0	?	1	0	1	1	1	9	0	0	9	9	0	1	2	0
Torvosaurus	?	1	0	0	0	?	1	0	1	0	1	9	1	0	9	9	0	0	2	0
Afrovenator	0	?	0	0	?	?	1	?	1	?	1	?	1	2	0	0	0	?	2	0
Megalosaurus	?	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	1	2	0
Poekilopleuron	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Edmarka	?	1	?	0	?	?	1	1	1	?	1	?	1	1	9	9	?	?	?	0
Brontoraptor	?	?	1	0	?	1	1	0	1	?	1	?	0	0	9	9	0	?	1	0
Eustreptospondylus	?	?	?	0	?	?	1	2	1	?	1	?	?	?	?	?	?	?	?	0
Piatnitzkysaurus	?	?	1	0	?	?	1	0	1	?	1	?	1	0	9	9	0	0	2	0
Sinraptor	?	1	2	0	0	1	1	1	1	2	1	0	1	2	0	0	0	?	1	0
Yangchuanosaurus	?	?	?	0	0	?	1	0	1	1	1	9	1	2	0	0	0	1	1	0
Gasosaurus	?	0	1	0	?	?	1	0	1	?	1	?	1	2	0	0	0	?	1	0
Szechuanosaurus	0	1	0	0	0	?	1	0	1	?	1	?	1	2	0	0	0	1	2	0
Metriacanthosaurus	?	?	0	0	?	?	1	?	?	2	?	?	?	?	?	?	?	?	1	0
Cryolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Allosaurus	0	1	0	0	0	1	1	2	2	2	2	1	0	2	0	0	0	0	1	0
Acrocanthosaurus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chilantaisaurus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saurophaganax	?	?	2	?	?	?	1	2	?	?	2	?	0	2	0	?	?	?	?	0
Monolophosaurus	?	1	0	0	0	0	1	0	0	?	1	?	1	1	9	9	0	0	?	0
Neovenator	?	?	?	0	?	?	?	2	?	?	2	?	0	2	?	?	0	1	2	0
Carcharodontosaurus	?	?	?	?	?	?	?	?	2	?	?	?	?	2	0	?	?	?	?	0
Giganotosaurus	?	1	?	0	?	?	1	2	1	?	2	?	0	2	0	0	0	?	1	0
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baronyx	0	1	?	?	?	?	?	?	?	?	?	?	?	2	0	?	?	?	?	0
Ornitholestes	-1	1	?	1	?	?	1	2	?	?	?	?	?	?	?	?	?	0	0	0
Compsognathus	0	0	?	0	0	?	?	?	1	0	2	?	1	2	0	1	1	?	1	?
Dromaeosauridae	1	0	0	1	0	1	1	2	1,3	0	2	?	1	2	1	1	1	1	0	0
Ornithomimosauria	0	1	0	0	1	0	1	2	1	2	2	0	0	2	0	1	0	1	2	0
Troodontidae	0	0	0	1	1	?	1	2	1	0	0	9	9	2	1	1	1	0	0	0
Tyrannosauridae	0	1	2	0	1	1	1	2	2	0	2	1	0	2	1	1	0	0	0	0
Oviraptorosauria	1	1	0	0,1	0	1	0	2	2	0	2	1	0	2	1	1	1	0	0	0
Therizinosauroidea	1	1	2	1	0	?	1	2	3	?	2	?	0	2	1	0	0	?	0	0
Archaeopteryx	1	0	0	1	?	?	1	2	3	0	1	?	1	2	1	0	-1	0	0	0

Appendix 3 *(continued)*

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
Herrerasaurus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Ceratosauria	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Abelisauroidea	1	0	0	0	1	?	?	?	?	1	?	?	0	0	0	?	?	?	?	?
Torvosaurus	?	?	?	?	?	?	?	?	?	0	1	?	0	1	0	0	1	?	?	0
Afrovenator	?	?	?	?	2	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Megalosaurus	1	0	0	0	2	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?
Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?	?
Edmarka	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brontoraptor	1	0	1	0	2	0	1	1	0	0	1	?	0	?	?	?	?	?	?	?
Eustreptospondylus	1	0	0	0	1	0	1	0	0	1	1	?	0	?	0	0	?	?	?	0
Piatnitzkysaurus	1	0	1	0	2	0	?	?	?	?	1	?	0	?	?	?	?	?	?	0
Sinraptor	1	0	1	1	2	0	2	1	0	0	1	1	0	1	0	1	1	0	1	0
Yangchuanosaurus	1	0	1	1	2	0	?	?	?	?	1	?	0	1	?	?	?	?	?	?
Gasosaurus	2	0	1	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Szechuanosaurus	1	0	1	0	2	0	?	?	?	?	?	?	0	?	?	1	?	?	1	0
Metriacanthosaurus	?	?	1	1	?	0	?	?	?	0	1	?	?	?	?	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	?
Allosaurus	1	0	1	1	2	0	2	1	0	0	1	1	0	1	1	1	1	0	1	0
Acrocanthosaurus	1	0	1	1	2	0	2	1	0	?	1	?	0	1	?	?	?	?	?	0
Chilantaisaurus	2	0	1	1	2	0	2	0	0	?	1	?	0	?	?	?	?	?	?	0
Saurophaganax	2	0	1	1	2	0	?	?	0	?	1	?	0	?	?	?	?	?	?	0
Monolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neovenator	2	0	1	1	2	0	?	?	0	?	1	?	?	?	?	?	?	?	?	0
Carcharodontosaurus	2	0	1	1	2	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?
Giganotosaurus	?	0	1	1	2	0	?	?	?	?	1	?	0	?	1	?	?	?	?	?
Sigilmassasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baronyx	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Ornitholestes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Compsognathus	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	0
Dromaeosauridae	1	1	0	1	1	2	?	?	0	1	?	1	0	1	2	1	0	0	1	0
Ornithomimosauria	1	0	1	1	2	1	1,2	0	0	0	1	1	0	1	2	1	0	9	1	1
Troodontidae	1	1	0	1	?	2	0	0	0	?	1	9	0	1	2	1	0	0	1	1
Tyrannosauridae	1	1	1	1	2	0	2	?	0	0	1	1	0	1	2	1	0	1	1	1
Oviraptorosauria	1	1	1	1	1	1	?	?	0	?	1	1	?	1	2	?	0	1	1	0
Therizinosauroidea	?	0	1	1	?	1	?	?	?	0	?	?	0	?	2	?	?	0	0	0
Archaeopteryx	1	?	0	1	1	2	?	?	?	?	?	?	1	1	1	1	?	1	1	0

	141	142	143	144	145
Herrerasaurus	0	0	0	0	0
Ceratosauria	0	0	0,1	1	0
Abelisauroidea	?	?	?	?	?
Torvosaurus	1	?	0	?	?
Afrovenator	?	?	?	?	?
Megalosaurus	1	?	0	?	?
Poekilopleuron	?	?	?	?	?
Edmarka	?	?	?	?	?
Brontoraptor	?	?	?	?	?
Eustreptospondylus	1	?	0	?	?
Piatnitzkysaurus	?	?	0	?	?
Sinraptor	1	1	0	0	0
Yangchuanosaurus	?	?	?	?	?
Gasosaurus	?	?	?	?	?
Szechuanosaurus	?	?	0	?	?
Metriacanthosaurus	?	?	?	?	?
Cryolophosaurus	?	?	?	?	?
Allosaurus	1	0	0	0	0
Acrocanthosaurus	1	?	0	?	?
Chilantaisaurus	1	?	0	?	?
Saurophaganax	?	?	?	?	?
Monolophosaurus	?	?	?	?	?
Neovenator	?	?	?	?	?
Carcharodontosaurus	?	?	?	?	?
Giganotosaurus	?	?	?	?	?
Sigilmassasaurus	?	?	?	?	?
Baronyx	?	?	?	?	?
Ornitholestes	?	?	?	?	?
Compsognathus	?	1	0	1	1
Dromaeosauridae	1	1	0	0	0
Ornithomimosauria	2	1	1	0	1
Troodontidae	2	1	1	0	1
Tyrannosauridae	2	1	1	0	0
Oviraptorosauria	1	1	0	0	?
Therizinosauroidea	?	1	0	?	0
Archaeopteryx	?	1	0	1	0