A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA

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ABSTRACT

A new skeleton of *Acrocanthosaurus atokensis* is the most complete specimen collected and has the only known complete skull. Aspects of the new skeleton are described in detail, with special attention directed to the morphology of the skull and forelimb. Although unquestionably one of the largest theropods ever found, it is smaller than *Carcharodontosaurus*, *Giganotosaurus* and *Tyrannosaurus*. Comparison with other theropods suggests that *Acrocanthosaurus* bears a strong resemblance to these taxa because of characters that are size determinate, and the evidence suggests *Acrocanthosaurus* is more closely related to Allosauridae than to Carcharodontosauridae. Three families (Allosauridae, Carcharodontosauridae, Sinraptoridae) are recognized in the Allosauroidea.

KEY WORDS
Dinosaurs,
theropods,
Early Cretaceous,
USA.

RÉSUMÉ

*Un nouveau specimen d'*Acrocanthosaurus atokensis *(Theropoda, Dinosauria) du Crétacé inférieur de la Formation Antlers (Crétacé inférieur, Aptien) de l'Oklahoma, États-Unis.*

Nous décrivons le squelette d'*Acrocanthosaurus atokensis* le mieux conservé jusqu'ici et possédant un crâne complet. La morphologie des structures inconnues sont décrites ; l'accent est mis sur la morphologie du crâne et du membre antérieur. Bien que ce théropode soit l'un des plus grands, ses dimensions restent inférieures à celles de *Carcharodontosaurus*, *Giganotosaurus* et *Tyrannosaurus*. Il présente un fort degré de ressemblance morphologique avec ces taxons, dont la nature serait liée à leur taille importante. Une analyse de parcimonie place *Acrocanthosaurus* comme plus proche parent des Allosauridae que des Carcharodontosauridae. Trois familles sont identifiées au sein des Allosauroidea : les Allosauridae, les Carcharodontosauridae et les Sinraptoridae.

MOTS CLÉS
Dinosaures,
théropodes,
Crétacé inférieur,
États-Unis.

INTRODUCTION

Acrocanthosaurus atokensis was described by Stovall & Langston (1950) on the basis of two partial skeletons (one with part of a skull) from the Lower Cretaceous Antlers Formation (Trinity Group, Aptian-Albian) of Atoka County, Oklahoma. The holotype is OMNH 10146 (MUO 8-0-S9 of Stovall & Langston 1950) and the paratype is OMNH 10147 (MUO 8-0-S8). *Acrocanthosaurus* Stovall & Langston, 1950 was the top predator of one of the richest faunas known from Early Cretaceous times (Cifelli *et al.* 1997). Although it seems to have been widely distributed (Lipka 1998) in North America, it was not the only large theropod of Aptian-Albian times (Harris 1998b).

Another partial skull and skeleton of *Acrocanthosaurus* was "discovered" in 1990 (the specimen was actually noticed for the first time more than 40 years earlier) near Weatherford, Texas in the Twin Mountain Formation (Trinity Group), which correlates with the lower part of the Antlers Formation (Harris 1998a). It was collected by a crew from Southern Methodist University. SMU 74646 includes about 70% of a skeleton (Harris 1998a).

Parts of another specimen (two posterior cervical or anterior dorsal centra, ischial fragment, distal end of a femur), described in this paper, were collected by the Oklahoma Museum of Natural History and were catalogued as OMNH 10168. Most of the specimen, however, was collected by Cephis Hall & Sid Love, who retrieved the skull, about two dozen vertebrae, ribs, chevrons, most of the front limbs, pelvic fragments, parts of both femora and tibiae, and most of the bones of the foot. This, the most complete skeleton of *Acrocanthosaurus* known, also comes from the Antlers Formation (Trinity Group) of McCurtain County, Oklahoma. The unprepared specimen was eventually acquired by Allen Graffham of Geological Enterprises, Inc., Ardmore, Oklahoma, who in turn arranged for the Black Hills Institute in Hill City, South Dakota, to prepare the specimen. The preparation was completed at the end of the summer of 1996, and the original skeleton went the following year to the North Carolina State Museum of Natural Sciences.

The total length of the skeleton (Fig. 1) as mounted for display by the Black Hills Institute is 11.5 m. This would make it one of the largest known theropods, comparable in total length with *Tyrannosaurus rex* Osborn, 1905 (the mounted skeletons of BHI 3033 and MOR 555 are 11.5 m)

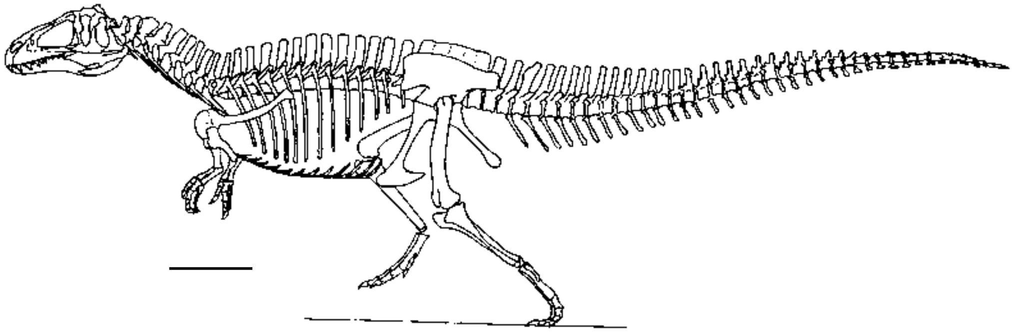

FIG. 1. — *Acrocanthosaurus atokensis*. Reconstruction of skeleton. Scale bar: 1 m.

and *Giganotosaurus* Coria & Salgado, 1995 (the mounted skeleton of MUCPv-CH1 is 12.2 m).

We have not attempted to describe the entire skeleton of *Acrocanthosaurus* in this paper, but have focused on new information available from NCSM 14345. This is especially true for the skull, pectoral girdle and forelimb and, to a lesser extent, the hindlimb. The reader is referred to papers by Stovall & Langston (1950) and Harris (1998a) for complementary information on the palate, braincase, vertebral column and pelvis. A more detailed description of the braincase of the holotype has been prepared by Welles *et al.*

Acrocanthosaurus (Fig. 1) was assigned to the Allosauridae by Stovall & Langston (1950). This was generally accepted by other authors until it was reassigned to the Carcharodontosauridae (Sereno *et al.* 1996). A more thorough analysis by Harris (1998a) supported the inclusion of *Acrocanthosaurus* within the Carcharodontosauridae. Information from the new specimen will be used in this paper to re-examine the relationships of *Acrocanthosaurus*.

ABBREVIATIONS

BYU	Brigham Young University, Provo;
FMNH	Field Museum of Natural History, Chicago;
GI	Paleontological Museum of the Geological Institute of Mongolia, Ulaan Baatar;
MACN-CH	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires;
MOR	Museum of the Rockies, Bozeman;
MUCPv-CH	Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén, Argentina;
NCSM	North Carolina State Museum of Natural Sciences, Raleigh;
NMMNH	New Mexico Museum of Natural History, Albuquerque;
OMNH	Oklahoma Museum of Natural History, University of Oklahoma, Norman;
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow;
SMU	Southern Methodist University, Dallas;
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller;
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington;
UUVP	University of Utah, Vertebrate Paleontology Collection, Salt Lake City.

FIG. 2. — *Acrocanthosaurus atokensis* NCSM 14345; **A**, skull in left view; **B**, skull in right view. Scale bar: 10 cm.

SYSTEMATIC PALEONTOLOGY

Subclass DINOSAURIA Owen, 1842
Order THEROPODA Marsh, 1881
Suborder CARNOSAURIA von Huene, 1920
Superfamily ALLOSAUROIDEA
Currie & Zhao, 1993
Family ALLOSAURIDAE Marsh, 1878

Acrocanthosaurus atokensis
Stovall & Langston, 1950

MATERIAL. — North Carolina State Museum of Natural Sciences, NCSM 14345, nearly complete skull and most of postcranium.

LOCALITY AND AGE. — NCSM 14345 was recovered from the Antlers Formation (Trinity Group, Lower Cretaceous) of McCurtain County, Oklahoma.

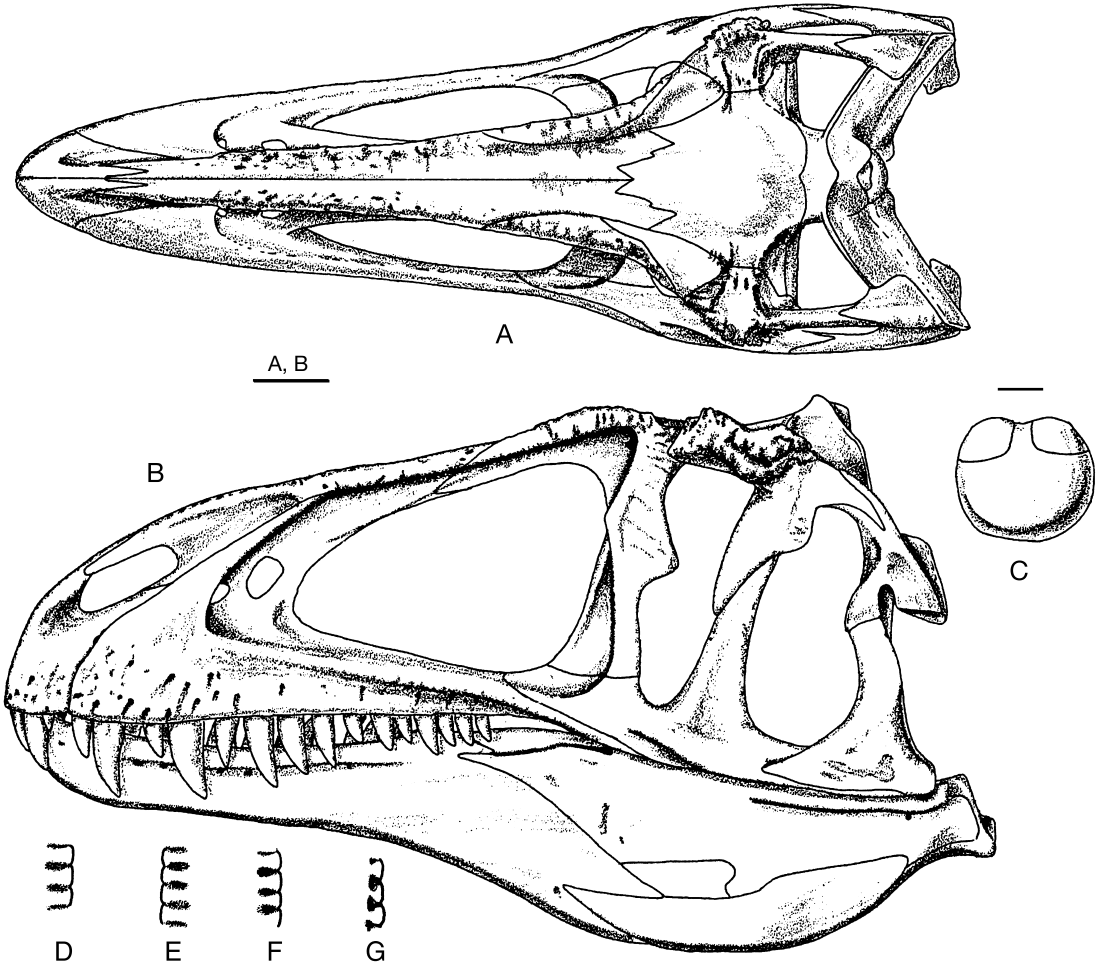

FIG. 3. — *Acrocanthosaurus atokensis*. Reconstruction of skull; **A**, dorsal view; **B**, left lateral view; **C**, occipital condyle; **D-G**, denticles of maxillary teeth. Scale bars: A, B, 10 cm; C, 2 cm.

REVISED DIAGNOSIS. — Large theropod with elongate neural spines that are more than 2.5 times corresponding presacral, sacral and proximal caudal lengths of the centra. Lacrimal contacts postorbital; supraoccipital expands on either side of the midline to protrude as a double boss behind the nuchal crest; pleurocoelous fossae and foramina pronounced on all presacral and sacral vertebrae; cervical neural spines have triangular anterior processes that insert into depressions beneath overhanging processes on preceding neural spines; accessory transverse processes on mid-caudal vertebrae.

DESCRIPTION

NCSM 14345 was found lying on its side, partially disarticulated. There has been some crushing and distortion of the skull, mostly towards the back (Fig. 2). For example, the left postorbital was broken in at least two places, and had pulled away from its suture with the frontal, the ventral part rotating medially. Minor crushing and distortion are also evident in the posterior half of the jaws.

The skull (Figs 2; 3) is almost 129 cm long (premaxilla to quadrate) with a preorbital length of 85 cm. The height of the skull in front of the orbit is 47 cm. Femur length (Table 1) is a relatively stable standard of measurement in theropods, and can be used to assess proportional differences of the skull. The skull/femur ratio is 1.17, which compares well with *Ceratosaurus* Marsh, 1884 (1.00, Gilmore 1920), sinraptorids (0.92-1.17, Currie & Zhao 1993) and tyrannosaurids (0.97-1.17). The skull of *Allosaurus* is apparently relatively short (0.76 in USNM 4734 and 1.03 in AMNH 5753).

In addition to the five major openings on each side of the skull (external naris, antorbital fenestra, orbit, upper and lateral temporal fenestrae), there are two accessory openings in the maxilla (Figs 2; 3). The external naris is relatively small and elongate, with a maximum length of 16 cm (anteroventral to posterodorsal axis). The naris is bound entirely by the premaxilla and nasal, and the maxilla is excluded from the opening. This is the plesiomorphic state found in primitive theropods like *Herrerasaurus* Reig, 1963 (Sereno & Novas 1992), in contrast with *Allosaurus* Marsh, 1877 (Madsen 1976), *Monolophosaurus* Zhao & Currie, 1993 and some Cretaceous theropods (Currie 1985). The triangular antorbital fenestra is enormous, covering almost half (42 cm) the preorbital skull length and two thirds (63%, 29 cm) of the height. The jugal forms part of the boundary in *Acrocanthosaurus*. In some reconstructions of *Allosaurus* (Madsen 1976), the jugal is excluded from the margin of the fenestra, although it does reach the antorbital fenestra in at least some specimens (Bakker, pers. comm. 1993). The keyhole shaped orbit is high (34 cm) but relatively short anteroposteriorly (12 cm). The outline of the lateral temporal opening is pear-shaped and is bordered above by a short intertemporal bar.

Anterior to the orbit, the side of the skull is a relatively flat, vertical face, clearly set off from the narrow skull roof as in most carnosaurs. A sharply defined ridge separates the dorsal and lateral surfaces of the nasal and lacrimal bones. The ridge, which overhangs the face by as much as 1.5 cm at the anteriormost nasal-lacrimal contact, is relatively straight in profile and is only slightly rugose as in *Allosaurus* (Madsen 1976). There are no nasal, lacrimal, frontal or postorbital horns as there are in *Allosaurus*, *Ceratosaurus*, *Carnotaurus* Bonaparte, Novas & Coria, 1990, *Monolophosaurus* and most tyrannosaurs, and in this character *Acrocanthosaurus* is similar to *Tyrannosaurus*. The paired premaxillae form the sharp, narrow tip of the skull (Fig. 3A). Each is pierced by more than half a dozen foramina (Fig. 3B) for branches of the medial ethmoidal nerve and subnarial artery. The maxillary body is higher than long as in *Ceratosaurus*, *Yangchuanosaurus* Dong, Zhou & Zhang, 1983 and *Torvosaurus* Galton & Jensen, 1979, whereas it is longer than high in *Allosaurus* (Britt 1991) and *Sinraptor* Currie & Zhao, 1993. In contrast with *Allosaurus*, the anterior margin slopes posterodorsally. There is a sloping, posteriorly concave (in lateral aspect) contact with the maxilla, which tapers into a posterodorsal (subnarial) process to contact the subnarial process of the nasal. As in *Allosaurus*, the subnarial foramen passes between the main bodies of the premaxilla and maxilla.

The maxilla is more than 82 cm long. It is excluded from the border of the external naris by the premaxilla and nasal, but forms most of the anterior margin of the antorbital opening. A maxillary fenestra (7 cm by 3.5 cm) pierces the maxilla between the external naris and the antorbital opening. As in most theropods, the smaller promaxillary fenestra (3.5 cm high) is tucked under the rim that forms the anteroventral corner of the antorbital fossa. The right maxilla has 15 teeth (counting one empty position), which is close to the counts for *Sinraptor* (15, Currie & Zhao 1993) and *Yangchuanosaurus* (14-15, Dong *et al.* 1983). As in *Allosaurus*, *Sinraptor*, *Yangchuanosaurus* and most other large theropods, the lateral surface of the maxilla is rugose only along its anterior edge and immediately above the tooth row. It is definitely not rugose in the way that the maxillae of *Abelisaurus*, *Carcharodontosaurus*, *Carnotaurus* and *Giganotosaurus* are. Most of the lateral surface of the maxilla is smooth and somewhat indented where it defines the extent of the antorbital fossa. The maxillae of *Carcharodontosaurus* (Stromer 1931; Sereno *et al.* 1996), *Carnotaurus* (Bonaparte *et al.* 1990), *Ceratosaurus* (Gilmore 1920), *Giganotosaurus* (MUCPv-CH-1), *Indosuchus* Chatterjee, 1978 and *Torvosaurus* (Britt 1991) are quite different in that most of the lateral surfaces are rugose, showing that the antorbital fossae are not as well developed.

The ventral margin of the promaxillary fenestra in the anteroventral apex of the antorbital fossa is at about the same level as the floors of the naris and the antorbital fenestra. This fenestra is found in most theropods; sometimes (e.g. *Ceratosaurus*) it is not visible in lateral aspect, and sometimes it is a relatively large opening (Witmer 1997). The larger maxillary fenestra is not consistently expressed in theropods, but tends to be present in advanced forms, including *Afrovenator* (Sereno *et al.* 1994), *Allosaurus* (Witmer 1997), tyrannosaurids and most small theropods. It is absent in *Abelisaurus* Bonaparte & Novas 1985, *Carnotaurus* (Bonaparte *et al.* 1990), *Ceratosaurus* (Gilmore 1920), *Carcharodontosaurus* Stromer, 1931 (Sereno *et al.* 1996 identify a maxillary fenestra, but it is in the position normally occupied by the promaxillary fenestra), *Giganotosaurus* (MUCPv-CH-1), *Indosuchus* Chatterjee 1978, *Majungatholus* Sues & Taquet, 1979 (Sampson *et al.* 1998) and *Torvosaurus* (Britt 1991), and is expressed as a variable complex of openings in sinraptorids (Currie & Zhao 1993; Witmer 1997). The posterodorsal process of the maxilla passes between the nasal bone and the antorbital fenestra, and bifurcates distally to embrace the anteroventral process of the lacrimal.

The nasal is 85 cm in length, more than four times the length of the frontal. The dorsal surface is flat and relatively narrow for most of its length, and is clearly delimited by a sharp inflection from the nasal contribution to the antorbital fossa as it is in *Allosaurus*, *Sinraptor* and *Yangchuanosaurus*. This is different in abelisaurids (Bonaparte & Novas 1985; Bonaparte *et al.* 1990), *Monolophosaurus* and tyrannosaurids, where at least half of the nasal has a convex and highly rugose dorsal surface. Like most theropods, the median internasal suture is not fused. The nasal is split anteriorly where the posterior tip of the premaxilla overlaps a shallow trough for a length of 11 cm. As in *Allosaurus*, *Ceratosaurus*, *Giganotosaurus*, *Monolophosaurus*, *Sinraptor* and *Yangchuanosaurus*, the nasal forms the anterodorsal rim of the antorbital fossa, and even extends slightly onto the medial wall. It appears as if pneumatic openings may have invaded the nasal along the margin of the antorbital fossa in the way they do in *Allosaurus* (Madsen 1976; Gilmore 1920), *Giganotosaurus* (R. Coria, pers. comm. 1996), *Monolophosaurus* (Zhao & Currie 1993) and *Sinraptor* (Currie & Zhao 1993). As in most other large theropods, there is a groove in the ventrolateral margin of the nasal for the maxillary articulation that would have permitted some lateral-medial rotation of the maxilla. Above the posterior end of the suture with the maxilla, the nasal overlaps the anterior tip of the lacrimal. Each nasal meets a prefrontal posterolaterally, and overlaps an anteroposteriorly elongate shelf of the frontal (Fig. 3A).

The lacrimal is 35 cm long and 37 cm high. The dorsolateral margin forms a low ridge at the front of the orbit comparable with *Carcharodontosaurus*, *Giganotosaurus* (R. Coria, pers. comm. 1996), *Sinraptor* (Currie & Zhao 1993) and *Yangchuanosaurus* (Dong *et al.* 1978). *Allosaurus, Ceratosaurus* (Gilmore 1920), the smaller genera of tyrannosaurids, and many other theropods have developed "horns" in this region. The lacrimal has a limited dorsal exposure. Anteriorly, there are interdigitating sutures with the maxilla and nasal. Its lateral surface is sculptured posterodorsally for close association with the skin. The lacrimal sends a narrow posterior extension along the ventrolateral margin of the prefrontal and seems to contact the postorbital beneath a thin lateral lappet of the prefrontal (Fig. 3B). In lateral aspect (Figs 2A; 3B), the posterior margin of the ventral (preorbital) process of the lacrimal has a double concavity separated by a short process (for attachment of the *Ligamentum suborbitale*) that marks the anteroventral extent of the eyeball itself (diameter was about 11 cm). Although less obvious in the holotype (Stovall & Langston 1950), the process is similar to those of *Abelisaurus* (Bonaparte & Novas 1985), *Majungatholus* (Sampson *et al.* 1998), *Monolophosaurus*, *Sinraptor* and *Yangchuanosaurus*. The posterior margin of the preorbital bar of other large theropods tends to be uniformly concave in lateral view. Below this low process of the lacrimal in *Acrocanthosaurus*, the preorbital bar narrows to 64 mm in lateral aspect. The posteroventral end of

TABLE 1. — Measurements of *Acrocanthosaurus* specimens. Abbreviations: **dw**, distal width; **l**, length; **pw**, proximal width; **sw**, shaft width.

	Acrocanthosaurus atokensis			
	NCSM 14345	**OMNH 10146, holotype**	**MUO 8.0.S8**	**SMU 74646**
Source	specimen	Stovall & Langston 1950	Stovall & Langston 1950	Harris, 1998
Weight Estimate	2400 kg			1869 kg
Estimated length	11.5 metres	9.9 metres		
Skull L (centre)	1160			
Skull L (side)	1230			
antorbital	852			
orbit length	115			
orbit height	340			
postorb.	340			
height	465			
Mx length	820			
Mx height	312			
Mx Tooth row	590			
occ.cond.wid		54		
for.mag.wid		32		
dentary	830			
dentary	500			
dentary	96			
dentary	280			
Jaw length	1315			
PMx tooth	4			
Mx tooth	15			
Mx tooth	118			
scap-cor.leng.	1180			
scap.blade len.	970			
scap. L on curve	1030			
scap. sw	95			95
scap. dw				
Coracoid height	210			
Coracoid Length	360			
H. length	370			
H. prox.width	183			
H. shaft width	55			
H. dist. width	140			
R. length	220			
R. pw	70			
R. sw	35			
R. dw	73			
U. length	255			
U.pw	120			
U. sw	38			
U. dw	95			
mc I	62			
mc II	116			
mc. III	89			
I-1	111			
II-1	101			
II-2	103			
II-3	124			
II-3	144			
III-1	50			
III-2	42			
III-3	60			
III-4	71			
III-4	75			

	Acrocanthosaurus atokensis			
	NCSM 14345	**OMNH 10146, holotype**	**MUO 8.0.S8**	**SMU 74646**
Pubis length				956+
Ischium length				844
F. length	1277	1153		1090
F. pw			251	
F. sw/ant-post	110			
F. sw/transverse	150			
F. shaft circumference	425			388
F. dw	280	216		248
T. length		865	958	
T. sw transverse		94		
T. dw	300	221	245	
Fib. length		801		
Fib. sw		40		
Fib. dw		58		
Calcan. H	99			
mt I	111			
mt II	410		416	
mt III	439e		445	
mt V	200			
I-1	70			
I-2	75+			
II-1	55			
II-2	122			
III-1	160		145	
III-2	115			
IV-1	85			
IV-2	70			
IV-3	58			

the lacrimal expands somewhat for its contact with the jugal. Much of the anterolateral surface of the preorbital bar is shallowly excavated for the antorbital fossa, which extends ventrally onto the jugal. Ventrally, the lacrimal is overlapped by the jugal, and does not contact the maxilla. In contrast, the lacrimal may contact the maxilla externally in *Allosaurus* and *Ceratosaurus* (Gilmore 1920).

As in other large theropods, there is a lateral, pneumatic opening into a vacuity in the main posterodorsal body of the lacrimal. The opening has a diameter of 2.7 cm in this specimen. It would have housed a pneumatic diverticulum of the nasal cavity (Osmolska 1985; Witmer 1997). The presence of two large openings in the lacrimal of the holotype (Stovall & Langston 1950) shows there is some variation of this feature, which is not surprising considering how variable pneumatic features are (Currie & Zhao 1993).

Posteromedial to the lacrimal, there is a relatively large, triangular prefrontal (11 cm long, 6 cm broad) as in *Allosaurus*, *Sinraptor* and other carnosaurs. It extends posteriorly to contact the postorbital and helps to roof over the orbit. A thin lappet appears to have extended over the lacrimal to reach the orbital margin.

The dorsal surface of the frontal is flat, as it is in *Allosaurus* and *Sinraptor* (Currie & Zhao 1993). The surface of the bone is smooth as in the majority of large theropods, but in contrast with the ornamented surface in *Abelisaurus* (Bonaparte & Novas 1985) and *Majungatholus* (Sampson *et al.* 1998). As in the holotype, the interfrontal suture is more or less completely fused. Like the frontals of the holotype, there is a slightly raised rugose bump along the midline near the frontoparietal suture. A shallow trough, emphasized anteriorly by a raised ridge, leads into a foramen at the junction of the frontal, prefrontal and postorbital (Fig. 3B), although the latter two bones contact each other to exclude the frontal from the margin of the orbital rim. To an extent, this is a size specific characteristic that is shared by the largest theropods, including *Carcharodontosaurus*, *Giganotosaurus, Tarbosaurus* and *Tyrannosaurus*.

The frontal forms the anterior rim of the supratemporal fossa, which it floors for a distance of almost 5 cm. At the dorsal limit of the upper temporal fenestra, the fused frontoparietal suture is strengthened by additional bone deposition that protrudes laterally into the fenestra as a sharply defined ridge. This has also been noted in *Giganotosaurus* (Coria & Currie in prep.) and *Sinraptor* (Currie & Zhao 1993). The frontoparietal suture can be followed laterally to the point where both bones contact the postorbital.

The parietal has limited dorsal exposure along the midline (about 3 cm) and compares well with the parietals of carcharodontosaurids and sinraptorids. However, the dorsal surface is almost perpendicular to the occiput (Stovall & Langston 1950: pl. II-2), which itself is almost vertical. This angle is distinctly obtuse in carcharodontosaurids and sinraptorids. Correlated with this, each posterolateral wing of the parietal forms an almost vertical posterior wall for the supratemporal fossa, whereas it strongly slopes in carcharodontosaurids and sinraptorids. The posterolateral wing extended along the top of the paroccipital process, tapering to a point that ends only 5 cm from the distal end of the process. There is no sharp sagittal crest along the midline of the parietal and, in this sense, *Acrocanthosaurus* is as primitive as all theropods except tyrannosaurids and troodontids. The nuchal crest is low and does not extend more than a few millimetres above the supraoccipital. Again, this situation is very different in tyrannosaurids and troodontids.

The orbital margin of the postorbital extends forward to contact the lacrimal and prefrontal, and has thickened into a prominent horizontal orbital boss as in abelisaurids, carcharodontosaurids and the largest tyrannosaurids. These are size-dependent characteristics that have uncertain taxonomic significance. The rugose rim of the postorbital is 4 cm thick dorsoventrally. The intertemporal ramus of the postorbital is relatively short and is oriented almost as much ventrally as it is posteriorly (Fig. 3B). The postorbital bar of the postorbital is relatively wide in lateral view, reaching a maximum anteroposterior length of 9.7 cm behind the orbit and has an anterior process beneath the orbit (Fig. 2A). This process is also evident in the holotype (Stovall & Langston 1950), and similar processes are found in *Carcharodontosaurus*, *Giganotosaurus*, *Gorgosaurus* Lambe, 1917, *Tarbosaurus* Maleev, 1974 and *Tyrannosaurus*. Presence of the process is in part size-related, and therefore has limited utility for assessing taxonomic relationships.

The jugal is similar to those of most other large theropods in that it separates the maxilla and lacrimal to take part in the rim of the antorbital fenestra. The long, sloping anteroventral edge sits in a shallow trough on the posterodorsal margin of the maxilla. The lateral surface is depressed anteriorly where it contributes to the antorbital fossa. This region has been damaged somewhat, but there were almost certainly pneumatic openings into the body of the jugal as in other specimens of *Acrocanthosaurus* (Stovall & Langston 1950; Harris 1998a), some specimens of *Allosaurus* (USNM 4734, UUVP 1403, UUVP 3894, UUVP 3981), *Monolophosaurus*, *Sinraptor* and tyrannosaurids. The postorbital process of the jugal (NCSM 14345, OMNH 10146) is a huge triangular plate of bone in lateral view, and has a long sloping contact with the postorbital bone that only reaches two thirds of the way up the postorbital bar. The lateral surface of this part of the jugal is shallowly concave as in *Daspletosaurus* Russell, 1970, *Tarbosaurus* and *Tyrannosaurus*. Similar to *Allosaurus*, *Ceratosaurus*, *Sinraptor* and *Deinonychus* Ostrom, 1969, the jugal forms the ventroposterior margin of the orbit. Like all theropods except *Sinraptor dongi*, the quadratojugal process of the jugal splits posteriorly into two. The uppermost prong of the quadratojugal process is much shorter than the ventral prong as in all large theropods except abelisaurids (Bonaparte *et al.* 1990; Sampson *et al.* 1998), *Ceratosaurus* and torvosaurs (Bakker *et al.* 1992).

The holotype of *Acrocanthosaurus* (Stovall & Langston 1950) has an inferior process on the squamosal that expands moderately ventrally for its contact with the quadratojugal. The two bones then invade the lateral temporal fenestra to a greater extent than is seen in *Allosaurus* and sinraptorids, but not as much as in tyrannosaurids. The inferior process of the squamosal is indented by a deep quadrate cotylus, and the head of the quadrate would have been exposed laterally. Posteroventrally, the squamosal extended along the dorsal surface of the paroccipital process, covering up the ventrolateral process of the parietal and wrapping around onto the anterodorsal surface of the distal end of the paroccipital process. The squamosal was inclined in such a manner that it would have roofed over the posterior temporal musculature.

A conspicuous midline ridge on the supraoccipital is comparable with those of carcharodontosaurids, sinraptorids and *Allosaurus* (Madsen 1976). Dorsally the supraoccipital expands on either side of the midline until it protrudes in a double boss 5 cm behind the nuchal crest. The dorsal surfaces of these knobs are rugose, and are only a few millimetres below the highest point on the parietal. Stovall & Langston (1950) reported that the supraoccipital was excluded from the margin of the foramen magnum by the exoccipitals, although fusion makes it difficult to be sure that this is the case. The lateral margins of the supraoccipital are nearly vertical, and are more similar to those of *Allosaurus* (Madsen 1976) than to *Sinraptor*.

The paroccipital process is relatively wide but shallow, in contrast with the deeper tyrannosaurid condition. Distally the process ends in a vertical sheet of bone 2.5 cm thick and 11 cm high. The paroccipital process turns downwards distally (Stovall & Langston 1950) as in *Allosaurus* and *Sinraptor*, and does not project as strongly backwards (Fig. 3A) as it does in *Carcharodontosaurus* (Sereno *et al.* 1996), *Giganotosaurus* (MUCPv-CH-1) and *Sinraptor* (Currie & Zhao 1993). In the holotype, at least two branches of the twelfth cranial nerve emerge through a depressed area between the occipital condyle and the paroccipital process.

The quadrate is a relatively tall bone (31 cm) as in almost all theropods except *Allosaurus* and tyrannosaurids, and is only shallowly concave posteriorly. The condyles of the jaw articulation are at least 11 cm across. There is a quadrate foramen with a diameter of 28 mm. Except for a narrow slit, it is completely surrounded by the quadrate as in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993). The gap is closed by the quadratojugal, which also curves onto the occiput where it overlaps the quadrate somewhat along the dorsolateral margin of the foramen.

The occipital condyle (Fig. 3C) is nearly circular in appearance, which contrasts with the flattened oval appearance of the occipital condyles of *Giganotosaurus*, *Piveteausaurus* Taquet & Welles, 1977 and *Tyrannosaurus*. The shape of the occipital condyle is characteristic of theropods that carry their skulls at the end of an extended neck. In spite of the large size of the specimen, the sutures between the exoccipital and basioccipital are still visible in the occipital condyle.

Palatal elements are generally obscured by the other bones of the skull. The palatine and ectopterygoid of *Acrocanthosaurus* have been described for SMU 74646 (Harris 1998a).

There are four premaxillary, 15 maxillary and an unknown number of dentary tooth positions. The third premaxillary tooth is the largest on the left side, attaining a dorsoventral length of 85 mm and a basal diameter of 27 mm. It is 72% the length of the largest maxillary tooth. *Allosaurus* and *Neovenator* Hutt, Martill & Barker, 1996 have five premaxillary teeth, *Ceratosaurus* and *Torvosaurus* (BYU 4882) have three, and most other theropods, including abelisaurids, *Eustreptospondylus* Walker, 1964, *Herrerasaurus*, *Marshosaurus* Madsen, 1976, *Monolophosaurus*, *Proceratosaurus* Woodward 1910, *Sinraptor*, tyrannosaurs and *Yangchuanosaurus*, have four. Because the premaxillae meet at an acute angle, the premaxillary teeth are not D-shaped in section as they are in tyrannosaurids (Currie *et al.* 1990). In fact, even in the first premaxillary tooth of *Acrocanthosaurus*, the anterior carina is positioned on the midline of the tooth at the tip. However, it curves onto the anteromedial surface closer to the root as in allosaurids and dromaeosaurids, but in contrast with *Torvosaurus* (Britt 1991). *Ceratosaurus* has no anterior carina on premaxillary teeth (Bakker, pers.

comm. 1993). There are 15 denticles per 5 mm on the anterior carina, and 13 on the posterior. The longest crown (fourth from the front) in the left maxilla is 118 mm high, with a FABL (fore-aft base length) of 41 mm. This is comparable in length with the longest tooth of a similar sized tyrannosaurid (GI 107/2, *Tarbosaurus*, has a skull length of 122 cm and a maximum maxillary tooth length of 115 mm), with the exception of *Tyrannosaurus* which seems to have had more elongate teeth (AMNH 5027 has a skull length of 136 cm and a maxillary tooth length of 142 mm). Although the maxillary teeth are narrower and more blade-like than those of tyrannosaurids, they are not as laterally compressed as the teeth of carcharodontosaurids (Sereno *et al.* 1996). For example, the ratio of length to width of a cross-section of the base of an *Acrocanthosaurus* tooth described by Harris (1998a) is 0.63, compared with 0.43 in a selection of carcharodontosaurid teeth (casts in Tyrrell Museum of privately owned specimens from Morocco). Furthermore, the teeth of *Acrocanthosaurus* do not have the wrinkles in the enamel that are characteristic of carcharodontosaurid teeth (Sereno *et al.* 1996; Harris 1998a).

In spite of the large size of the teeth in NCSM 14345, the denticles are minute (the second premaxillary tooth has 12.5 per 5 mm on the posterior carina; the fourth maxillary tooth has 17.5 per 5 mm on the anterior carina, and from 12.5 to 17.5 on the posterior edge). This is even less than the denticle size of *Carcharodontosaurus*, where there are 10 serrations per 5 mm in a tooth with a FABL of 36 mm (Russell 1996). Harris (1998a) pointed out that the denticles extend across the tips of *Acrocanthosaurus* teeth, and suggested this is unusual. However, it is the same situation in a diverse assemblage of theropods that includes carcharodontosaurids, velociraptorine dromaeosaurids, and tyrannosaurids, so this feature has limited taxonomic utility.

Lower jaw

The lower jaw (132.5 cm long) is well-preserved on both sides, although crushing has damaged some of the thinner bones, especially along the intramandibular articulation and around the margins of the external mandibular fenestra. The external mandibular fenestra is preserved on both sides, although it is difficult to precisely define the margins. It appears to have been about 20 cm long, which is significantly larger than that of *Allosaurus* (Madsen 1976). It is positioned at the junction of the dentary, angular and surangular. The jaw is shallow anteriorly, and deep posteriorly. The depth has been emphasized somewhat by collapse of the adductor fossa.

As in almost all theropods (Bakker *et al.* 1988), including *Herrerasaurus* (Sereno & Novas 1992), there is an intramandibular joint. A posteriorly projecting lateral process of the dentary near the dorsal margin, referred to by Currie & Zhao (1993) as the intramandibular process of the dentary, fits into a slot in the labial side of the surangular. An anteriorly projecting tongue, the intramandibular process of the surangular, extends ventrolateral to the intramandibular process of the dentary to form a combination sliding and pivoting joint. Ventrally, the anterior end of the angular had a sliding joint along the top of a shelf formed by the dentary and the splenial.

The dentary is relatively long and low, with generally concave upper and lower margins in lateral view. It is unusual in having a distinctive ventral process at the bottom of the symphysis, which gives the front of the jaw (10 cm high) an angular, squared off appearance. This is even more conspicuous in *Giganotosaurus*, but is also present to a lesser degree in large tyrannosaurids, suggesting that it may be a size-dependent character. The lateral surface, especially at the front of the bone, is pierced by a dorsal row of relatively large mental foramina for innervation and vascularization of the skin and lips. The smooth surface of the bone contrasts with the ornamented surface in *Abelisaurus* (Bonaparte & Novas 1985). The front of the jaw is relatively shallow and is only 96 mm deep at mid-length. For comparison, the same measurement in AMNH 5881, a specimen of *Tyrannosaurus rex* with a slightly shorter jaw, is 170 mm. Posteriorly, the dentary is deep (19 cm at the front of the intramandibular articulation, and almost 10 cm deeper at the back). Its posterior margin slopes posteroventrally from the lock-

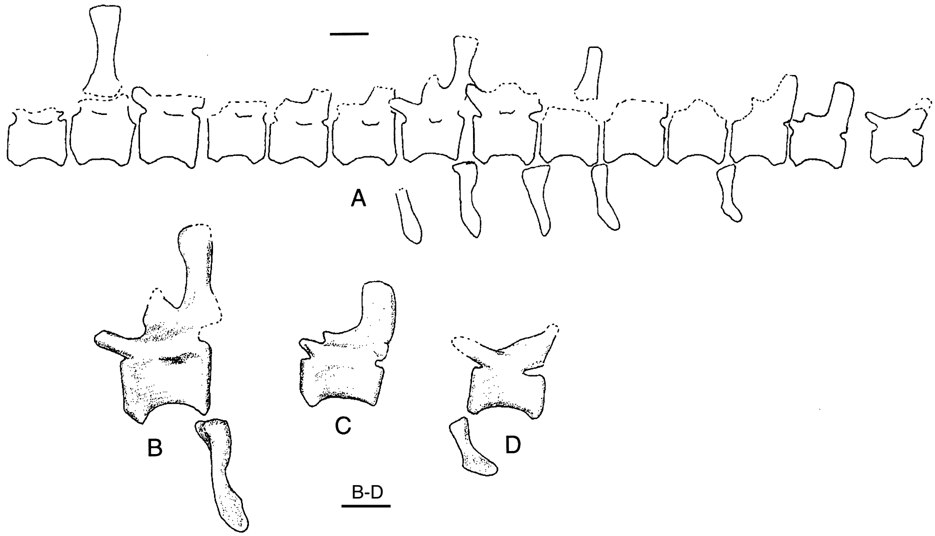

FIG. 4. — *Acrocanthosaurus atokensis* NCSM 14345, caudal vertebrae; **A**, preserved series in left lateral view; **B**, mid-caudal (seventh one in preserved series) vertebra with haemal arch; **C**, ninth caudal in preserved series; **D**, distal caudal (twelfth in preserved series) with preceding haemal spine. Scale bars: A, 10 cm; B-D, 5 cm.

ing intramandibular joint. Two notches in the back of the dentary on the lower, left side are probably the result of postdepositional damage, but are fortuitous in that they expose part of the sliding joint with the angular.

The splenial presumably wrapped around the ventromedial margin of the angular, thereby forming part of the sliding intramandibular joint. However, it does not wrap around far enough to be exposed in lateral view as in *Herrerasaurus* (Sereno & Novas 1992), *Ceratosaurus* (USNM 4735), dromaeosaurids (Currie 1995) and other primitive theropods.

The anterior surangular foramen of the surangular is continuous anteriorly with a groove as in *Allosaurus*, *Monolophosaurus*, *Sinraptor* and other theropods. The lower margin of the groove is formed anteriorly by a finger-like process that extends laterally over the labial surface of the dentary. A similar finger-like process of the dentary contacts the medial and dorsal margins of the groove. There is an extensive squamose suture for the angular, and posterolaterally the surangular covers part of the prearticular. Stovall & Langston (1950) suggested that the posterior surangular foramen of OMNH 10146 was relatively large, as it is in tyrannosaurs. However, it is relatively small (diameter of 12 mm) in NCSM 14345, where this region is better preserved. It is found anterolateral to the glenoid beneath a powerful lateral ridge that overhangs the lateral surface of the jaw by about 5 cm. This ridge is more powerfully developed than in any other known large theropod other than *Giganotosaurus* (MUCPv-CH-1), although it is also pronounced in abelisaurids (MACN-CH 894). Harris (1998a) noted the presence of a conspicuous knob on the surangular shelf close to the jaw articulation. As in other theropods, the surangular of *Acrocanthosaurus* forms part of the lateral mandibular glenoid (Harris 1998a).

The angular is a shallowly curved plate of bone strengthened by a thick ventral margin. An extensive part of the bone is overlapped laterally by the dentary, but the contact is smooth, and sliding movement was possible. Posteriorly, the angular laterally overlaps the surangular. The ventral edge of the angular is thickest where it forms the ventral margin of the jaw behind the intramandibular joint. Unlike *Allosaurus* but like most other theropods, the posterior end of the angular terminates anterior to the posterior surangular foramen. The dorsal edge of the supradentary can be seen behind the last mandibular tooth extending pos-

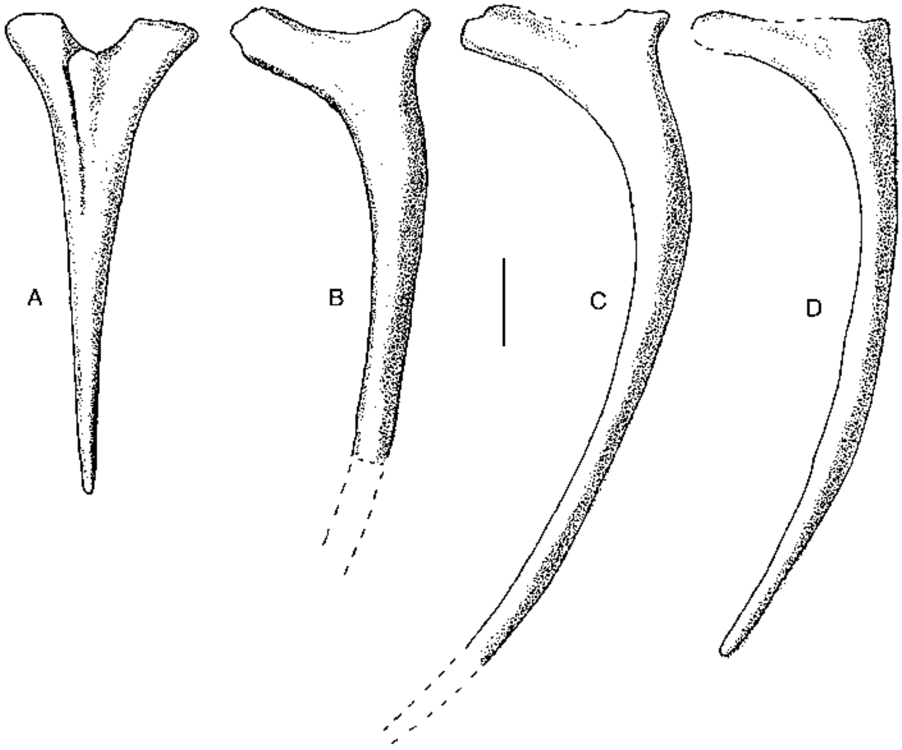

FIG. 5. — *Acrocanthosaurus atokensis* NCSM 14345; **A**, posterior cervical rib; **B**-**D**, dorsal ribs. Scale bar: 10 cm.

teriorly across the intramandibular joint. It cannot be determined whether it was fused to the coronoid or not, although it was presumably capable of restricted sliding movement against the surangular laterally and the prearticular medially as in *Monolophosaurus* (Zhao & Currie 1993). The posteroventral margin of the prearticular is exposed in lateral view where it extends to the back of the jaw.

The medial glenoid and most of the interglenoid ridge for the jaw articulation are found on the articular. Harris (1998a) reported that the interglenoid ridge of SMU 74646 is relatively low compared with that of *Allosaurus*. Overall, the articular looks relatively short in lateral view because of the posteromedial orientation of the retroarticular process, but is in fact much larger than it is in *Allosaurus* (Gilmore 1920; Madsen 1976) and tyrannosaurids (Lambe 1917; Osborn 1912; Molnar 1991).

Axial skeleton

Almost two dozen partial vertebrae were recovered from the skeleton, but, with the exception of three caudals, none are complete (Fig. 4). From what can be seen of the vertebrae and a number of isolated neural spines, vertebrae of NCSM 14345 did not differ in any substantial way from those found with the holotype (Stovall & Langston 1950) and SMU 74646 (Harris 1998a). A fragment of a posterior cervical or anterior dorsal centrum is pierced by two pneumatopores as in OMNH 10146 and SMU 74646. The internal pneumatization is of the complex type (Britt 1993), in contrast with the simple pneumatization found in *Allosaurus* and *Sinraptor*. This has also been noted in SMU 74646 (Harris 1998a). The neural spines in the middle and distal parts of the tail are restricted to the posterior region of the vertebrae. As in the caudal vertebrae described by Stovall & Langston (1950) and Harris (1998a), there is a “cranial process” above the anterior insertion region for the interspinous ligaments (Fig. 4B, C). Mid-caudal centra are about 16 cm long, 10 cm wide and 11.5 cm high, whereas the most distal one preserved is 12 by 7.5 by 7.5 cm. The distal caudal has a moderately elongate prezygopophysis (Fig. 4D).

Six chevrons (Fig. 4) from the mid-caudals are directly comparable in overall shape with those of *Allosaurus* (Madsen 1976), and in spite of elongation of the neural spines, do not appear to be any more elongate than in the Jurassic theropod.

One elongate cervical rib (Fig. 5A) has a prominent knob projecting anterolaterally from between the tuberculum and capitulum. Most of the ribs from the dorsal region are represented in the collection, but fewer than half a dozen are complete. They are directly comparable with those of *Allosaurus* (Madsen 1976), and show that *Acrocanthosaurus* had a rather high, narrow body. There were also many fragmentary gastralia recovered, but there is nothing to suggest that the gastral basket was different in any substantial way from other specimens of *Acrocanthosaurus* (Harris 1998a).

Appendicular skeleton

All elements of the pectoral girdle (Fig. 6) and front limb (Fig. 7) are represented except for some of the unguals. The arm is relatively short. The sum of the lengths of the humerus, ulna (excluding the olecranon process), ulnare, metacarpal II and digit II is 105 cm, which is shorter than either the scapulocoracoid (118 cm) or the femur (128 cm). In contrast, *Allosaurus* has a relatively longer arm. That of MOR 693 is 94 cm long, which is 30% longer than the scapulocoracoid. The arm of *Acrocanthosaurus* is 81% the length of the femur, whereas the arm of *Allosaurus* is 26% longer than the femur in MOR 693 and 12% longer in USNM 4734. The differences are less evident in the humerus than they are in the forearm and hand, where specimens of *Allosaurus* (MOR 693, TATE 11, USNM 4734) that are 20% smaller than *Acrocanthosaurus* have radii, ulnae and metacarpals that are absolutely longer than the same elements in *Acrocanthosaurus*. This shows that the differences in arm length between the taxa cannot be attributed to allometric scaling. Tyrannosaurids, on the other hand, have even shorter arms than *Acrocanthosaurus*. The humerus is about 30% the

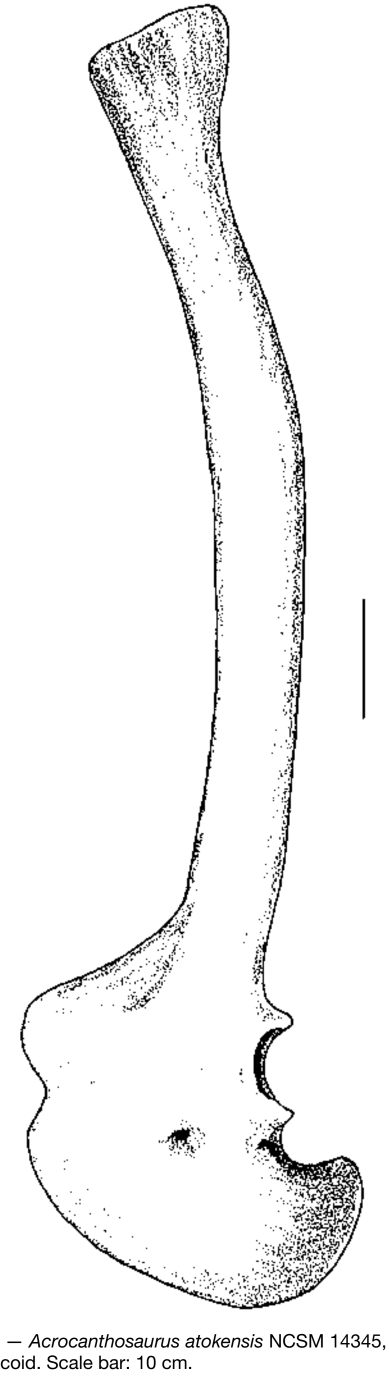

FIG. 6. — *Acrocanthosaurus atokensis* NCSM 14345, left scapulocoracoid. Scale bar: 10 cm.

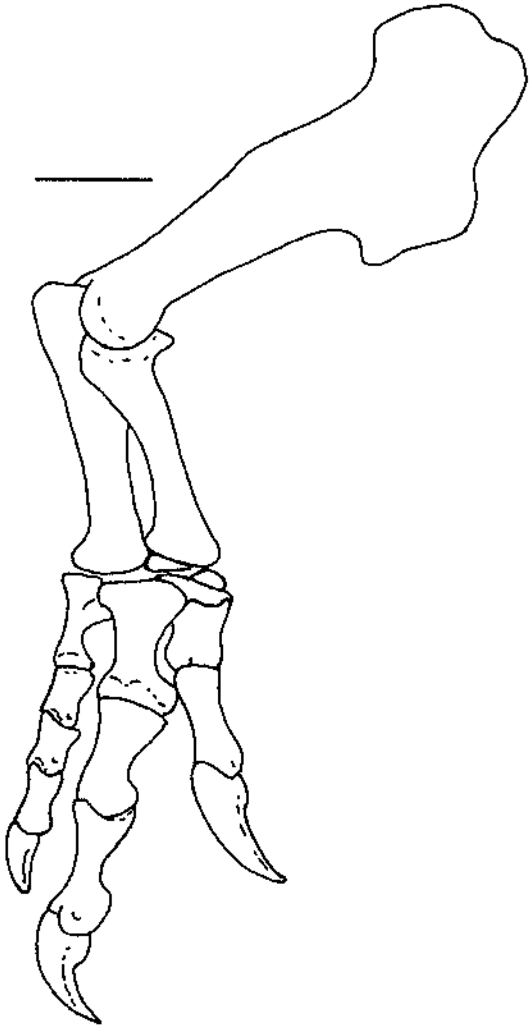

FIG. 7. — *Acrocanthosaurus atokensis* NCSM 14345, reconstruction of right arm. Scale bar: 10 cm.

length of the femur in both *Acrocanthosaurus* and *Tyrannosaurus*, but the forearm is relatively shorter in the latter. The front limb of *Tarbosaurus* (GI 107/2) is 65 cm in length, which is 93% the length of the scapulocoracoid and 60% the length of the femur, whereas that of one *Tyrannosaurus rex* (FMNH PR2081) is 89 cm long, which is less than 70% of either scapulocoracoid or femur length.

The scapula is a long, slender, gently curved element (Fig. 6), 97 cm (103 cm measured on the outside curve) long. It is only 9.5 cm wide at its narrowest point when seen in lateral aspect, and the distal end is only moderately expanded. The acromial process is pronounced and is sharply offset from the anterodorsal margin of the scapular blade as in *Allosaurus* (Madsen 1976), *Sinraptor* (Currie & Zhao 1993) and tyrannosaurids (Maleev 1974). The scapular blades of *Ceratosaurus* (Madsen 1976), *Carnotaurus* (Bonaparte *et al.* 1990), *Edmarka* Bakker *et al.*, 1992 and *Torvosaurus* (Bakker *et al.* 1992), and *Megalosaurus* Buckland, 1824 (Walker 1964) are more robust, and the anterior margin grades smoothly into the acromion process.

The outline of the coracoid (Fig. 6) is also closer to that of *Allosaurus* than it is to *Ceratosaurus* (Madsen 1976) or megalosaurs (Bakker *et al.* 1992). The coracoid foramen is a small but conspicuous opening close to the centre of the bone. The coracoid extends posteroventrally well beyond its contribution to the glenoid as in advanced theropods plus abelisaurids.

The humerus (Fig. 8) is a rather massive element 37 cm long. The proximal end is expanded to such a degree that its maximum width is half the length of the bone. The deltopectoral crest is large (9.5 cm) and well-developed, protruding 6.5 cm from the shaft (Fig. 8E). Unlike *Allosaurus*, which has a deltopectoral crest that tapers steadily away from the shaft, that of *Acrocanthosaurus* is quadrilateral in outline. There is a well-developed scar for the humeroradialis muscle (Fig. 8E). The transverse shaft diameter is only about a third the width of the proximal end, and slightly less than half of the distal expansion. The distal end is rotated outward from the plane of the proximal end (Fig. 8B), and the deltopectoral crest is oriented at right angles to the distal end of the bone (Fig. 8G) as in *Allosaurus*. There is a deep pit on the anteroventral side proximal to the radial condyle and the ulnar groove (Fig. 3C). The entepicondyle is a small (1.5 cm) but pronounced tubercle (Fig. 8D) separated from the radial condyle by a groove of finished bone, although finished bone continues from the distal end of the humerus up along the crest of the tubercle. In

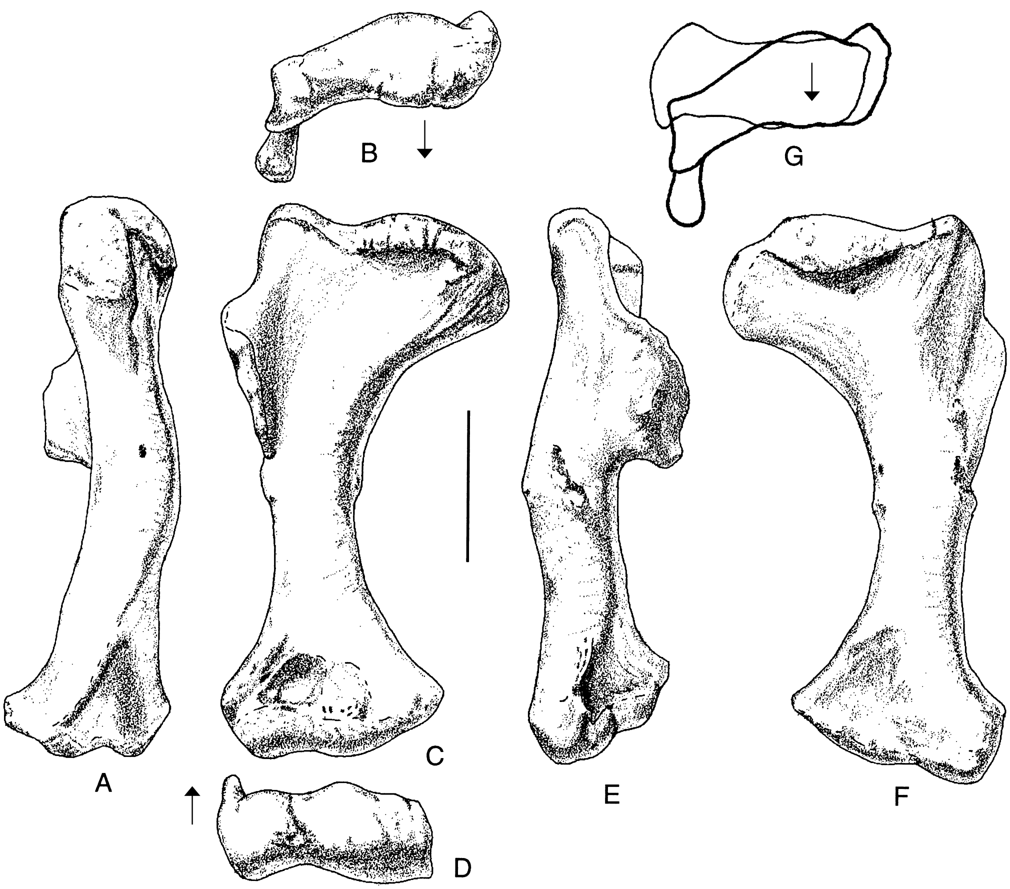

FIG. 8. — *Acrocanthosaurus atokensis* NCSM 14345, right humerus; **A**, medial aspect; **B**, proximal aspect; **C**, posterodorsal aspect; **D**, distal aspect; **E**, lateral aspect; **F**, anteroventral aspect; **G**, outlines of proximal (bold) and distal (light) ends. Scale bar: 10 cm.

most characters, the humerus of *Acrocanthosaurus* is like that of *Allosaurus*, and most of the differences seem to be allometric changes related to the larger size of the Cretaceous form. However, the shaft is not as twisted along its length as it is in *Allosaurus*.

The ulna is a robust bone with a total length of 25.5 cm, almost 15% of which is composed of the olecranon process (Fig. 9). The proximal concavity that contacts the proximal end of the radius has neither articular facets nor strong ligamentous attachments. However, there is a well-defined distal articulation for the radius, which consists of a convex surface of unfinished bone elevated almost a centimetre from the general contour of the ulna by a pedestal of bone (Fig. 9C, lower right). Amongst described theropods, the ulna most closely resembles that of *Allosaurus* (Madsen 1976), although it is relatively shorter (69% the length of the humerus, compared with 85% the length in USNM 4734). The radial notch of the ulna is not as deep or prominent as in *Allosaurus*.

The radius (Fig. 9) is a curved, slender element that is difficult to measure. The straight line length is 22 cm, whereas the distance between the closest points of the articular surfaces is only 20 cm. It is therefore 55% to 60% of the length of the humerus, whereas the radius of *Allosaurus* is more than 70% of humerus length (Gilmore

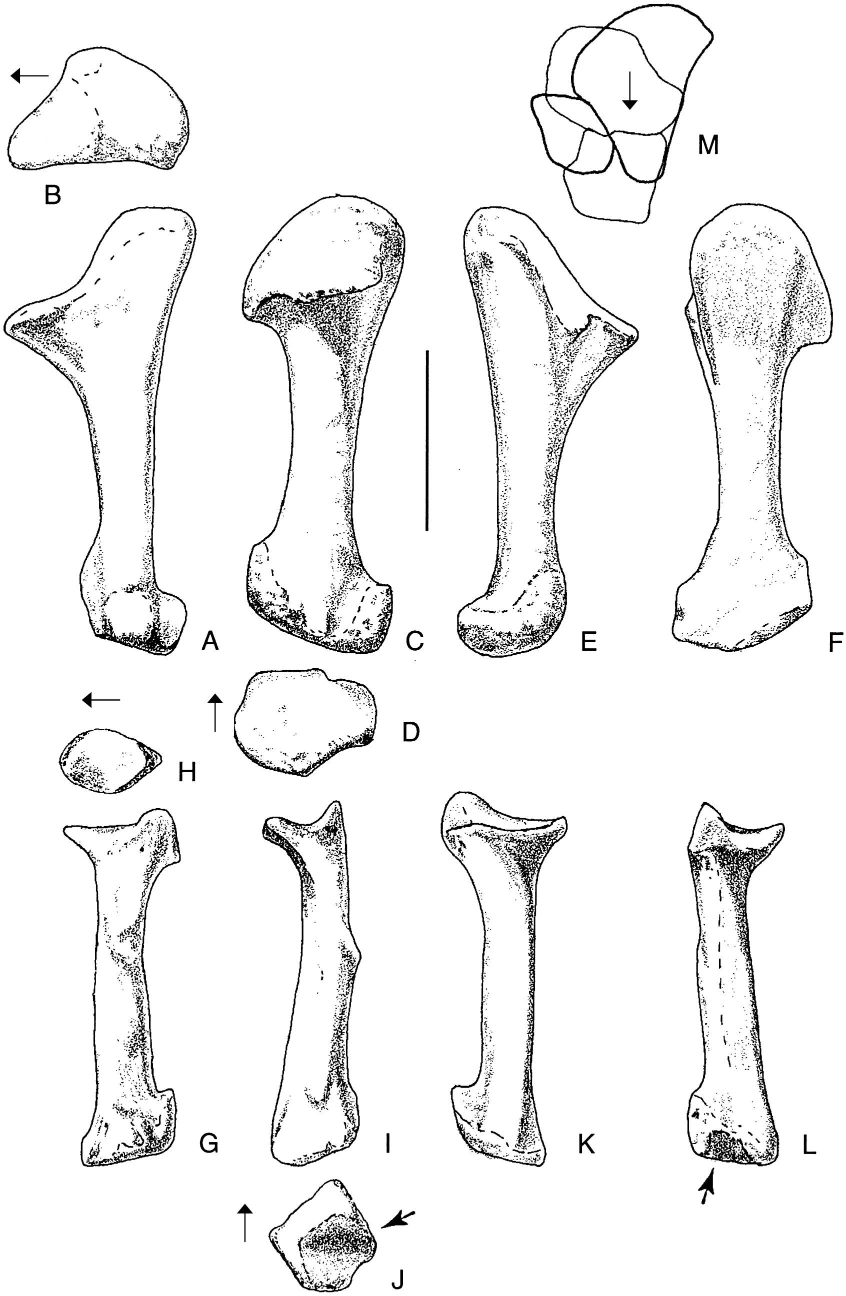

FIG. 9. — *Acrocanthosaurus atokensis* NCSM 14345; **A**-**F**, right ulna; **A**, medial view; **B**, proximal view; **C**, anterior view; **D**, distal view; **E**, lateral view; **F**, posterior view; **G**-**L**, radius; **G**, medial view; **H**, proximal view; **I**, anterior view; **J**, distal view; **K**, lateral view; **L**, posterior view; **M**, outlines of proximal (bold) and distal (thin) ends of articulated ulna (upper) and radius (lower) with the arrow pointing towards the anterior side of the forearm. Scale bar: 10 cm.

1920). The proximal articulation is trapezoidal (Fig. 9H) with a maximum mediolateral width of 6 cm and an anteroposterior length of 5.2 cm. It is saddle-shaped with strong anterior and posterior ridges. The trough-like articulation continues medially onto the ulna. The edge of the proximal end is rugose where it contacts the ulna. Distal to the proximal articulation, the shaft of the radius curves anteromedially (Fig. 9I) as it twists around the front of the ulna, closely following the curvature of that bone. A well-defined, twisting ridge with a rugose surface (Fig. 9I) lies close to the anterior margin of the ulna and presumably marks the line of ligamentous attachments with its neighbor. The lower half of the bone has an almost straight shaft, although the distal end is set off at an angle to it (Fig. 9I, K). There is an extensive elevated area (about 4 cm wide and 2 cm high) posteromedially near the distal articulation for contact with the ulna. Its rugose surface, and that of the corresponding region of the ulna, suggests that the ligamentous attachments were strong and movement between the bones was limited. This also would have restricted rotation of the wrist. The distal articular surface is a shallow concavity that would have articulated with the radiale.

Three carpals were recovered with the specimen (Figs 10; 11). One of these elements was preserved in articulation with the metacarpals of the right hand. Furthermore, it fits perfectly across the head of metacarpal I and extends about a quarter of the way across the head of metacarpal II. This element has been identified as the intermedium in other theropods, including *Allosaurus* (Gilmore 1920), *Gorgosaurus* (Lambe 1917) and *Tarbosaurus* (Maleev 1974), although Madsen (1976) identified it as distal carpal I (with carpal II fused into it in 14 out of 18 specimens of *Allosaurus*), as did Osborn (1917) for *Struthiomimus*, Russell & Dong (1993) for *Alxasaurus* and Padian & Chiappe (1997) for maniraptorans. Colbert identified the carpal in this position in *Coelophysis* Cope, 1889 as distal carpal I + II. In this paper, we refer to it as distal carpal I because it occupies the primitive position (Sereno 1993) of this element above the contact between metacarpals I and II. However, we also recognize that it was probably formed by the fusion of several elements as in *Allosaurus*. Regardless of what name should be put on this element, it is morphologically similar to the same unit in *Allosaurus*, therizinosaurids and tyrannosaurids.

Distal carpal I is a complex element that is closely appressed to metacarpals I and II. This close association shows that little movement would have been possible amongst these three elements, all of which were tightly integrated. At its thickest point above the posterior junction of metacarpals I and II, it is 16.2 mm thick proximodistally. Lateromedially it measures 60.8 mm close to the extensor surface and is 52.4 mm anteroposteriorly. In comparison, one of the larger distal carpals from the Cleveland-Lloyd collection of *Allosaurus* elements is thicker (24 mm), narrower (50 mm at the extensor surface) and anteroposteriorly longer (54 mm). The anterior (extensor) surface (Figs 10C; 11B) is a thin edge of finished bone (it is tall in *Allosaurus*, Madsen 1976) that aligns with the anterior margin of metacarpal I. This surface is rugose and pitted like the proximoanterior surface of the first metacarpal, suggesting there were strong ligamentous attachments between these bones. Lateral to the junction of metacarpals I and II, the distal surface (Fig. 10B) becomes concave, rising up to cover the proximal articular surface of the second metacarpal. Concurrent with this, the carpal thins laterally and withdraws from the extensor surface to leave part of the proximal articular surface of metacarpal II exposed anteromedially (Fig. 11A). The posterior (flexor) surface of the carpal is partially composed of a surface of finished bone above the junction of the two metacarpals (Figs 10D; 11D). Medial to this, the carpal thins and withdraws from the flexor surface (Fig. 11A) to wrap around the margin of a depression in the proximoposterior surface of the first metacarpal. This is where the troughlike “pulley” articulation of the carpal passes onto the metacarpal. Medial to the depression in the metacarpal, the posterior edge of the carpal approaches the flexor surface of the metacarpal, although it remains a thin edge between convex proximal and distal articular surfaces (Fig. 11C).

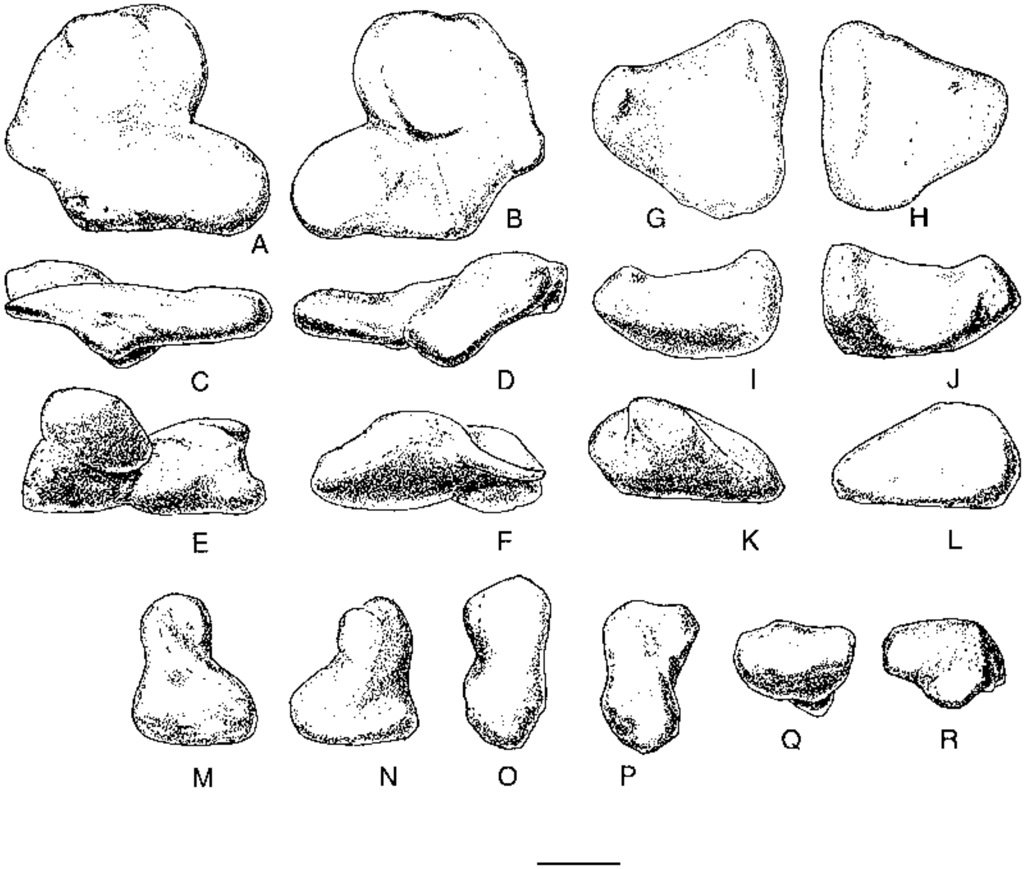

FIG. 10. — *Acrocanthosaurus atokensis* NCSM 14345, carpals; **A**-**F**, distal carpal I; **A**, dorsal view; **B**, ventral view; **C**, anterior view; **D**, posterior view; **E**, medial view; **F**, lateral view; **G**-**L**, ulnare; **G**, dorsal view; **H**, ventral view; **I**, medial view; **J**, lateral view; **K**, anterior view; **L**, posterior view; **M**-**R**, radiale; **M**, dorsal view; **N**, ventral view; **O**, medial view; **P**, lateral view; **Q**, anterior view; **R**, posterior view. Scale bar: 2 cm.

The proximal surface has a distinct trough that starts from the emarginated posteromedial region (Fig. 10A) and extends anterolaterally to the lateral surface (Fig. 10F). A less prominent trough-like depression isolates the convex anteromedial region of the proximal surface. The distal surface of the carpal (Fig. 10B) has a prominent ridge that follows the junction of the first and second metacarpals. The more lateral articular surface for the second metacarpal consists of shallow anterior and posterior depressions separated by a weak lateromedial ridge (emphasized anteriorly by a shallow trough). The lateral articular surface fits perfectly on a pair of low convex surfaces on the second metacarpal. The medial articulation on the distal surface is more complex. It contacted the first metacarpal in three areas. The most medial one is the largest, and is a flattened saddle-shaped articulation. This is separated from the other articulations by a channel that seems to have been utilized by blood vessels or nerves. It is deep and well-defined on the distal surface of the carpal where it enters posteriorly the region of articulation with the first metacarpal from the flexor surface, but becomes less distinct as it divides into two troughs. The more medial one exits the extensor surface via a well-marked canal in the proximal surface of the first metacarpal. The other branch turns to become the shallow trough anterior to the low mediolateral ridge that

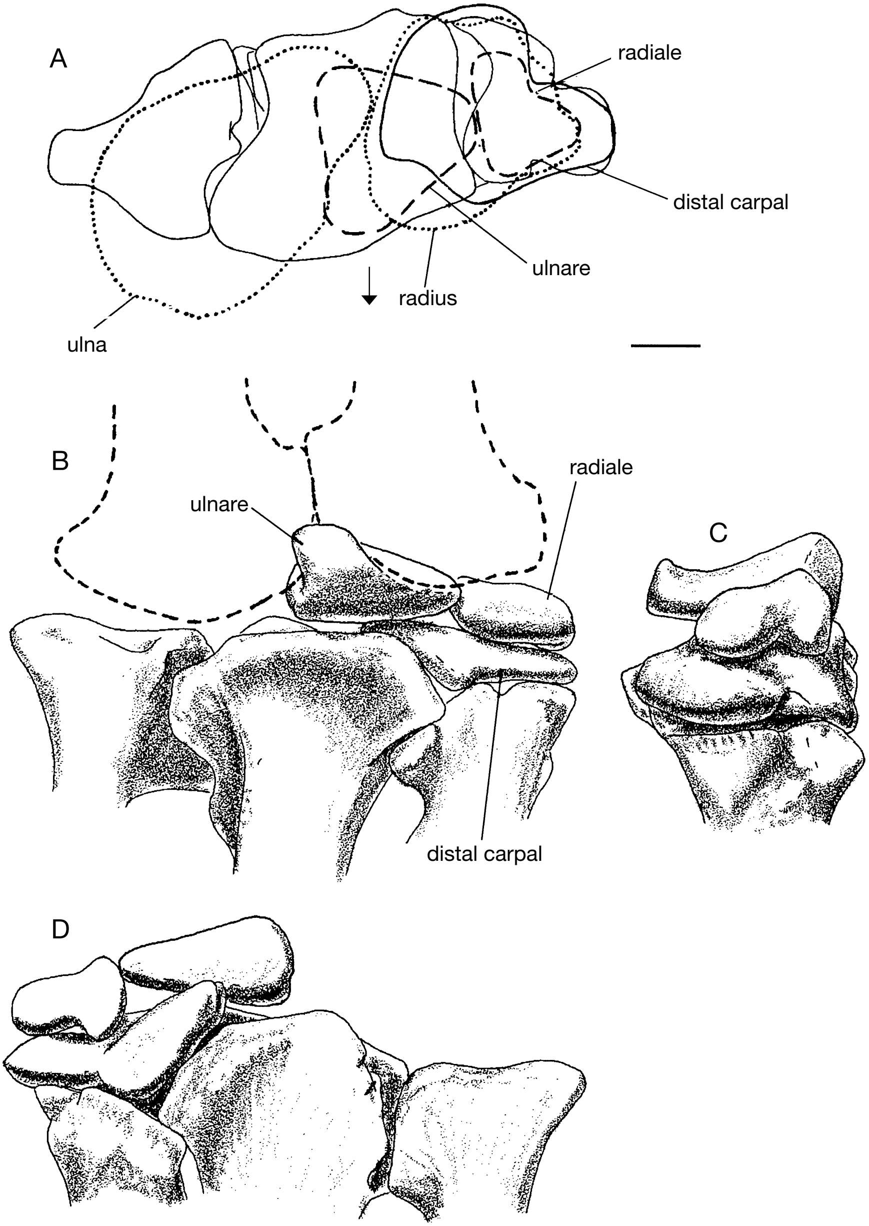

FIG. 11. — *Acrocanthosaurus atokensis* NCSM 14345, reconstruction of the right wrist; **A**, dorsal aspect; **B**, anterior aspect; **C**, medial aspect; **D**, posterior aspect. Scale bar: 2 cm.

divides the lateral articulation into anterior and posterior components. Overall, then, the distal articular surface has a total of five contacts with the first and second metacarpals.

The ulnare closely resembles that of *Allosaurus* (Madsen 1976). In proximal and distal aspects (Fig. 11G, H), the bone is quadrangular, although the anterolateral side is so short that it looks trian-

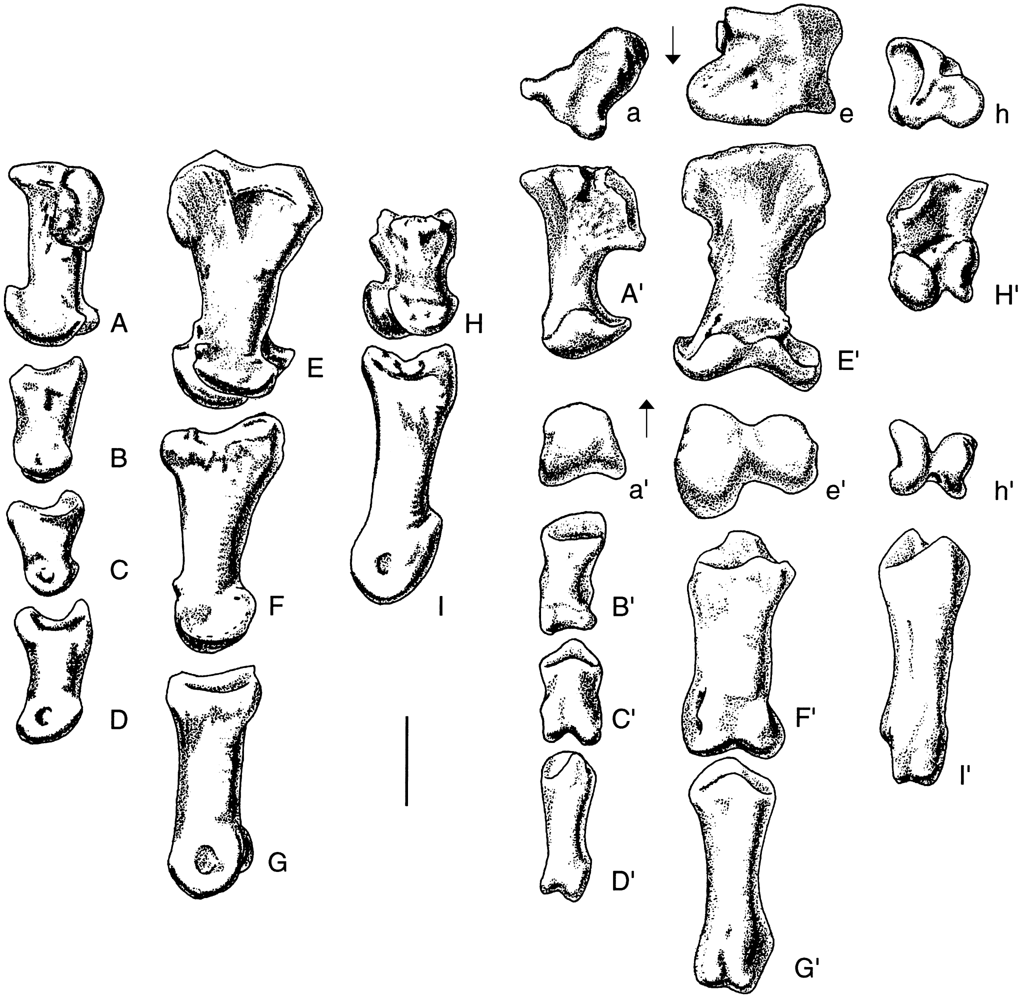

Fig. 12. — *Acrocanthosaurus atokensis* NCSM 14345, right manus. Metacarpals (**A**, **E**, **H**) and phalanges (**B**, **C**, **D**, **F**, **G**, **I**) in proximal (**a**, **e**, **h**), medial (far left), anterior (‘), lateral (“) and posterior (“‘, far right). Scale bar: 5 cm.

gular. The anterolateral face has a convex surface and an oval outline (Fig. 10K). The longitudinal axis of the oval is 18 mm long. The posterior side of the carpal (Fig. 10L) is triangular (41 mm wide and 23 mm high) and has an almost flat surface. The proximal surface is saddle-shaped (in section it is concave along the anteroposterior axis, and convex perpendicular to that axis) and the distal surface (Fig. 10H) is mostly convex.

The smallest of the carpals is the radiale (Figs 10; 11), which is 4 cm across and 2.8 cm deep. Most surfaces are convex, and the bone had a sliding anteromedial-posterolateral contact with distal carpal I.

There are three powerfully built metacarpals in *Acrocanthosaurus* (Fig. 12). With the exception of the broadly expanded proximal and distal ends, the metacarpals resemble those of *Allosaurus* (Madsen 1976), *Sinraptor* (Currie & Zhao 1993) and other carnosaurs. *Szechuanosaurus zigongensis* (Gao 1993) also has broadly expanded ends on some of its metacarpals. However, there are many highly significant differences showing this animal is not closely related to *Acrocanthosaurus*, which

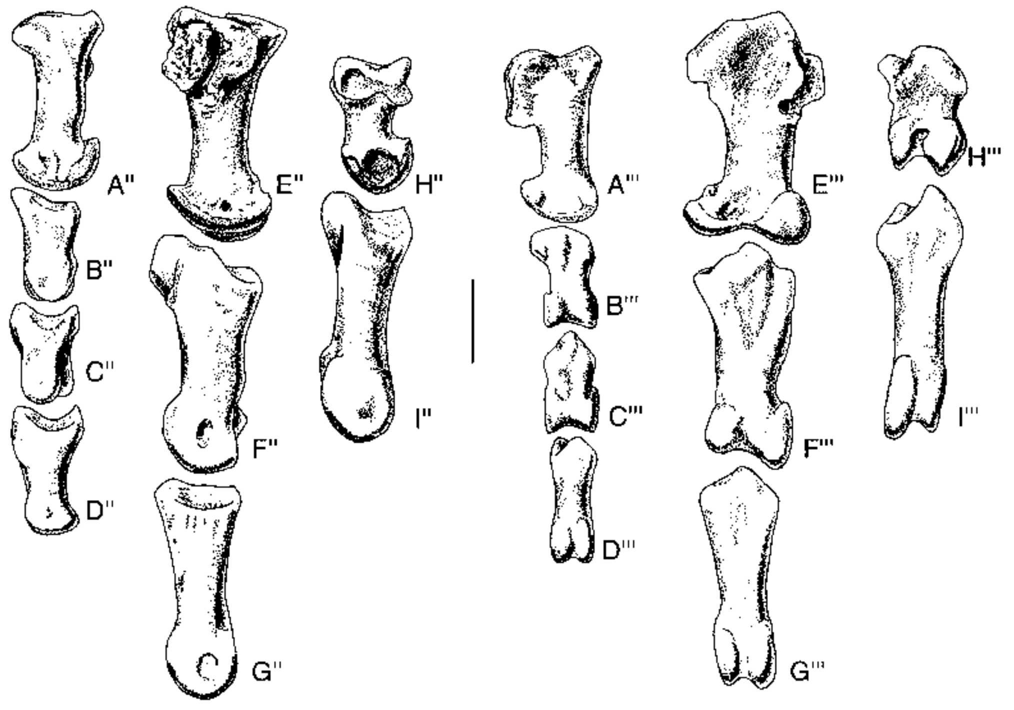

FIG. 12. — *Acrocanthosaurus atokensis* NCSM 14345, right manus. Metacarpals (**A**, **E**, **H**) and phalanges (**B**, **C**, **D**, **F**, **G**, **I**) in proximal (**a**, **e**, **h**), medial (far left), anterior ('), lateral ('') and posterior (''', far right). Scale bar: 5 cm.

suggests that the expanded metacarpal ends probably have functional significance.

The first metacarpal is 62 mm in length. Its proximal and distal heads expand to 50 mm, while the shaft is a flattened oval in section (36 mm transversely, 24 mm anteroposteriorly). In comparison, one of the larger first metacarpals from the Cleveland-Lloyd collection of *Allosaurus* elements is 68 mm long with a proximal expansion of 47, shaft diameters of 45 × 36, and a distal expansion of 53 mm. The proximal end in *Acrocanthosaurus* is closely applied to the lateral surface of the second metacarpal. The roughly triangular proximal articular surface (50 mm lateromedially, 47 mm anteroposteriorly compared with 45 × 50 mm in *Allosaurus*) is complex (Fig. 12A). The lateral half slopes lateroventrally, especially where it articulates with the second metacarpal. This articulation consists mainly of a deep depression close to the flexor surface, but it extends anteriorly to the extensor surface as well. The posteromedial face is emarginated for a distinct, smooth-walled depression that is continuous with an emargination on the posteromedial edge of the first distal carpal. This is continuous with the "trough" of the pulley-like surface of the distal carpal. It may represent the end of a sliding articulation of the "pulley-like" wrist joint. As pointed out, a canal for a blood vessel or nerve enters the region between these two bones on the lateral side of this depression. This canal becomes more obvious on the metacarpal as it passes forward and subdivides, forming a deep trough that cuts into the proximal surface of the metacarpal on the anterior (flexor) surface where the bone is emarginated. The Y-shaped system divides the proximal surface into three articular surfaces for the first distal carpal. The deep lateral depression for the second metacarpal and the posteromedial depression for the end of the "trough" of the "pulley" are characteristic of all avetheropodans (= carnosaurs + coelurosaurs).

There are prominent tubercles with rugosities for the attachment of ligaments in the proximolateral (Fig. 12H") and distomedial regions of the extensor surface (Fig. 12H'). The distal condyles are separated by a deep sulcus (Fig. 12H'). The articular surfaces extend high on the extensor surface, allowing the digit to hyperextend until its shaft is almost perpendicular to the shaft of the metacarpal. In contrast, the first phalanx could not flex much more than 30 degrees. The condyles are asymmetrical so that the first phalanx would have rotated somewhat during extension, when the tip of the claw would have turned more medially. In the degree of rotation and the asymmetry of the condyles, *Acrocanthosaurus* seems to be different from *Allosaurus* (Madsen 1976). There is a deep ligament pit distolaterally (Fig. 12H"), but there is not one medial to the medial condyle (Fig. 12H).

The second metacarpal is 116 mm long, with a maximum proximal breath of 74.5 mm, a transverse shaft diameter of 32 mm, and a distal width of 69.5. In comparison, one of the larger second metacarpals from the Cleveland-Lloyd collection of *Allosaurus* elements is 120 mm long with a proximal expansion of 58, a shaft width of 34 and a distal expansion of 56 mm. In proximal outline (Figs 11A; 12E), the lateral, medial and flexor edges are concave, and the extensor margin is mostly convex. The proximal articular surface extends onto the medial surface posteriorly (Fig. 12E) to form a surprising small facet that articulates with the first metacarpal. On the lateral surface, there are two rugose surfaces on the proximal end for a firm, almost suture-like contact with metacarpal III (Fig. 12E"). There is a 3 mm wide canal between the two surfaces that undoubtedly was used by blood vessels and/or nerves (Fig. 12E"). The course of the canal starts in a deep notch in the anteromedial surface of the third metacarpal (Fig. 12A'), continues distally in the canal on metacarpal II, and exits on the flexor surface distal to the contact between metacarpals II and III, just proximal to a prominent ligament tubercle (Fig. 12E'"). Shallow depressions are all that represent the colateral ligament pits on the medial and lateral condyles. These are highly developed in *Allosaurus* (Madsen 1976), *Sinraptor* (Currie & Zhao 1993) and most other large theropods. The condyles are highly asymmetrical (Fig. 12E'), the lateral one having a much greater anteroposterior surface. The joint allows the first phalanx of the second digit to hyperextend as much as it flexes (about 40 degrees), and turns the digit so that the tip of the claw would have rotated medially during flexion and laterally during hyperextension. As in the first metacarpal, the disparity in distal condyle size and function is much greater than it is in *Allosaurus*.

The third metacarpal is 89 mm long, about 53 mm across proximally, has a shaft diameter of 22 mm, and a distal width of 39 mm. The equivalent measurements in a large *Allosaurus* are 105 (length), 38 (proximal), 12 (shaft diameter) and 29 mm (distal width). The bone has a pronounced posteromedial expansion (Fig. 12A) where it contacts the second metacarpal in what must have been a virtually immobile joint. There is a suture-like contact with the adjacent metacarpal on the posteromedial expansion, bound anteriorly by a well-defined canal for a blood vessel or nerve (Fig. 12A). The canal divides, part of it passing distoanteriorly into the sutural contact, and the other branch transferring distomedially onto the lateral surface of the second metacarpal (Fig. 12E"). When articulated, the long axis of the third metacarpal is rotated posteriorly so that the centre of the distal end of the bone is about 3 cm behind the centre of metacarpal II.

The length of the phalanges of the second digit is almost 90% the length of the humerus. The third digit is 93% as long as the first, which in turn is 73% the length of the second. These proportions are very close to what is found in *Allosaurus* (USNM 4734, Gilmore 1920), which suggests that the stocky appearance of the hand of *Acrocanthosaurus* is a function of allometric changes. As in *Allosaurus*, the longest phalanx (excluding the unguals) is I-1, followed by II-2, II-1 and III-3. Phalanges I-1 and II-1 have ginglymoid articulations with their metacarpals, whereas III-1 has a shallowly concave, undivided articulation. Collateral ligament pits are shallow and poorly defined on the manual phalanges (Fig. 12).

Although the femur is incomplete (Fig. 13), it was at least 110 cm long. The length of the femur can

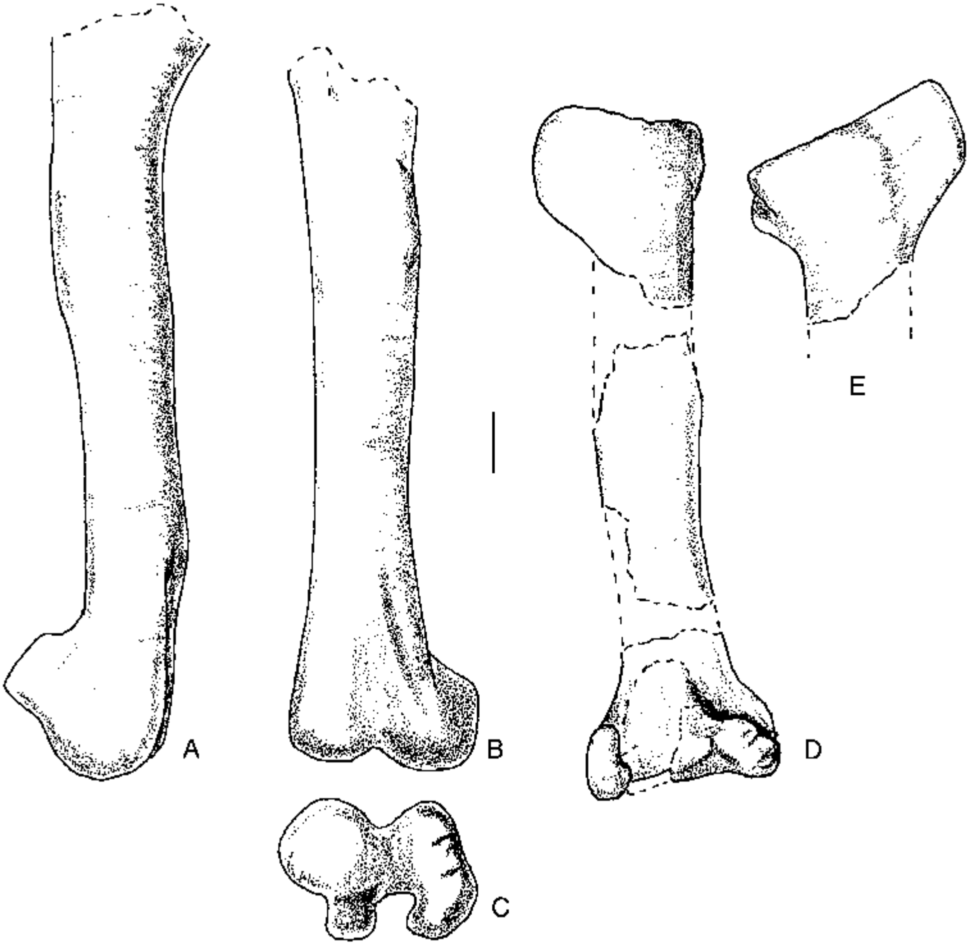

FIG. 13. — *Acrocanthosaurus atokensis* NCSM 14345, right hindlimb elements; **A-C**, femur ; **A**, lateral view; **B**, anterior view; **C**, distal view; **D**, tibia, astragalus and calcaneum in anterior aspect; **E**, proximal head of tibia in medial view. Scale bar: 10 cm.

be estimated as 128 cm by comparison with previously described specimens of *Acrocanthosaurus* (Stovall & Langston 1950; Harris 1998a). As in other carnosaurs, the relatively straight shaft of the femur is pierced by a nutrient foramen proximal to the fourth trochanter. Like *Allosaurus*, *Sinraptor* and other carnosaurs, the fourth trochanter is represented by a low but prominent ridge next to the depression for the *M. caudifemoralis longus*. The minimum transverse diameter of the shaft is 15 cm, which is less than the same dimension in adult specimens of *Tyrannosaurus* (BHI 3033, MOR 555, TMP 81.12.1). This indicates that *Acrocanthosaurus* was a lighter animal than *Tyrannosaurus*, even though the overall length of the body was similar. The distal end of the femur has a ridge along the medial margin of the anterodorsal surface (Fig. 13B) similar to *Allosaurus* (Madsen 1976), but not as sharply defined as those of *Giganotosaurus* (MUCPv-CH-1) and *Sinraptor* (Currie & Zhao 1993). The ridge bounds the adductor fossa medially. The fossa is continuous with the intercondylar trough of the distal end. There are well-developed distal condyles (Fig. 13C), the lateral one associated with a distinct crista tibiofibularis. The tibia is incomplete. However, similarity in size of the distal end of the tibia and the lengths of the

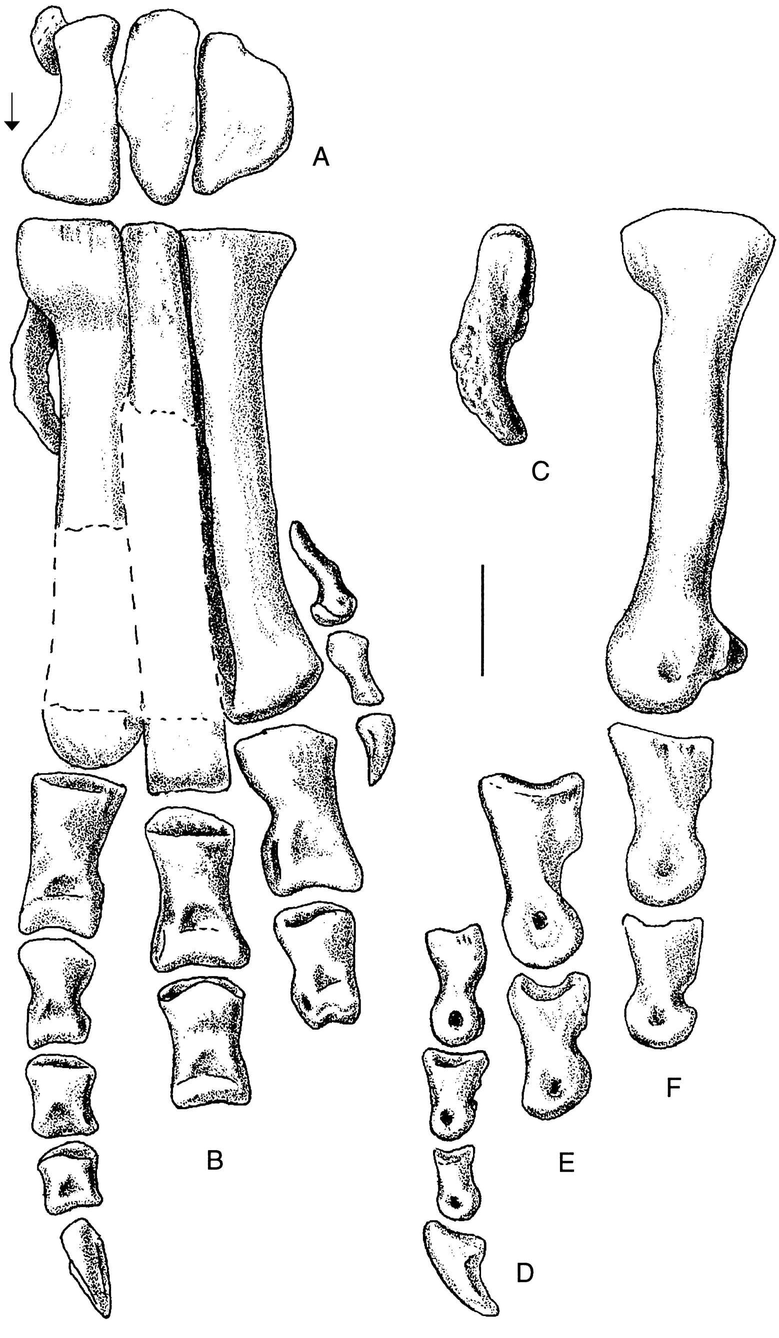

FIG. 14. — *Acrocanthosaurus atokensis* NCSM 14345, right pes; **A**, proximal aspect of metatarsus; **B**, anterior view of preserved elements; **C**, anteromedial view of fifth metatarsal; **D**, medial views of digit IV; **E**, medial views of digit III; **F**, medial views of digit II. Scale bar: 10 cm.

second metatarsals suggests that it would have been close to the same length as that of OMNH 10147 (96 cm). There is a well-developed cnemial crest (Fig. 13D, E) and a fibular crest. The tibia flares distally in anterior view (Fig. 13D) where it contacts the astragalus and calcaneum. The anterior surface is flat to accommodate the ascending process of the astragalus. Only the medial portion of the main body of the astragalus was recovered. Overall it appears to have been quite similar to that of *Allosaurus* with a relatively high, proximolaterally sloping ascending process. The calcaneum is relatively large disk of bone (122 mm anteroposteriorly, 66 mm mediolaterally and 99 mm high) with a distinct process that plugged into a depression in the lateral margin of the astragalus as in *Allosaurus* and *Sinraptor*.

The first, second, and fifth metatarsals are complete, but only the proximal ends of the third and fourth ones were recovered (Fig. 14). The second metatarsal (41 cm) is 99% of the length of that of OMNH 10147, so the total length of metatarsal III can be estimated as 44 cm. Only the smallest specimens of tyrannosaurids have such short third metatarsals. For example, TMP 91.36.500 is a 5.1 m long skeleton of *Gorgosaurus libratus* that has a 46 cm long metatarsal III. The length the metatarsus does, however, fall within the range expected for all other large theropods. Generally the foot is closely comparable to those of *Allosaurus* and *Sinraptor*, but is more robust. In proximal view, the outlines of the metatarsals (Fig. 14A) are almost identical to those of *Allosaurus*.

Digit I of the pes, which is complete, is 15 cm long. The first two phalanges of pedal digit III are 16.0 and 11.5 cm, suggesting that the total length of the toe would have been about half a metre. The fourth toe is missing the last two phalanges. The unguals have triangular cross-sections and resemble the pedal unguals of other carnosaurs.

DISCUSSION

Acrocanthosaurus is one of the largest theropods known. Amongst the four described specimens, NCSM 14345 is larger than either the holotype (OMNH 10146) or SMU 74646. It appears to have been about the same size as OMNH 10147, which has a 958 mm long tibia (Stovall & Langston 1950). In total length, NCSM 14345 was comparable with *Giganotosaurus* (Coria & Salgado 1995) and *Tyrannosaurus*. Femur length, a relatively stable measurement for gauging overall size (Christiansen 1998), suggests it was bigger than the largest known specimens of *Carcharodontosaurus* (Stromer 1931), *Saurophaganax* (Chure 1996), *Suchomimus* Sereno *et al.*, 1998 and *Tarbosaurus* (GI 107/2), but was smaller than *Giganotosaurus* (MUCPv-CH-1) and *Tyrannosaurus* (at least five specimens). In terms of skull size (the premaxilla to quadrate length of NCSM 14345 is 123 cm), *Acrocanthosaurus* is surpassed by one specimen of *Tarbosaurus* (PIN 551-1 has a skull 135 cm long), five specimens of *Tyrannosaurus* (with skull lengths of 127 to 153 cm), *Carcharodontosaurus* (estimated length of 160 cm, Sereno *et al.* 1996) and *Giganotosaurus* (estimated length of MUCPv-CH-1 is 160 cm). Finally, the circumference of the femur (425 mm in NCSM 14345) can be used to estimate weight (Anderson *et al.* 1985), suggesting that the new specimen of *Acrocanthosaurus* was heavier at 2.40 metric tons than most specimens of *Tarbosaurus* and all but one (NMMNH P-26083, Williamson & Chure 1996) of *Allosaurus*, weighed a little less than *Saurophaganax* (Chure 1996), and was lighter than *Carcharodontosaurus*, *Giganotosaurus* (4.16 metric tons) and *Tyrannosaurus* (weight estimate of MOR 555 is also 4.16 metric tons).

The total length of *Acrocanthosaurus* is comparable with *Tyrannosaurus* because like *Allosaurus*, it has relatively longer vertebrae when compared with the skull or femur. For example, the 19th presacral vertebral centrum of *Tyrannosaurus* (MOR 555) is 148 mm long and 180 mm wide. The widths of the centra should be proportional to the weights of the animals, and should scale to the two thirds power of lengths (Currie 1978). Because the femur of SMU 74646 (*Acrocanthosaurus*) is 0.85 the length of the femur of the *Tyrannosaurus*, one would expect that the width of the dorsal vertebra of the smaller animal should be $0.85^{2/3}$ (= 0.78) that of the width of the larger animal. The actual width of the 19th centrum of *Acrocanthosaurus* is 138 mm, which is 0.77 the width of the *Tyrannosaurus* centrum, very close to the predicted value. The length of the vertebra should scale linearly with femur length, and therefore should be 0.85 time (126 mm) the length of the *Tyrannosaurus* centrum. In fact it is 135 mm long in *Acrocanthosaurus*, showing that the dorsal vertebrae are significantly longer than in tyrannosaurs. Another way of demonstrating the relatively longer lengths of *Acrocanthosaurus* vertebrae is by examining their relative proportions. In large tyrannosaurs, the presacral vertebrae are shorter than they are wide, whereas in carnosaurs they are always longer than wide.

Overall, *Acrocanthosaurus* compares most closely morphologically with *Allosaurus*. *Acrocanthosaurus* was assigned to the Allosauridae by Stovall & Langston (1950). It is more primitive than *Allosaurus* in that it has only four premaxillary teeth like most other theropods, whereas allosaurids have five. The jugal takes part in the border of the antorbital fenestra, a character listed by Holtz (1994) as a derived condition. However, it is far more likely that this is the primitive condition because it is present in *Herrerasaurus* and most theropods. In *Allosaurus*, the jugal is excluded from the border of the antorbital fenestra by the maxilla and lacrimal. *Acrocanthosaurus* is also more primitive than *Allosaurus* in having a tall quadrate, in lacking a downturned paroccipital process, and in lacking the neomorph antarticular (Madsen 1976). Furthermore, the surangular of *Acrocanthosaurus* does not contact the angular in front of the external mandibular fenestra. Unlike *Allosaurus* but like most other theropods, the posterior end of the angular terminates anterior to the posterior surangular foramen, which is relatively small. The neural spines of the vertebrae are relatively much higher than in any other theropod except *Spinosaurus*. Pleurocoels are found in at least the first 21 presacral vertebrae (Harris 1998a), but are only found in the cervicals and first four or five dorsals of *Allosaurus*. The arms of *Acrocanthosaurus*, especially the forearm and metacarpus, are shorter than those of *Allosaurus*.

Acrocanthosaurus was assigned to the Carcharodontosauridae by Sereno *et al.* (1996), a view supported by a more extensive analysis by Harris (1998a). However, Harris (1998a) went on to point out problems with paleogeographic interpretations if *Acrocanthosaurus* is related to *Carcharodontosaurus* and *Giganotosaurus*.

In fact, there are few characters that can be used to unite *Acrocanthosaurus* with *Carcharodontosaurus* and *Giganotosaurus*. Sereno *et al.* (1996) used eight characters to define the Carcharodontosauridae. Of these, the broad postorbital-lacrimal contact is probably size-related. Although both *Acrocanthosaurus* and carcharodontosaurids have pronounced shelves of bone over the orbits, this is also true of abelisaurids and big tyrannosaurids. In *Acrocanthosaurus*, this shelf is formed by both the prefrontal and lacrimal, which extend backwards over the eye to contact the postorbital. In the carcharodontosaurid *Giganotosaurus* (R. Coria, pers. comm. 1998) and possibly *Tyrannosaurus* (N. Larson, pers. comm. 1997), the gap is bridged by a new bone, possibly similar to the ornithischian palpebral. This suggests carcharodontosaurids are roofing over the orbit in a different way than *Acrocanthosaurus*. The suborbital flange found on the postorbital of *Carcharodontosaurus* can also be seen in *Giganotosaurus* (Coria & Salgado 1995), abelisaurids (Bonaparte 1991; Sampson *et al.* 1998), some tyrannosaurids, and to a lesser extent in *Cryolophosaurus* Hammer & Hickerson, 1994. The holotype of *Acrocanthosaurus* has a postorbital flange (Stovall & Langston 1950), but this feature is not evident in the new specimen. The ventral extension of the basisphenoid that unites *Giganotosaurus* with *Carcharodontosaurus* is not present in *Acrocanthosaurus*. A pronounced process that extends the ventral end of the intermandibular symphysis is supposedly a character shared by the three taxa. However, there are no jaws of *Carcharodontosaurus* that are complete enough to show this, and it is no more pronounced in NCSM 14345 than it is in large specimens of *Tyrannosaurus rex*. The mid-cervical vertebrae of carcharodontosaurids are supposed to be at least 20% broader than tall. This may be true for *Carcharodontosaurus* (Sereno *et al.* 1996), but not for *Giganotosaurus* (MUCPv-CH-1) which has almost round cervical centra in end view. Furthermore, the cervical centra of *Acrocanthosaurus* are only slightly wider than they are high (Stovall & Langston 1950;

Harris 1998a). The degree of elevation of the anterior intervertebral articulation in midcervical vertebrae is determined by neck posture, and is widely variable throughout the Theropoda. Although there are depressions in the lateral surfaces of the proximal caudal centra, they are not pneumatic in *Acrocanthosaurus* (Harris 1998a). Pleurocoels have been reported in the caudal vertebrae of *Carcharodontosaurus* and *Bahariasaurus* Stromer, 1931 (Rauhut 1995), but are not present in the caudals of *Giganotosaurus* (R. Coria, pers. comm.). The pubic boot of carcharodontosaurids, according to Sereno *et al.* (1996), is 30% of the total length of the bone. Similar pubic proportions are found in a wide range of theropods, including *Allosaurus*, ornithomimids, oviraptorids and tyrannosaurs.

The analysis by Harris (1998a) united *Acrocanthosaurus* with the Carcharodontosauridae on the basis of the reniform cervical centra (at least 20% wider than tall), but did state that the feature is much more accentuated in *Carcharodontosaurus*. Russell (1996) set up a new genus (*Sigilmassasaurus*) for a Moroccan animal with reniform cervical centra, and described a posterior cervical of *Carcharodontosaurus* with an essentially round centrum in posterior view. Furthermore, as pointed out previously, the cervical centra of *Giganotosaurus* are round in posterior view, not reniform. This character, therefore, is a very weak one for placing *Acrocanthosaurus* in the Carcharodontosauridae.

There are many differences between *Acrocanthosaurus* and the two unquestionable carcharodontosaurids — *Carcharodontosaurus* and *Giganotosaurus*. *Acrocanthosaurus* lacks the pronounced sculpturing on the maxilla, and has an antorbital fossa that extends farther beyond the bounds of the antorbital fenestra than the situation in carcharodontosaurids. Carcharodontosaurids lack the maxillary fenestra that is found in most tetanurine theropods, including *Acrocanthosaurus*. The braincase of *Acrocanthosaurus* (Welles *et al.* in prep.) is similar to that of *Allosaurus*, and strikingly different from the highly modified braincases of carcharodontosaurids (Larsson 1996; Coria & Currie in prep.). The lateral temporal fenestrae of *Acrocanthosaurus* and *Allosaurus* are similar in outline, and contrast strongly with the relatively larger openings of carcharodontosaurids and other more primitive theropods. Correlated with this, the quadrates of carcharodontosaurids are positioned much farther behind the occiput than they are in *Acrocanthosaurus*. This is the major reason that carcharodontosaurid skulls are so much longer than the skulls of other theropods, including *Acrocanthosaurus*. The occiput of *Acrocanthosaurus* is nearly vertical in contrast with the strongly sloping posterior occipital region of carcharodontosaurids. There is a double boss on the supraoccipital of *Acrocanthosaurus*, compared with the more normal medial boss of a carcharodontosaurid supraoccipital. There are also many differences in the postcranial skeleton, although few are so striking as those of the femur. Whereas the femur of *Acrocanthosaurus* is closely comparable with that of *Allosaurus* (Stovall & Langston 1950), femora of *Giganotosaurus* (MUCPv-CH-1) and *Carcharodontosaurus* (Stromer 1931) are more primitive in appearance with the heads angled upwards from the shaft (not perpendicular) and lesser trochanters that are well below proximal head level. Novas (1997) pointed out other features in carcharodontosaurid skeletons that may indicate that this family is more closely related to Abelisauridae than Allosauridae.

We set up a data matrix (Appendix 2) based mostly on that used by Harris (1998a) in his analysis of carcharodontosaurids. Some corrections and additions were made to his character list, mostly because of the new information provided by NCSM 14345 and new specimens of *Giganotosaurus* from Argentina. The matrix consisted of 42 cranial, 24 axial and 44 appendicular characters (Appendix 1). We also included some different taxa in our analysis. *Herrerasaurus* was retained as the outgroup to all other theropods, and the Abelisauridae was included in the analysis as a second outgroup. The data matrix was analyzed using the beta version of PAUP 4.0b2 (Swofford 1998). The Branch-and-Bound search method produced three equally parsimonious trees (tree length = 235, C.I. = 0.638, R.I. = 0.600, R.C. = 0.382). Both accelerated and delayed transformations (Acctran & Deltran) were performed for character state optimization. MacClade 3.07 (Maddison & Maddison 1992) was used to produce Figure 15. The results of this analysis show that, in all three trees, *Allosaurus* is the closest thero-

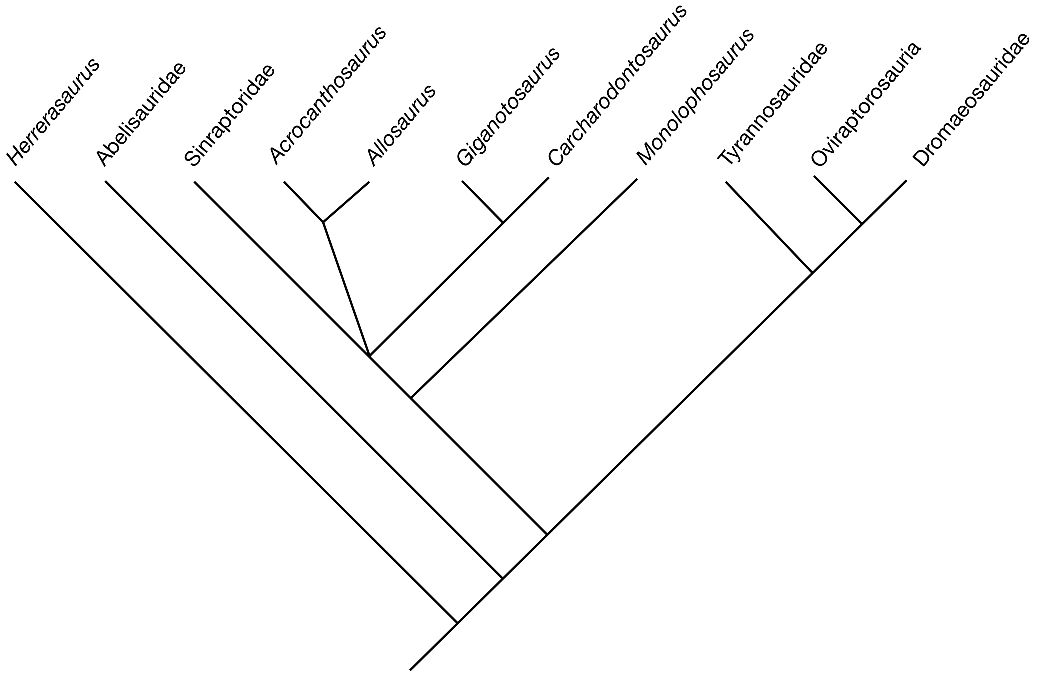

FIG. 15. — Strict consensus of three trees generated in analysis of phylogenetic relationships of *Acrocanthosaurus* using 110 morphological characters.

pod to *Acrocanthosaurus*, and that *Giganotosaurus* and *Carcharodontosaurus* form a second clade. The trees differ only in inter-relationships of the Allosauridae, Carcharodontosauridae and Sinraptoridae. Padian *et al.* (1997) defined the Allosauroidea as all descendants of the most recent common ancestor of *Allosaurus* and *Sinraptor*. In the present analysis, it could not be determined if carcharodontosaurids should be included within the Allosauroidea.

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REFERENCES

Anderson J. F., Hall-Martin A. & Russell D. A. 1985. — Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology* (A) 207: 53-61.

Bakker R. T., Kralis D., Siegwarth J. & Filla J. 1992. — *Edmarka rex*, a new, gigantic theropod dinosaur from the middle Morrison Formation, Late Jurassic of the Como Bluff outcrop region. *Hunteria* 2 (9):1-24.

Bakker R. T., Williams M. & Currie P. J. 1988. — *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria* 1 (5): 1-30.

Bonaparte J. F. 1991. — The Gondwanian theropod families Abelisauridae and Noasauridae. *Historical Biology* 5: 1-25.

Bonaparte J. F. & Novas F. E. 1985. — *Abelisaurus comahuensis*, n. gen, n. sp., Carnosauria del Cretacico Tardio de Patagonia. *Ameghiniana* 21: 259-265.

Bonaparte J. F., Novas F. E. & Coria R. A. 1990. — *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County, Contributions in Science* 416: 1-41.

Britt B. B. 1991. — The theropods of the Dry Mesa Quarry (Morrison Formation), Colorado: with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University, Geology Studies* 37: 1-72.

Britt B. B. 1993. — *Pneumatic Postcranial Bones in Dinosaurs and Other Archosaurs*. PhD thesis, University of Calgary, Calgary, Canada, 383 p.

Chatterjee S. 1978. — *Indosuchus* and *Indosaurus*, Cretaceous carnosaurs from India. *Journal of Paleontology* 52: 570-580.

Christiansen P. 1998. — *Biomechanical and Biometric Aspects of the Appendicular Skeleton of Non-Avian Theropods (Dinosauria: Theropoda) in comparison with Extant Mammalia.* PhD thesis, University of Copenhagen, Dept of Historical Geology and Palaeontology, Copenhagen, The Netherlands.

Chure D. J. 1996. — A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA : 103-106 *in* Sun S. & Wang Y. (eds), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing.

Cifelli R. L., Gardner J. D., Nydam R. L. & Brinkman D. L. 1997. — Additions to the vertebrate fauna of the Antlers Formation (Lower Cretaceous), southeastern Oklahoma. *Oklahoma Geology Notes* 57 (4): 124-131.

Coria R. A. & Currie P. J. **in review.** — The braincase of *Giganotosaurus carolinii* (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina.

Coria R. A. & Salgado L. 1995. — A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377: 224-226.

Currie P. J. 1978. — The orthometric linear unit. *Journal of Paleontology* 52: 964-971.

Currie P. J. 1985. — Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Canadian Journal of Earth Sciences* 22: 1643-1658.

Currie P. J. 1995. — New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology* 15: 576-591.

Currie P. J., Rigby K. Jr & Sloan R. E. 1990. — Theropod teeth from the Judith River Formation of southern Alberta, Canada : 107-125, *in* Carpenter K. & Currie P. J. (eds), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, New York.

Currie P. J. & Zhao X. J. 1993. — A new large theropod (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30: 2037-2081.

Dong Z. M., Zhang Y. H., Li X. & Zhou S. W. 1978. — Note on a new carnosaur *Yangchuanosaurus shangyuensis* gen. et sp. nov. from the Jurassic of Yangchuan District, Sichuan Province. *Kexue Tongbao* 23: 298-302 (in Chinese).

Dong Z. M., Zhou S. W. & Zhang Y. H. 1983. — The dinosaurian remains from Sichuan Basin, China. *Palaeontologia Sinica*, New Series C 23, 162, 145 p., 43 plates (in Chinese).

Gao Y.-H. 1993. — A new species of *Szechuanosaurus* from the Middle Jurassic of Dashanpu, Zigong, Sichuan. *Vertebrata PalAsiatica* 31: 308-314.

Gilmore G. W. 1920. — Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *United States National Museum, Bulletin* 110: 1-159.

Hammer W. R. & Hickerson W. J. 1994. — A crested theropod dinosaur from Antarctica. *Science* 264: 828-830.

Harris J. D. 1998a. — A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science, Bulletin* 13, 75 p.

Harris J. D. 1998b. — Large, Early Cretaceous theropods in North America. *New Mexico Museum of Natural History and Science, Bulletin* 14: 225-228.

Holtz T. R. Jr. 1994. — The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68: 1100-1117.

Hutt S., Martill D. M. & Barker M. J. 1996. — The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 10: 635-644.

Lambe L. M. 1917. — The Cretaceous theropodous dinosaur *Gorgosaurus*. *Geological Survey of Canada, Memoir* 100: 1-84.

Larsson H. C. E. 1998. — Cranial morphology of the African theropod, *Carcharodontosaurus saharicus* (Allosauroidea). *Journal of Vertebrate Paleontology* 16: 47A.

Lipka T. R. 1998. — The affinities of the enigmatic theropods of the Arundel Clay facies (Aptian), Potomac Formation, Atlantic coastal plain of Maryland. *New Mexico Museum of Natural History and Science, Bulletin* 14: 229-234.

Maddison W. P. & Maddison D. R. 1992. —*MacClade: Analysis of Phylogeny and Character Evolution, version 3.01.* Sinauer Associates, Sunderland, Massachusetts.

Madsen J. H. 1976. — *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey, Bulletin,* 109 xii + 163 p.

Maleev E. A. 1974. — Gigantic carnosaurs of the family Tyrannosauridae. *Joint Soviet-Mongolian Paleontological Expedition, Transactions* 1: 132-191 (in Russian).

Molnar R. E. 1991. — The cranial morphology of *Tyrannosaurus rex*. *Paleontographica* A 217: 137-176.

Novas F. E. 1997. — Abelisauridae : 1-2, *in* Currie P. J. & Padian K. (eds), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.

Osborn H. F. 1912. — Crania of *Tyrannosaurus* and *Allosaurus*. *American Museum of Natural History, Memoirs*, New Series, 1: 1-30.

Osborn H. F. 1917. — Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *American Museum of Natural History, Bulletin* 35: 733-771.

Osmólska H. 1985. — Antorbital fenestra of archosaurs and its suggested function. *Vertebrate Morphology* 30: 159-162.

Padian K. & Chiappe L. M. 1997. — Bird origins: 71-79, *in* Currie P. J. & Padian K. (eds), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.

Padian K. & Hutchinson J. 1997. — Allosauroidea: 6-9, *in* Currie P. J. & Padian K. (eds), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.

Rauhut O. W. M. 1995. — Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934. *Berliner geowissenshaft Abhandlungen* E16: 357-375.

Russell D. A. 1996. — Isolated Dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Muséum national d'Histoire naturelle,* série 4, C 18 (2-3) : 349-402.

Russell D. A. & Dong Z. M. 1993. — The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30: 2107-2127.

Sampson S. D., Witmer L. D., Forster C. A., Krause D. W., O'Connor P. M., Dodson P. & Ravoavy F. 1998. — Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science* 280: 1048-1051.

Sereno P. C. 1993. — The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* 13: 425-450.

Sereno P. C., Beck A. L., Dutheil D. B., Gado B., Larsson H. C. E., Lyon G. H., Marcot J. D., Rauhut O. W. M., Sadleir R. W., Sidor C. A., Varricchio D. D., Wilson G. P. & Wilson J. A. 1998. — A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science* 282: 1298-1302.

Sereno P. C., Dutheil D. B., Iarochene S. M., Larsson H. C. E., Lyon G. H., Magwene P. M., Sidor C. A., Varricchio D. J. & Wilson J. A. 1996. — Late Cretaceous dinosaurs from the Sahara. *Science* 272: 986-991.

Sereno P. C. & Novas R. E. 1992. — The complete skull and skeleton of an early dinosaur. *Science* 258: 1137-1140.

Sereno P. C., Wilson J. A., Larsson H. C. E., Dutheil D. B. & Sues H.-D. 1994. — Early Cretaceous dinosaurs from the Sahara. *Science* 266: 267-271.

Stovall J. W. & Langston W. L. Jr. 1950. — *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist* 43: 696-728.

Stromer E. 1931. — Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Bajarîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematik-Naturwissenschaftern* 9: 1-23.

Swofford D. L. 1998. — *PAUP 4.0, beta version*. Sinauer Associates, Sunderland, Massachusetts.

Taquet P. & Welles S. P. 1977. — Redescription du crâne de dinosaure théropode de Dives (Normandie). *Annales de Paléontologie (Vertébrés)* 63: 191-206.

Walker A. D. 1964. — Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions (B)* 248: 53-134.

Welles S. P., Langston W. Jr. & Currie P. J. in prep. — The braincase of the Early Cretaceous theropod dinosaur *Acrocanthosaurus atokensis* Stovall & Langston.

Williamson T. E. & Chure D. J. 1996. — A large allosaurid from the Upper Jurassic Morrison Formation (Brushy Basin Member), West-central New Mexico. *Museum of Northern Arizona Bulletin* 60: 73-79.

Witmer L. M. 1997. — The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir* 3, 73 p.

Woodward A. S. 1910. — On a skull of *Megalosaurus* from the Great Oolite of Minchinhampton (Gloucestershire). *Quarterly Journal of the Geological Society of London,* 66: 111-115

Zhao X. J. & Currie P. J. 1993. — A large crested theropod from the Jurassic of Xinjiang People's Republic of China. *Canadian Journal of Earth, Sciences* 30: 2027-2036.

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APPENDIX 1

Morphological characters (all unordered) used in this paper, most of which are derived from Holtz (1994) and Harris (1998). "0" represents the primitive state.

1. Premaxilla, shape of symphysis from below:
0 - V-shaped.
1 - U-shaped.

2. Premaxilla-nasal contact below nasal:
0 - yes.
1 - no.
2 - extensive contact behind naris.

3. Antorbital fossa, additional openings:
0 - none.
1 - promaxillary only.
2 - promaxillary and maxillary.
3 - all of above plus more.

4. Lateral temporal fenestra:
0 - large and triangular.
1 - reduced and keyhole shaped.
2 - constricted midheight.

5. Maxilla, tooth row:
0 - extends beneath orbit.
1 - ends before orbit.

6. Facial bones (maxilla, nasal), sculpturing:
0 - moderate.
1 - heavily sculptured to edge of antorbital fenestra.

7. Nasal, participates in antorbital fossa:
0 - no or slightly.
1 - broadly.

8. Nasals, fused on midline:
0 - no.
1 - yes.

9. Prefrontal:
0 - large.
1 - reduced.
2 - absent.

10. Postorbital, ventral end above ventral margin of orbit:
0 - yes.
1 - no.

11. Postorbital-lacrimal contact:
0 - absent.
1 - present.

12. Postorbital, suborbital flange:
0 - absent.
1 - small.
2 - large.

13. Lacrimal pneumatic recess:
0 - absent.
1 - present.

14. Lacrimal horn:
0 - non-existent.
1 - low crest or ridge.
2 - high-pointed cone.

15. Jugal pneumatic:
0 - no.
1 - yes.

16. Jugal, foramen on medial surface:
0 - absent.
1 - present.

17. Jugal, expressed on rim of antorbital fenestra:
0 - no.
1 - yes.

18. Jugal, qj process, length of upper prong to lower:
0 - subequal.
1 - upper shorter.
2 - upper longer.

19. Preorbital bar, suborbital process:
0 - not present.
1 - present.

20. Quadrate short:
0 - no.
1 - yes.

21. Quadrate fenestra:
0 - none.
1 - between quadrate and quadratojugal.
2 - surrounded by quadrate.

22. Orbit, expanded and circular:
0 - no.
1 - yes.

23. Braincase, pneumatism:
0 - apneumatic.
1 - moderately.
2 - highly pneumatic.

24. Basioccipital participates in basal tubera:
0 - yes.
1 - no.

25. Occiput:
0 - nearly vertical.
1 - slopes posteroventrally.

26. Paroccipital processes downturned distally:
0 - no.
1 - moderate.
2 - distal ends below level of foramen magnum.

27. Exoccipital-opisthotic, posteroventral limit of contact with basisphenoid separated from basal tubera by notch:
0 - no.
1 - yes.

28. Trigeminal nerve, separation of ophthalmic branch:
0 - no.
1 - incipient.
2 - complete.

29. Internal carotid artery, pneumatized opening:
0 - no.
1 - yes.

30. Basipterygoid processes:
0 - long.
1 - short.

31. Palatine:
0 - subrectangular or trapezoidal.
1 - tetraradiate.

32. Palatine, subsidiary palatal fenestra:
0 - absent.
1 - present.

33. Palatine, meet medially:
0 - no.
1 - yes.

34. Palatine, jugal process expanded distally:
0 - no.
1 - yes.

35. Palatine, pneumatic recess:
0 - none.
1 - small fossa.
2 - small foramen.
3 - large fossa.
4 - large fossa with at least one foramen.

36. Ectopterygoid, pneumatic recess:
0 - elongate.
1 - subcircular.

37. Surangular, dorsoventral height:
0 - less than two times the maximum height of angular.
1 - more than two times.

38. External mandibular fenestra:
0 - large.
1 - reduced.

39. Splenial forms notched anterior margin of internal mandibular fenestra:
0 - absent.
1 - present.

40. Articular, retroarticular process broad and faces posteriorly:
0 - no.
1 - yes.

41. Teeth, premaxillary ones asymmetrical in cross-section:
0 - no.
1 - yes.
2 - yes, D-shaped.
9 - not applicable.

42. Teeth, flat and blade-like in maxilla and dentary with wrinkles in the enamel next to the serrations:
0 - no.
1 - yes.
2 - no but greatly thickened and enlarged.

43. Atlas, neurapophysis in lateral view:
0 - not triangular.
1 - triangular.

44. Axis, strong tilt of axial intercentrum to axial ventral margin:
0 - subparallel.
1 - tilted dorsally.

45. Axis, ventral keel:
0 - absent.
1 - present.

46. Axis, epipophyses:
0 - none.
1 - small.
2 - large.

47. Axis, distal end of neural spine:
0 - not expanded.
1 - expanded (spine table).

48. Cervical vertebrae:
0 - not opisthocoelous.
1 - weakly opisthocoelous.
2 - strongly opisthocoelous.

49. Cervical vertebrae, anterior facets reniform:
0 - no.
1 - yes.

50. Cervical vertebrae, posterior facets reniform and more than 20% broader than tall:
0 - no.
1 - yes.

51. Cervical vertebrae, prezygopophyses:
0 - planar.
1 - flexed.

52. Cervical vertebrae, postaxial pleurocoels:
0 - absent.
1 - fossa only.
2 - fossa with one foramen.
3 - more than one foramen.

53. Cervical vertebrae, interior:
0 - apneumatic.
1 - simple camerate.
2 - complex camellate.

54. Cervical vertebrae, hypapophyses of posterior cervicals and anterior dorsals:
0 - absent.
1 - anterior dorsals only.
2 - posterior cervicals and anterior dorsals.

55. Dorsal vertebrae, 10th presacral in dorsal series:
0 - no.
1 - yes.

56. Dorsal vertebrae, anterior dorsals opisthocoelous:
0 - no.
1 - yes.

57. Dorsal vertebrae, pleurocoels:
0 - none.
1 - on anterior dorsals.
2 - on all dorsals.

58. Dorsal vertebrae, posterior neural spines incline anterodorsally:
0 - no.
1 - yes.

59. Sacral vertebrae, pleurocoelous:
0 - no.
1 - yes.

60. Sacral vertebrae, synsacrum:
0 - absent.
1 - present.

61. Caudal vertebrae, pleurocoels in proximal tail:
0 - no.
1 - yes.

62. Caudal vertebrae, double ventral keel:
0 - absent.
1 - present.

63. Caudal vertebrae, subsidiary foramina in proximal and distal excavations in neural spines:
0 - absent.
1 - present.

64. Haemal arches, paired anterior and posterior processes at base:
0 - no.
1 - yes.

65. Haemal arches, L-shaped in distal chevrons:
0 - no.
1 - yes.

66. Caudal vertebrae, transverse processes:
0 - more than 15.
1 - fewer than 15.

67. Cervical ribs, aliform process at base of anterior rib shafts:
0 - no.
1 - yes.

68. Scapula-coracoid, pronounced notch between acromial process and coracoid:
0 - no.
1 - yes.

69. Scapula, elongate blade set off from glenoid and acromial process:
0 - grades smoothly.
1 - abrupt.

70. Coracoid:
0 - not rectangular.
1 - subrectangular.

71. Sternum, sternal plates fused in adults:
0 - no.
1 - yes.
9 - not applicable.

72. Humerus:
0 - straight.
1 - sigmoidal.

73. Ulna, bowed strongly posteriorly:
0 - no.
1 - yes.

74. Manus, manus length to length of humerus plus radius:
0 - less than two thirds.
1 - more than two thirds.

75. Carpals, semi-lunate carpal articular facets:
0 - none (not a true semi-lunate).
1 - proximal and distal facets.

76. Metacarpal I, at least half of proximal end closely appressed to Mc II:
0 - no.
1 - yes.

77. Metacarpal I, ratio mcI/mcII:
0 - more than one third.
1 - less than one third.

78. Metacarpal III, long and slender:
0 - no.
1 - yes.

79. Metacarpal IV, retained:
0 - yes.
1 - no.

80. Forelimb length: presacral column; manus length: pes length:
0 - < 75%, pes greater.
1 - > 75%, manus and pes subequal.

81. Ilium, hook-like ventral process on anteroventral margin forming preacetabular notch:
0 - absent.
1 - present.

82. Ilium, pronounced ridge on lateral side divides ilium into pre- and postacetabular fossae:
0 - absent.
1 - present.

83. Ilium, posterodorsal margin in lateral view:
0 - subvertical.
1 - angled posteroventrally.

84. Ilium, pubic peduncle twice as long anteroposteriorly as mediolaterally:
0 - no.
1 - yes.

85. Pubis, obturator opening:
0 - foramen.
1 - incipient notch.
2 - notch.

86. Pubis, in lateral view:
0 - curves posteriorly.
1 - straight.
2 - curves anteriorly.
3 - retroverted.

87. Pubis, distal opening:
0 - none.
1 - pubic notch.
2 - pubic foramen.

88. Pubis, distal end:
0 - not expanded.
1 - 30% pubis length.
2 - more than 30%.

89. Pubis, distal view of conjoined pubic boots:
0 - not triangular.
1 - triangular.
9 - not applicable.

90. Pubis, anterior projection of pubic boot compared to posterior:
0 - large.
1 - small or absent.
9 - not applicable.

91. Ischium, obturator opening:
0 - none.
1 - foramen.
2 - notch.

92. Ischium, obturator process:
0 - proximal.
1 - distal.
9 - not applicable.

93. Ischium, obturator process:
0 - not triangular.
1 - triangular.
9 - not applicable.

94. Ischium, less than two thirds of the length of pubis:
0 - no.
1 - yes.

95. Ischium, fusion of distal halves:
0 - no.
1 - yes.

96. Ischium, distal expansion:
0 - absent.
1 - present but not boot-shaped.
2 - boot-shaped.

97. Femur, angle of caput to shaft in anterior or posterior view:
0 - less than 90 degrees.
1 - perpendicular.
2 - more than 90 degrees.

98. Femur, mound-like greater trochanter:
0 - no.
1 - yes.

99. Femur, deep notch between greater and lesser trochanters:
0 - no.
1 - yes.

100. Femur, lesser trochanter:
0 - distal in position, at or below level of lower margin of head.
1 - proximal in position.

101. Femur, lesser trochanter:
0 - shelf.
1 - non aliform.
2 - aliform.

102. Femur, fourth trochanter:
0 - robust.
1 - weak.
2 - absent.

103. Femur, extensor groove on distal end:
0 - absent.
1 - shallow and broad.
2 - deep and narrow.

104. Femur, ridge for cruciate ligaments in flexor groove:
0 - absent.
1 - present.

105. Femur, distal end:
0 - shallow, round depression bound laterally by low ridge.
1 - sharp anteromedial ridge.
2 - low, rounded anteromedial ridge.

106. Tibia, fibular fossa occupied all of medial aspect of proximal end:
0 - no.
1 - yes.

107. Astragalus and calcaneum fuse to each other and tibia:
0 - no.
1 - yes.

108. Fibula, distal end:
0 - expanded more than twice shaft width.
1 - less than twice width.

109. Astragalus, height of ascending process:
0 - less than a sixth of tibial length.
1 - one sixth to one quarter.
2 - more than a quarter.

110. Astragalus, condyle orientation:
0 - ventrally.
1 - posteroventrally.

APPENDIX 2

Data matrix used for phylogenetic analysis. 0, primitive state; 1, 2, 3, 4, derived character states; 9, not applicable; ?, missing data.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
Abelisauridae (outgroup)	0	0	1	0	0	1	0	1	1	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Acrocanthosaurus	0	0	2	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	2
Allosaurus	0	1	2	1	1	0	1	0	1	0	0	0	1	2	1	0	0	1	0	1	2	0	1	1	0	2
Carcharodontosaurus	0	?	1	0	1	1	1	0	1	0	1	1	1	1	1	?	1	1	0	0	1	0	2	0	1	1
Dromaeosauridae	0	0	2	2	1	0	0	0	2	0	0	0	0	0	1	?	1	1	0	1	1	1	1	0	0	0
Giganotosaurus	0	0	1	0	?	1	1	0	1	?	1	1	1	1	?	?	?	?	0	0	1	0	2	0	1	1
Herrerasaurus (outgroup)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Monolophosaurus	0	1	1	1	1	0	1	1	1	1	0	1	0	2	1	?	1	1	1	0	1	0	?	0	0	0
Oviraptorosauria	1	2	2	2	1	0	0	?	2	1	0	0	0	0	0	0	0	?	0	1	?	1	1	0	0	0
Sinraptoridae	0	0	3	0	1	0	1	0	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	0	1	1
Tyrannosauridae	1	0	2	2	1	0	0	1	1	0	1	(02)	1	2	1	1	1	1	0	1	1	0	1	0	0	0

	27	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**
Abelisauridae (outgroup)	0	1	0	1	?	?	?	?	?	?	1	0	0	?	1	0	0	0	1	2	0	1	0	0	0	2
Acrocanthosaurus	?	2	1	0	1	?	?	1	4	0	?	1	1	1	1	0	?	0	1	2	1	2	0	0	0	3
Allosaurus	1	2	1	0	1	0	1	1	2	0	0	1	1	1	1	0	1	0	0	1	1	2	0	0	0	1
Carcharodontosaurus	?	1	0	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	2	1	1	0	1
Dromaeosauridae	0	0	1	1	1	1	?	0	3	1	?	0	1	1	1	0	0	0	1	1	1	0	1	1	1	2
Giganotosaurus	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	1	2	?	2	0	0	?	3
Herrerasaurus (outgroup)	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Monolophosaurus	1	?	?	1	?	?	?	?	?	?	1	?	1	?	1	0	1	1	?	1	1	2	?	0	?	1
Oviraptorosauria	0	?	1	?	0	0	0	0	0	1	1	0	?	0	9	?	0	0	?	1	0	0	1	1	1	2
Sinraptoridae	1	1	0	1	1	0	1	1	4	0	0	0	1	1	1	0	1	1	0	2	1	2	0	0	0	1
Tyrannosauridae	0	2	1	0	1	1	?	?	4	1	1	1	1	1	2	2	?	0	?	1	0	0	0	1	0	3

	53	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**
Abelisauridae (outgroup)	?	0	0	0	1	0	0	1	0	?	0	0	?	?	1	0	0	0	0	0	0	0	0	0	0	0
Acrocanthosaurus	2	?	1	1	2	1	1	0	0	1	1	1	1	0	1	1	1	0	?	1	0	1	0	1	0	0
Allosaurus	1	1	1	1	1	1	0	0	0	1	?	1	1	0	0	1	1	0	0	1	0	1	0	1	0	0
Carcharodontosaurus	?	?	?	1	?	?	?	?	0	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Dromaeosauridae	1	2	0	0	2	0	1	1	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1
Giganotosaurus	?	?	?	1	1	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Herrerasaurus (outgroup)	0	?	0	0	0	0	?	0	0	0	0	?	?	0	?	0	1	0	?	0	0	0	0	0	0	0
Monolophosaurus	?	0	1	1	1	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Oviraptorosauria	2	1	0	0	2	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1
Sinraptoridae	1	(01)	1	1	1	1	0	?	0	1	?	?	?	1	1	?	1	?	1	?	?	?	?	1	0	0
Tyrannosauridae	2	0	0	0	1	0	1	1	0	0	?	0	1	1	?	0	1	1	1	0	0	1	0	1	0	1

	79	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**
Abelisauridae (outgroup)	0	0	1	0	0	?	0	1	1	1	9	1	0	9	9	0	1	2	1	0	0	0	1	?	?	?
Acrocanthosaurus	1	0	?	?	?	?	2	2	2	2	1	0	2	0	0	0	0	2	1	0	1	1	2	0	2	1
Allosaurus	1	0	1	0	0	1	2	2	2	2	1	0	2	0	0	0	0	1	1	0	1	1	2	0	2	1
Carcharodontosaurus	?	?	?	?	?	?	?	2	?	?	?	?	2	0	?	?	?	?	2	0	1	0	2	0	2	?
Dromaeosauridae	1	1	0	0	1	1	2	3	0	2	?	1	2	1	1	1	1	0	1	1	0	1	1	2	1	0
Giganotosaurus	?	?	1	?	0	?	2	1	?	2	?	0	2	0	0	0	?	1	2	0	1	0	2	0	?	?
Herrerasaurus (outgroup)	0	0	0	0	0	0	0	0	1	2	9	0	0	9	9	0	1	0	0	0	0	0	0	0	0	0
Monolophosaurus	?	?	1	0	0	0	0	0	?	1	?	1	1	9	9	0	0	?	?	?	?	?	?	?	?	?
Oviraptorosauria	1	1	1	0	-	1	2	2	0	2	1	0	2	1	1	1	0	0	1	1	1	1	1	1	1	0
Sinraptoridae	0	?	1	2	0	1	1	1	(12)	1	(09)	1	2	0	0	0	1	1	1	0	1	1	2	0	2	1
Tyrannosauridae	1	0	1	2	0	1	2	2	0	2	1	0	2	1	1	1	0	0	1	1	1	1	2	0	2	0

	105	**106**	**107**	**108**	**109**	**110**
Abelisauridae (outgroup)	?	1	1	0	0	?
Acrocanthosaurus	1	?	0	1	1	1
Allosaurus	2	0	0	1	1	1
Carcharodontosaurus	1	?	?	?	?	?
Dromaeosauridae	2	1	0	1	2	0
Giganotosaurus	1	?	0	1	1	?
Herrerasaurus (outgroup)	0	1	0	0	0	0
Monolophosaurus	?	?	?	?	?	?
Oviraptorosauria	?	?	0	1	2	0
Sinraptoridae	1	0	0	1	0	1
Tyrannosauridae	2	0	0	1	2	0