



A NEW PHYLOGENY OF THE CARNIVOROUS DINOSAURS

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ABSTRACT: The last several years have seen the discovery of many new theropod dinosaur taxa. Data obtained from these and from fragmentary forms not previously utilized in cladistic analyses are examined. An analysis of forty one primary ingroup taxa and 386 characters yielded a set of most parsimonious cladograms which preserves many previously discovered relationships (e.g., a basal split between Ceratosauria and Tetanurae; a carnosaur-coelurosaur clade Avetheropoda outside of more primitive "megalosaur" - grade tetanurines; Dromaeosauridae as the sister taxon to birds, and so forth). The Middle Jurassic English *Proceratosaurus* was discovered to be a basal coelurosaur, as was (on less secure evidence) the Middle Jurassic Chinese *Gasosaurus*: these are among the oldest coelurosaurs yet described. Several characters previously considered to be restricted to birds and other advanced coelurosaurs (e.g., furcula, semilunate carpal block) were found to be more broadly distributed among tetanurines. Other characters, once considered synapomorphies for Avetheropoda (e.g., loss of metacarpal IV, possession of a pubic obturator notch) were found to be convergent between advanced carnosaurs and advanced coelurosaurs, lacking in the basal members of both clades. At least three (and possibly four) separate origins for the arctometatarsalian pes were supported in this study. The mosaic of derived character state distributions for troodontids relative to the dromaeosaurid-bird clade, the tyrannosaurid-ornithomimosaur clade, and the therizinosauroid-oviraptorosaur clade suggests that relationships alternative to the most parsimonious found here may be supported in future studies.

INTRODUCTION

Since the pioneering work of GAUTHIER (1986), there has been great scientific interest in the phylogeny of the Theropoda MARSH, 1881. Much of this interest stems from the recognition that the origin of birds lies within the theropod dinosaurs, an hypothesis advanced by OSTROM (e.g., 1974, 1975a, 1975b, 1976) primarily from his work on the dromaeosaurid *Deinonychus antirrhopus* OSTROM, 1969a (see PADIAN & CHIAPPE, 1998 for a recent review of bird origins). The results of Gauthier's phylogenetic analysis are shown in Fig. 1A, B.

Numerous authors have proposed phylogenetic hypotheses subsequent to Gauthier's initial 1986 study: BAKKER, WILLIAMS & CURRIE, 1988; NOVAS, 1992, 1997a; CURRIE & ZHAO, 1993a; RUSSELL & DONG, 1993a, b; PÉREZ-MORENO *et al.*, 1993, 1994; HOLTZ, 1994, 1995a, 1996a; SERENO *et al.*, 1994, 1996, 1998; SERENO, 1997, 1998; SUES, 1997; HARRIS, 1998; FORSTER *et al.* 1998; MAKOVICKY & SUES, 1998. Results of some of these studies are presented in Fig. 1.

The present analysis attempts to synthesize the proposed phylogenetic data from these studies, beginning as an update of previous work by the present author (HOLTZ, 1994). Among the changes from that work include correction of typographical errors in the character descriptions and elimination or modification of poorly coded characters (see CLARK, PERLE & NORELL, 1994; HUTT, MARTILL & BARKER, 1996; CHARIG & MILNER, 1997; NORELL & MAKOVICKY, 1997 for specific examples). Furthermore, many significant new theropod taxa and more complete remains of hitherto poorly known forms (therizinosauroids, basal ornithomimosaurids, spinosaurids, sinraptorids, alvarezsaurids, etc.) which were not previously used have been incorporated into the new analysis. Additionally, new characters drawn from the studies listed previously are included (some in a modified form) here, as are some previously unused characters.

To fully describe each of the characters in this study in detail will require a much longer work (in preparation by the present author). This paper, how-

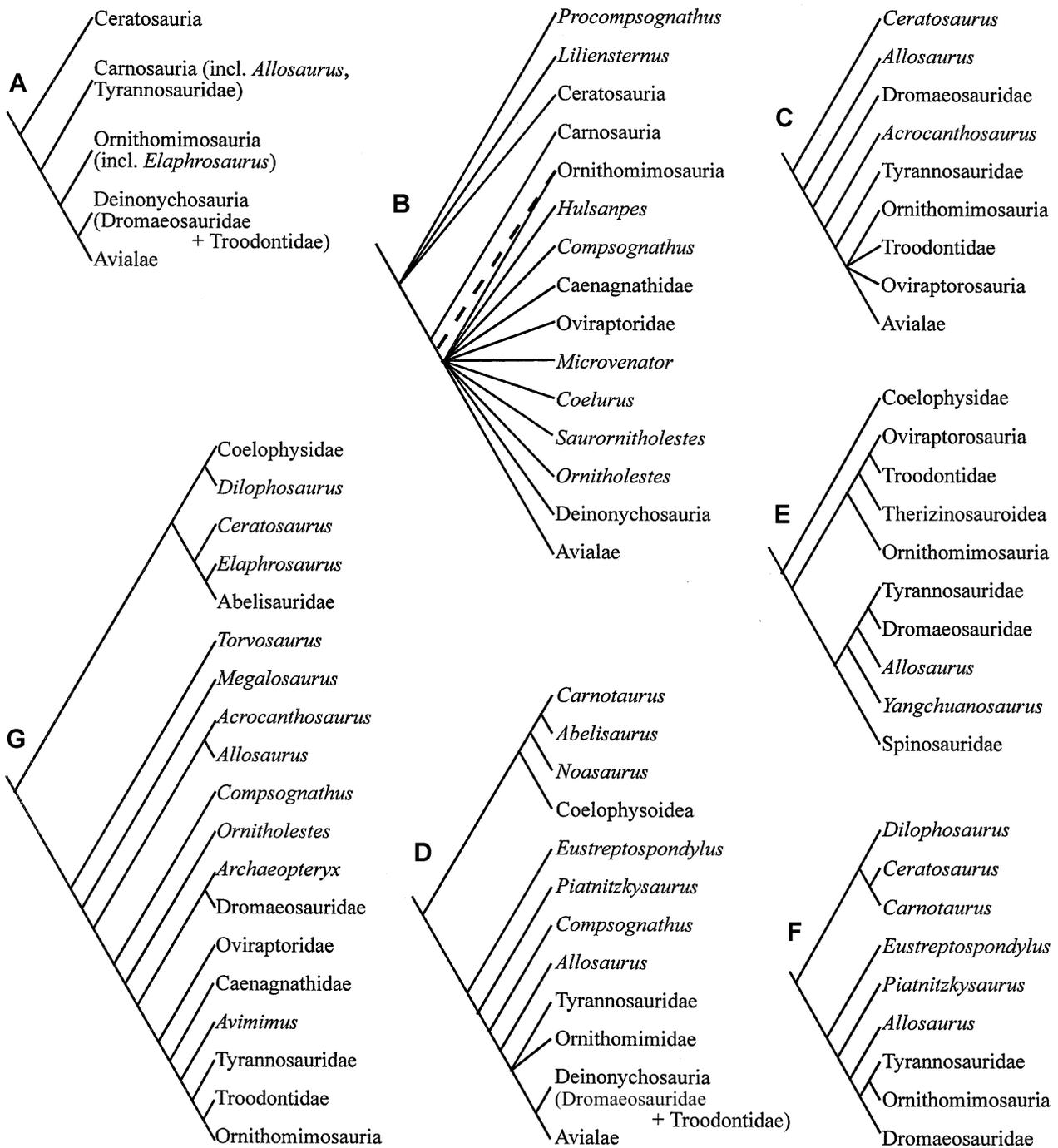


Fig. 1 - Previously proposed phylogenies of theropod relationships. Taxonomy of listed forms revised to match the names used here. **A** - Cladogram of comparatively well known theropods from GAUTHIER (1986). **B** - Cladogram of all theropods included in GAUTHIER (1986), dashed line for Ornithomimosauria represents topology from GAUTHIER (1986), solid line after WILKINSON (1995) (differs from that presented in GAUTHIER (1986) due to incomplete computational analysis in that study: see WILKINSON (1995) for details). **C** - BAKKER, WILLIAMS & CURRIE (1988). **D** - NOVAS (1992). **E** - RUSSELL & DONG (1993a). **F** - PÉREZ-MORENO *et al.* (1993). **G** - HOLTZ (1994). (Continued)

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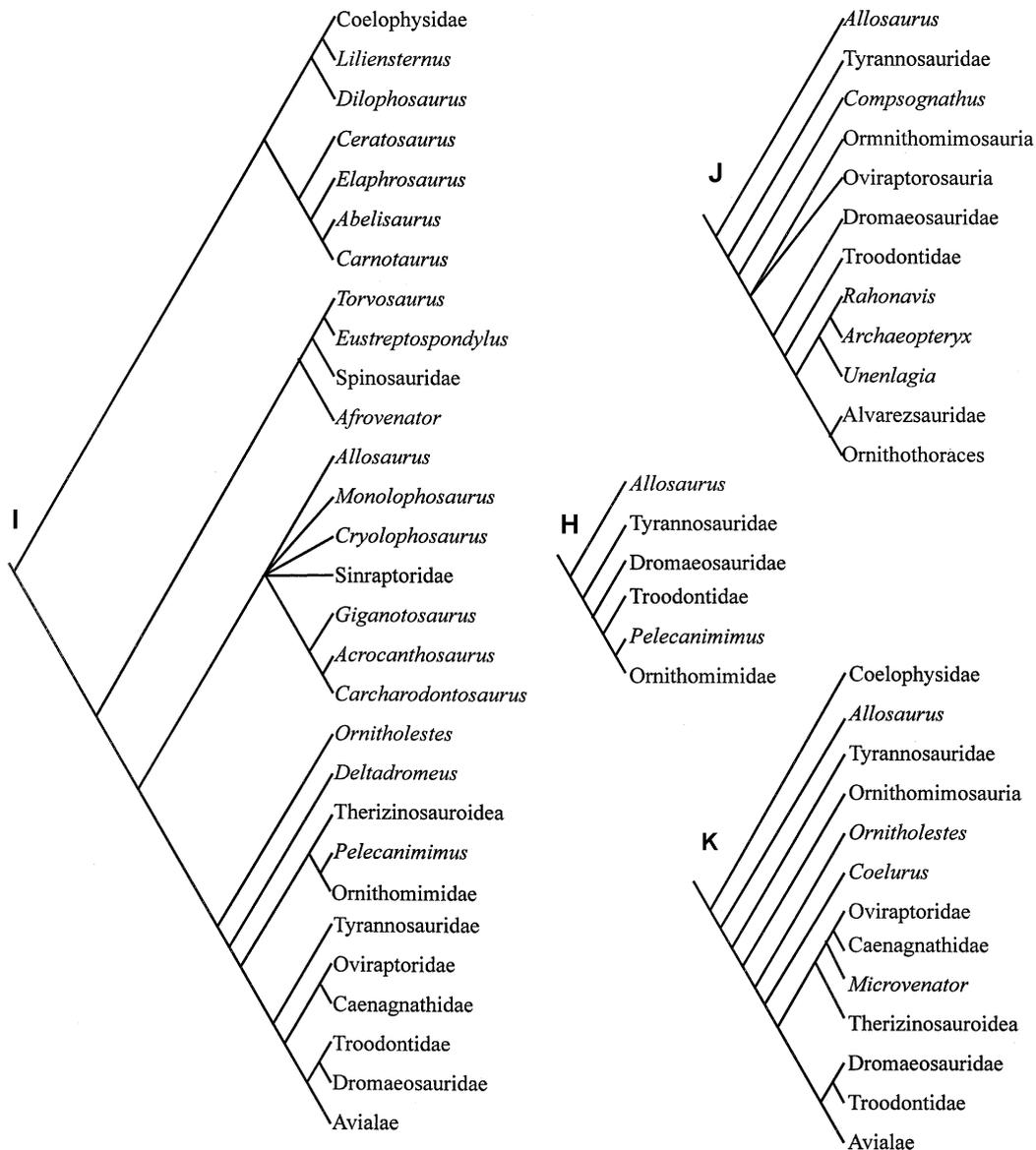


Fig. 1 (continued) - Previously proposed phylogenies of theropod relationships. Taxonomy of listed forms revised to match the names used here. **H** - PÉREZ-MORENO *et al.* (1994). **I** - SERENO (1997, 1998). **J** - FORSTER *et al.* (1998). **K** - MAKOVICKY & SUES (1998).

To fully describe each of the characters in this study in detail will require a much longer work (in preparation by the present author). This paper, however, will serve as an interim study pending that more detailed phylogenetic analysis.

METHODS AND MATERIALS

The operational taxonomic units (OTUs) employed in this study are listed in TABLE I. Forty one in-group taxa were used in the primary analysis. The phylogenetic positions of three very fragmentary forms (*Deltadromeus agilis*, "*Megalosaurus*" *hes-*

peris, and *Unenlagia comahuensis*) were examined in subsequent analyses.

The sister taxon to those theropods used here is a matter of some recent debate. NOVAS (1994, 1997b), SERENO (1997, 1998), and SERENO & NOVAS (1992, 1994) have proposed that the Late Triassic taxa *Eoraptor lunensis* SERENO *et al.*, 1993 of Argentina and the more globally distributed *Herrerasauridae* BENEDETTO, 1973 share a more recent common ancestor with the taxa used in this analysis than do any other known forms (Fig. 2A). Under this phylogeny, *Eoraptor* and the herrerasaurids would

TABLE I
Theropod taxa used in this analysis.

OPERATIONAL TAXONOMIC UNITS

TAXA INCLUDED IN PRIMARY ANALYSIS

Abelisaurus comahuensis BONAPARTE & NOVAS, 1985
Acrocanthosaurus atokensis STOVALL & LANGSTON, 1950
Afrovenator abakensis SERENO, WILSON, LARSSON, DUTHEIL & SUES, 1994
Allosaurus spp. MARSH, 1877¹
 Alvarezsauridae BONAPARTE, 1991
Archaeopteryx spp. MEYER, 1861²
Bagaraatan ostromi OSMÓLSKA, 1996
 Caenagnathidae STERNBERG, 1940
Carcharodontosaurus saharicus (DEPÉRET & SAVORNIN, 1927)
Camotaurus sastrei BONAPARTE, 1985
Ceratosaurus nasicornis MARSH, 1884
 Coelophysidae WELLES, 1984
Coelurus fragilis MARSH, 1879b
 Compsognathidae COPE, 1871
Dilophosaurus wetherilli (WELLES, 1954)
 Dromaeosauridae RUSSELL, 1969
Dryptosaurus aquilunguis (COPE, 1866)
Elaphrosaurus bambergi JANENSCH, 1920
Eustreptospondylus oxoniensis WALKER, 1964
Gasosaurus constructus DONG & TANG, 1985
Giganotosaurus carolinii CORIA & SALGADO, 1995
Megalosaurus bucklandi MEYER, 1832
Microvenator celer OSTROM, 1970
Monolophosaurus jiangi ZHAO & CURRIE, 1993
Neovenator salierii HUTT, MARTILL & BARKER, 1996
Ornitholestes hermanni OSBORN, 1903
 Ornithomimidae MARSH, 1890
 Ornithothoraces CHIAPPE & CALVO, 1994
 Oviraptoridae BARBOLD, 1976a
Pelecanimimus polyodon PÉREZ-MORENO, SANZ, BUSCALIONI, MORATALLA, ORTÉGA & RASSKIN-GUTMAN, 1994
Piatnitzkysaurus floresi BONAPARTE, 1979
Proceratosaurus bradleyi (WOODWARD, 1910)
Rahonavis ostromi (FORSTER, SAMPSON, CHIAPPE & KRAUSE, 1998)
Scipionyx samniticus DAL SASSO & SIGNORE, 1998
Sinraptor spp. CURRIE & ZHAO, 1993a³
 Spinosauridae STROMER, 1915
 Therizinosauridae RUSSELL & DONG, 1993a
Torvosaurus tanneri GALTON & JENSEN, 1979
 Troodontidae GILMORE, 1924
 Tyrannosauridae OSBORN, 1906
Yangchuanosaurus spp. DONG, CHANG, LI & ZHOU, 1978⁴

TAXA INCLUDED IN SUPPLEMENTARY ANALYSES

Deltadromeus agilis SERENO, DUTHEIL, IAROCHENE, LARSSON, LYON, MAGWENE, SIDOR, VARRICCHIO & WILSON, 1996
 “*Megalosaurus*” *hesperis* WALDMAN, 1974
Unenlagia comahuensis NOVAS & PUERTA, 1997

1 - PAUL (1988), SMITH (1998), CHURE (1998), HENDERSON (1998) and BAKKER (1998) argue that more than one species (or higher level taxa) are present in the Morrison Formation genus *Allosaurus*. 2 - WELLNHOFER (1993) suggests that two species are present in the Solnhofen Lithographic Limestone genus *Archaeopteryx*: *A. lithographica* MEYER, 1861 and *A. bavarica* WELLNHOFER, 1993. 3 - *Sinraptor* includes two species, *S. dongi* CURRIE & ZHAO, 1993a and *S. hepingensis* (GAO, 1992). 4 - *Yangchuanosaurus* includes two species, *Y. shangyouensis* DONG, CHANG, LI & ZHOU, 1978 and *Y. magnus* DONG, ZHOU & ZHANG, 1983.

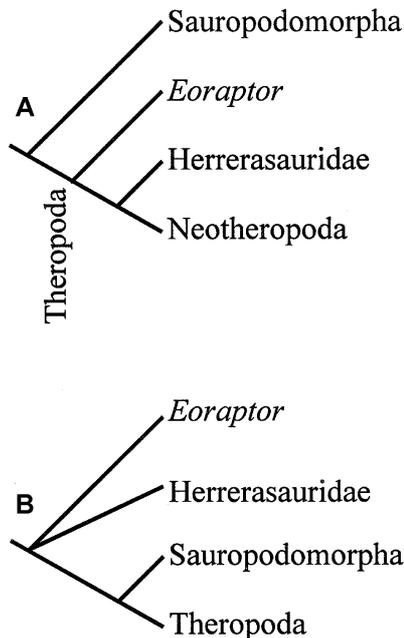


Fig. 2 - Alternative phylogenies for sister taxon to theropods used in this study. **A** - Herrerasaurids and *Eoraptor* share a more recent common ancestor with (more advanced) theropods than do sauropodomorphs, after NOVAS (1994, 1997a), SERENO (1997, 1998), and SERENO & NOVAS (1992, 1994). **B** - Sauropodomorphs share a more recent common ancestor with theropods than do either herrerasaurids or *Eoraptor*, after HOLTZ & PADIAN (1995) and BONAPARTE & PUMARES (1995).

phylogeny, *Eoraptor* and the herrerasaurids would be considered true theropods (given the definition of Theropoda following GAUTHIER (1986): birds and all taxa sharing a more recent common ancestor with birds than with sauropodomorphs). Among the potential derived characters supporting such a hypothesis are prominent postaxial cervical epiphyses; greatly reduced manual digits IV and V; an intramandibular joint; and a distal enlargement of the pubis (NOVAS, 1994, 1997a; SERENO, 1997).

Alternatively, HOLTZ & PADIAN (1995) and BONAPARTE & PUMARES (1995) have argued that sauropodomorphs share a more recent common ancestor with the forms in this analysis than do *Eoraptor* or herrerasaurids (Fig. 2B). Derived characters supporting such a hypothesis include pollex ungual larger than other manual unguals; manual digit II longest digit in the hand; vertebrae 6-9 longest in the cervical column; and a distal expansion of the ischium.

The question of the sister taxon to the forms used here is the subject of a separate study by the present author and PADIAN, in preparation. For this analysis, a compromise outgroup was used. Character states shared in common in *Eoraptor*, herrerasaurids, and

basal sauropodomorphs (as well as those in common in all three of these and in more distantly related forms such as ornithischians, basal ornithodirans, and non-ornithodiran archosauriforms) were considered to the primitive relative to the taxa in the current study. Character states found in the taxa in the present analysis and in some (but not all three) of *Eoraptor*, herrerasaurids, and basal sauropodomorphs were coded as derived for the ingroup forms: these are discussed below. Finally, character states found in some or all of the ingroup taxa but none of the three potential sister taxa are coded as derived. Based on these codings, an "all zero" outgroup with all primitive states was created to approximate a compromise ancestral condition. The character states observed in herrerasaurids (primarily *Herrerasaurus*) and basal sauropodomorphs ("prosauropods") are also included here, and use of these taxa rather than an "all zero" outgroup are briefly discussed. In the longer study in preparation by the present author, differences between the results using this method and various arrangements of the known potential outgroups will be examined.

The characters employed in this analysis are listed in APPENDIX I. 386 characters were used (135 craniodental, 75 axial, 74 pectoral and forelimb, and 102 pelvic and hindlimb characters). 301 of the characters are coded as binary; 85 as multistate. All binary characters were considered unordered; multistate characters were considered unordered unless otherwise indicated (see APPENDIX I). Descriptors of facial pneumatic structures follow WITMER (1997). In APPENDIX I a brief description of the primitive and derived state(s) is provided; in work in preparation, each of these characters will be described in greater detail (as in GRANDE & BEMIS (1998) or WILSON & SERENO (1998)). However, some characters of particular phylogenetic significance in this or previous studies will be discussed below. APPENDIX II is the data matrix analyzed.

The resulting data matrix was analyzed using PAUP 3.1.1 (SWOFFORD, 1993). The unwieldy size of the data matrix required the use of the Heuristic search option, as the Branch-and-Bound and Exhaustive search methods would require prohibitively long run times given current computer calculation speeds. In all cases, random branch addition was run with thirty replicates, to reduce the chance of falsely accepting a local rather than global minimum (that is, a tree or set of trees with less than maximum parsimony). The set of most parsimonious trees discovered under these runs was analyzed using MacClade 3.07 (MADDISON & MADDISON, 1997), in order to determine character state distribution under accelerated and delayed transformation (ACCTRAN and DELTRAN, respectively) optimizations and to examine alternate topologies. The tree length, con-

TABLE II
Phylogenetic taxonomic definitions used in this study, based primarily on PADIAN, HUTCHINSON & HOLTZ (1999)

TAXON	TYPE	A	B
Theropoda MARSH, 1881	Stem	Neornithes	<i>Cetiosaurus</i>
Neotheropoda BAKKER, 1986	Node	<i>Ceratosaurus</i>	Neornithes
Ceratosauria MARSH, 1884	Stem	<i>Ceratosaurus</i>	Neornithes
Coelophysoidea HOLTZ, 1994	Stem	<i>Coelophysis</i>	<i>Ceratosaurus</i>
Neoceratosauria NOVAS, 1992	Stem	<i>Ceratosaurus</i>	<i>Coelophysis</i>
Abelisauridae NOVAS, 1992	Stem	<i>Carnotaurus</i>	<i>Ceratosaurus</i>
Abelisauridae BONAPARTE & NOVAS, 1985	Node	<i>Abelisaurus</i>	<i>Carnotaurus</i>
Tetanurae GAUTHIER, 1986	Stem	Neornithes	<i>Ceratosaurus</i>
Avetheropoda PAUL, 1986	Node	Neornithes	<i>Allosaurus</i>
Carnosauria HUENE, 1920	Stem	<i>Allosaurus</i>	Neornithes
Allosauridae CURRIE & ZHAO, 1993a	Node	<i>Allosaurus</i>	<i>Sinraptor</i>
Allosauridae MARSH, 1879a	Stem	<i>Allosaurus</i>	<i>Sinraptor</i>
Sinraptoridae CURRIE & ZHAO, 1993a	Stem	<i>Sinraptor</i>	<i>Allosaurus</i>
Coelurosauria HUENE, 1914	Stem	Neornithes	<i>Allosaurus</i>
Maniraptoriformes HOLTZ, 1996b	Node	<i>Ornithomimus</i>	Neornithes
Arctometatarsalia HOLTZ, 1994	Stem	<i>Ornithomimus</i>	Neornithes
Bullatosauria HOLTZ, 1994	Node	<i>Ornithomimus</i>	<i>Troodon</i>
Ornithomimosauria BARSBOLD, 1976b	Node	<i>Ornithomimus</i>	<i>Pelecanimimus</i>
Maniraptora GAUTHIER, 1986	Stem	Neornithes	<i>Ornithomimus</i>
Oviraptorosauria BARSBOLD, 1976b	Node	<i>Oviraptor</i>	<i>Chirosstenotes</i>
Paraves SERENO, 1997	Stem	Neornithes	<i>Oviraptor</i>
Eumaniraptora PADIAN, HUTCHINSON & HOLTZ, 1999	Node	<i>Deinonychus</i>	Neornithes
Deinonychosauria COLBERT & RUSSELL, 1969	Stem	<i>Deinonychus</i>	Neornithes
Avialae GAUTHIER, 1986	Stem	Neornithes	<i>Deinonychus</i>
Aves LINNE, 1758	Node	<i>Archaeopteryx</i>	Neornithes
Metornithes PERLE, NORELL, CHIAPPE & CLARK, 1993	Node	<i>Mononykus</i>	Neornithes

Taxon, taxon type, and reference taxa for phylogenetic definitions employed in this paper. Definitions and justifications discussed in PADIAN, HUTCHINSON & HOLTZ (1999). Type: Stem, stem-based; Node, node-based. Stem-based taxon definitions are of the form "reference taxon A and all taxa sharing a more recent common ancestor with reference taxon A than with reference taxon B". Node-based taxon definitions are of the form "all descendants of the most recent common ancestor of reference taxa A and B."

sistency index (CI), retention index (RI), and rescaled consistency index (RC) for each tree was calculated on MacClade, while the homoplasy index (HI) was calculated on PAUP: see pp. 364-368 of MADDISON & MADDISON (1997) for the differences in metric calculations between these two programs. Bremer support values were calculated by means of the AutoDecay program, version 4.0 (ERIKSSON, 1998).

Names of clades found in this analysis are based on the standardized phylogenetic definitions provided in PADIAN, HUTCHINSON & HOLTZ (1999), and are summarized in TABLE II. See the reference above, SERENO (1998), and the references therein for a discussion of the principles of phylogenetic taxonomy. SERENO (1997, 1998) provides some different definitions for the same names, and some different names for the same definitions as used here: see PADIAN, HUTCHINSON & HOLTZ (1999) for discussion of these taxonomic conflicts.

RESULTS

The primary analysis produced a set of 20 equally parsimonious trees of 1404 steps. The CI for these trees was 0.442, the RI was 0.618, the RC was 0.273, and the HI was 0.647. The strict consensus of these trees is presented in Fig. 3A. The normalized consensus fork index, a measure of consensus tree resolution (number of nodes in the strict consensus tree over number of nodes in a fully resolved dichotomous tree of the same number of taxa: COLLESS, 1980) is 0.825. Use of Herrerasauridae as an outgroup does not alter tree topology, but instead produces the same 20 trees at a tree length of 1412, a CI of 0.439, an RI of 0.614, an RC of 0.269, and an HI of 0.649. Use of basal sauropodomorphs ("pro-sauropods") yields 120 trees of tree length 1458, CI 0.433, RI 0.619, RC 0.268, and HI 0.658: the tree topologies are identical to those analyses using the all zero outgroup or the herrerasaurid outgroup, except that *Megalosaurus*, *Torvosaurus*, *Eustreptospondylus*

lus, and *Piatnitzkysaurus* are equally parsimoniously placed in six different possible configurations relative to the *Afrovenator*-avetheropod clade. The increase in tree length and decrease in CI, RI, RC, and HI is explained by homoplasy in some conditions found in herrerasaurids or prosauropods and various derived theropod clades, but not hypothesized for basal neotheropods under either accelerated or delayed transformation.

Examination of the resulting trees in the primary analysis (using the all zero outgroup) found that the polytomies in the strict consensus cladogram could be decomposed as instability at three different regions. The variability at each these three regions is independent of the variability at the other three. This independence (five different possible topologies in one region of the tree, two in the other two) results in the 20 different equally parsimonious trees recovered.

In the first of these cases, the instability occurred because of the incompletely known taxon *Proceratosaurus bradleyi*, known only from cranial remains from the Middle Jurassic (Bathonian) of England, was found to occupy five different possible positions with respect to the other basalmost coelurosaur *Gasosaurus* and *Dryptosaurus* without change in tree length, CI, or other tree metrics (Fig. 3B). The second region of tree instability concerns two alternative placements for the fragmentary Aptian-Albian form *Microvenator celer*, as either the sister taxon to Oviraptoridae or the sister taxon to the clade Oviraptoridae plus Caenagnathidae (Fig. 3C).

The third instability is of greater interest, as it concerns two alternative placements of the well known taxon Troodontidae as the sister group to two very different clades: a sister group relationship with the dromaeosaurid-bird clade on the one hand, and a sister group relationship with Ornithomimosauria on the other. Both topologies are equally parsimonious, and result in the apparent lack of resolution among maniraptoriform coelurosaur shown in Fig. 3A. In fact there is much greater structure than revealed under strict consensus: all the other taxa have resolved positions relative to each other, with the exception of Troodontidae itself. The structure within Maniraptoriformes is presented in Fig. 4, which shows the two alternative positions for troodontids.

A summary cladogram (Fig. 5) is used to discuss the distribution of characters in the present analysis. This represents one of the twenty most parsimonious trees in the analysis. For this summary cladogram, *Proceratosaurus* was placed between *Gasosaurus* and *Dryptosaurus*, and *Microvenator* placed as outside of an oviraptorid-caenagnathid clade (the position preferred by the lower stratigraphic position of this form). A tree in which Troo-

odontidae is more closely related to dromaeosaurids and birds than to ornithomimosaur was selected for the summary cladogram, as this topology more closely reflects the results of most other workers (e.g., GAUTHIER, 1986; NOVAS, 1992; SERENO, 1997, 1998; SUES, 1997; MAKOVICKY & SUES, 1998; FORSTER *et al.*, 1998; NOVAS & POL, in press). However, the analyses of HOLTZ (1994) and PÉREZ-MORENO *et al.* (1994) (and previously the non-numerical study of THULBORN (1984)) recovered a troodontid-ornithomimosaur clade to the exclusion of dromaeosaurids or birds, which represents the al-

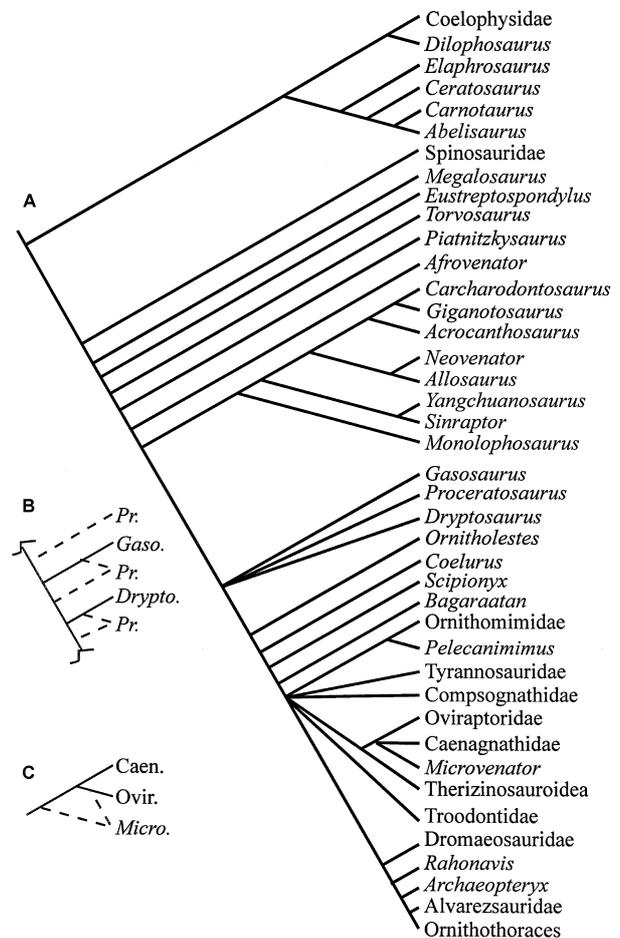


Fig. 3 - Relationships among theropod dinosaurs based on maximum parsimony analysis of 386 morphological characters. **A** - Tree represents the strict consensus of twenty equally most parsimonious trees (tree length=1404, CI=0.442, RI=0.618, RC=0.273, HI=0.647, normalized consensus fork index=0.825). Characters used in analysis included in Appendix I. **B** - Dashed lines indicate the five equally parsimonious alternative positions of *Proceratosaurus* (*Pr.*) relative to *Gasosaurus* (*Gaso.*) and *Dryptosaurus* (*Drypto.*). **C** - Dashed lines indicate the two equally parsimonious alternative positions of *Microvenator* (*Micro.*) relative to Oviraptoridae (*Ovir.*) and Caenagnathidae (*Caen.*).

ternative topology of this study. Characters supporting this position will be discussed below.

Note that this particular configuration (Fig. 5) is used to facilitate discussion only, and is not preferred by the data analysis over the nineteen other potential arrangements. Future analyses may help to resolve the uncertainty with regards to the relationships presented here (if not overturn some or all of those in the current analysis, pending the addition of new data).

Addition of the fragmentary *Deltadromeus* of the Cenomanian of northern Africa results in 80 equally parsimonious trees two steps longer than the primary analysis (tree length 1406, CI 0.441, RI 0.618, RC 0.272, HI 0.627). This addition does not change the tree topology: rather, *Deltadromeus* is equally parsimoniously placed in five different positions. These positions are: as the sister taxon to *Ornitholestes*; as the sister taxon to *Coelurus*, or as the sister taxon to nodes ff, gg, or jj. Similarly, inclusion of the poorly known *Unenlagia* of the Late Cretaceous of Argentina does not alter overall tree structure. Instead, its presence results in a total of 50 trees eleven steps longer (tree length 1415, CI 0.438, RI 0.619, RC 0.271, HI 0.649) than that in the primary analysis. *Unenlagia* is equally parsimoniously placed as the sister taxon to *Rahonavis*, as the sister taxon to the *Archaeopteryx*-Metornithes clade (node mm), or as the sister group to Ornithothoraces. Inclusion of "*Megalosaurus*" *hesperis* (known only from cranial material of the Middle Jurassic of

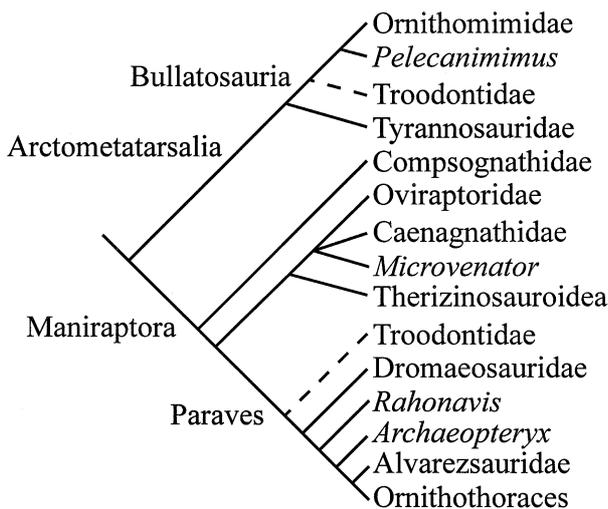


Fig. 4 - Maniraptoriform theropod cladogram as recovered in this analysis. Solid lines indicate positions shared by all twenty most parsimonious trees; dashed line indicates two equally parsimonious positions for Troodontidae (as bullatosaurian arctometatarsalians or as paravian maniraptorans). See text for discussion.

England) results in 220 trees 1 step longer than the primary analysis (TL 1405, other metrics identical to main analysis). "*M.*" *hesperis* is equally parsimoniously placed as the sister group to nodes G, H, I, J, K, or L or as the sister group to Spinosauridae, *Megalosaurus*, *Eustreptospondylus*, *Torvosaurus*, or *Platnitzkysaurus*.

In the following section, the character states found at each node are listed. The nodes are listed by the corresponding letter from the summary cladogram (Fig. 5). Taxon names are listed for some of the clades mentioned here, following the definitions proposed in PADIAN, HUTCHINSON & HOLTZ (1999), and listed in TABLE II. Stem-defined names are underlined in the description headings, whereas node-defined names are not. Where two names are listed, the first represents the stem-defined taxon name and the second is the node-defined taxon name. Not all nodes are named.

For purposes of description of the nodal character state changes, ALL refers to those derived character states present in all optimizations, ACCTRAN refers to those derived character states present at that node under accelerated transformation (i.e., at the basalmost point on the tree where this character could appear without requiring additional evolutionary steps), and DELTRAN refers to those present at that node under delayed transformation (i.e., at the terminal-most point on the tree where this character could appear without requiring additional evolutionary steps). Characters are listed by the character number (before the period) and state (after the period): for example, **17.1** refers to the condition "maxillary fenestra present." Characters listed with a minus sign (-) before them represent a reversal to a state found at a more basal position in the tree: for example, **-17.0** would indicate "maxillary fenestra absent" for a form nested within a clade otherwise characterized by the state **17.1**.

NODE A. THEROPODA - NEOTHEROPODA

ALL: **10.1** Premaxilla and nasal do not meet subnarily; **26.1** Narial prominences present; **30.1** Lacrimal broadly exposed on skull roof; **45.1** Orbit oval or key-shaped, rounded dorsally, constricted ventrally; **54.1** Postorbital frontal process about same level or slightly higher than squamosal, producing T-shaped postorbital; **73.1** Vomera fused rostrally; **110.1** Reduced overlap of dentary onto postdentary bones; **111.1** Intramandibular joint; **117.1** Rostral prong of angular penetrates the dentary-splenic cavity; **137.1** First intercentrum with large occipital fossa (two or less times as wide as tall) and small odontoid notch; **138.1** Second intercentrum cranial articulation with first intercentrum with broad crescentic fossa; **148.1** Postaxial cervical pleurocoels, one pair present; **152.1** Caudal cervical epiphophy-

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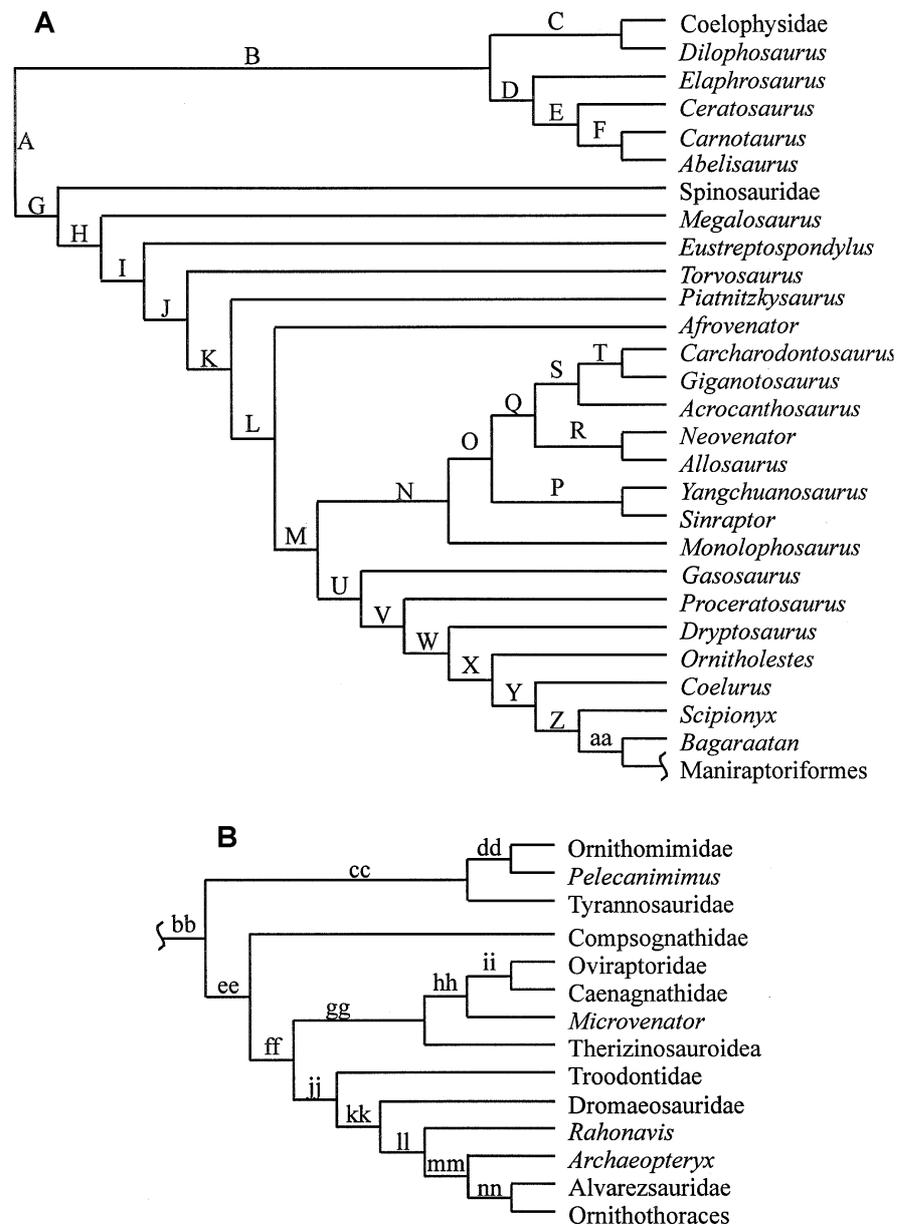


Fig. 5 - Summary cladogram of theropod relationships, representing one of the twenty equally parsimonious trees in this analysis. See text for character state changes at each node, listed by letter indicated. Note that the topology shown here is not preferred by the data over other potential topologies, but was instead chose to facilitate discussion of character distribution. See text for details. **A** - Ceratosauria and non-maniraptoriform Tetanurae section of tree. **B** - Maniraptoriformes.

ses elongate; **164.1** Longest postaxial cervicals VI-IX; **180.1** Cranial and median dorsal pleurocoels, one pair present; **181.1** Presacral pleurocoels camerate; **185.3** Number of sacrals five; **197.1** Transition point in distal half of tail; **219.1** Coracoid biceps tubercle conspicuous and well developed; 256.3 Metacarpal V absent; **257.1** Metacarpal IV present, without ungual; **270.1** Digit II longest in manus; **271.1** Penultimate phalanx longest nonungual phalanx; **286.1** Ilium dolichoiliac; **290.1** Brevis fossa deep; **301.1** Acetabular height/craniocaudal length

about 50%; **312.1** Pubic blade at least six times as long as broad; **329.1** Femur shape bowed in convex arc with less pronounced sigmoidality; **336.1** Proximalmost point of anterior trochanter below femoral head; **372.1** Metatarsal V vestigial or absent; **378.1** Metatarsal I reduced but retains phalanges; **379.1** Metatarsal I placed near midpoint of metatarsal II shaft.

ACCTRAN: **16.1** Promaxillary fenestra present, visible in lateral view; **24.1** Nasal participates in an-

torbital cavity; **44.1** Orbit shorter than internal antorbital fenestra length; **58.1** Jugal participates in internal antorbital fenestra; **67.1** Quadrate foramen reduced or absent; **81.1** Ventral ectopterygoid recess present and comma-shaped; **253.1** Distal carpal I block does not overlap metacarpal II dorsally, but does so ventrally; **254.1** Distal carpal I fused to distal carpal II; **278.1** Pollex larger than other manual unguals; **317.2** Pubic boot rounded, angle between shaft and caudal portion of boot acute; **319.1** Pubic boot present, less than 30% as long as pubic shaft; **339.1** Muscle scar in craniodistal region of femur present, non-elliptical in shape; **344.1** Ectocondylar tuber proximodistally long, pronounced, and extends almost to distal end of femur; **350.1** Crista fibularis present, not well developed.

DELTRAN: None

As defined by GAUTHIER (1986) Theropoda is a stem-based taxon, comprised of birds and all taxa sharing a more recent common ancestor with birds than with sauropodomorphs. The term Neotheropoda BAKKER, 1986 has been used by SERENO *et al.* (1993), SERENO (1997, 1998), and PADIAN, HUTCHINSON & HOLTZ (1999) for the node-defined taxon comprised of all descendants of the most recent common ancestor of Ceratosauria and Tetanurae (or, more explicitly, of *Ceratosaurus* and Neornithes: see PADIAN, HUTCHINSON & HOLTZ (1999)).

How and if the diagnosis of Theropoda and Neotheropoda differ hinges on the question of the immediate sister group of Neotheropoda (see above, and Fig. 2). The following characters from the above list are shared by basal theropods and basal sauropodomorphs, and would therefore diagnose a clade more inclusive than Theropoda if herrerasaurids and *Eoraptor* are not theropods themselves: **10.1**, **67.1**, **117.1**, **164.1**, **270.1**, **278.1**, and **301.1**. Those shared in common with Herrerasauridae and/or *Eoraptor* (see below) would either have evolved convergently between these Triassic forms and true theropods or have been present in the common ancestor of these taxa, theropods, and sauropodomorphs, and subsequently lost in the latter. The remaining characters of the above list would be diagnostic of Theropoda and Neotheropoda (which would share the same diagnosis, as all known theropods would be neotheropods).

If instead herrerasaurids and *Eoraptor* are true theropods, then character **197.1** (Transition point in distal half of tail) would be considered synapomorphic for Theropoda, and the following for an herrerasaurid-neotheropod clade: **67.1**, **111.1**, **117.1**, **138.1**, and **152.1**. It should be noted, however, that the condition represented by character state **111.1** (Intramandibular joint) may not be ho-

mologous in Herrerasauridae and Neotheropoda, as SERENO & NOVAS (1994) noted the geometry of the joint are reversed between the two taxa: in herrerasaurids, the splenial has a concave surface which slides against the convex ventral margin of the angular, while in neotheropods the splenial has a convex dorsal surface which slides against a concave depression on the angular (p. 471). No characters were observed which were present in *Eoraptor* and basally within Neotheropoda that were not also found in herrerasaurids. Under this scheme, the seven derived characters shared by neotheropods and basal sauropodomorphs mentioned previously would either have had to developed independently in these two lineages, or have been present and subsequently lost in *Eoraptor* and Herrerasauridae.

There remain many characters found basally in Ceratosauria and Tetanurae which are not also found in basal sauropodomorphs, *Eoraptor*, or Herrerasauridae. These are diagnostic for Neotheropoda, regardless of either particular sister group scenario.

NODE B. CERATOSAURIA

ALL: **31.2** Lacrimal prominences comprised of ridge continuous with raised surface of lateral edge of nasals; **148.2** Postaxial cervical pleurocoels, two pairs present; **170.1** Dorsal transverse processes strongly backturned caudally and triangular in dorsal view; **180.2** Cranial and median dorsal pleurocoels, two pairs present; **193.1** Ventral groove in cranial caudals; **201.1** Shaft of cervical ribs extremely long (four or more times centrum length) and slender; **291.2** Brevis fossa distal end broad; **300.1** Supracetabular shelf on ilium present; **309.1** Pubis orientation propubic, proximal portion of shaft approximately 30 degrees from horizontal; **321.1** Ischial antitrochanter large; **335.1** Anterior trochanter conical prominence; **338.1** Trochanteric shelf of femur well developed; **340.1** Medial epicondyle (= mediolateral crest) of femur pronounced, extends one quarter or more the length of the femoral shaft; **342.1** Groove in lateral condyle of femur; **345.1** Sulcus along medial side of base of crista tibiofibularis; **356.1** Sulcus in proximomedial region of fibula; **359.1** Anterior surface of distal fibula overlaps ascending process of astragalus cranially; **375.1** Metatarsal III dorsal surface area clearly larger than either metatarsal II or metatarsal IV

ACCTRAN: **189.1** Synsacrum present in adults; **285.1** Pelvic girdle sutures fused in adults; **366.1** Astragalocalcaneum (astragalus fused to calcaneum)

DELTRAN: **24.1** Nasal participates in antorbital cavity; **44.1** Orbit shorter than internal antorbital fenestra length; **67.1** Quadrate foramen reduced or ab-

sent; **319.1** Pubis and ischium proximal shafts narrow

As first proposed by GAUTHIER (1986), Ceratosauria forms a major clade of theropods containing such forms as *Ceratosaurus*, *Dilophosaurus*, and *Coelophysis*. As in HOLTZ (1994), Ceratosauria is divided into two primary branches, the relatively gracile Late Triassic and Early Jurassic Coelophysoidea and the more robust Late Jurassic and Cretaceous Neoceratosauria.

ROWE (1989) and ROWE & GAUTHIER (1990) considered the Early Jurassic (?Sinemurian-Pliensbachian) *Sarcosaurus woodi* ANDREWS 1921 to be a ceratosaur. This taxon (known only from a partial pelvis) was not included in the present analysis, so its relationship with other ceratosaurians is not resolved here.

NODE C. COELOPHYSOIDEA

ALL: **11.1** Subnarial gap; **26.2** Narial prominences comprised of paired ridges along lateral edges of nasals; **64.1** Dorsal ramus of quadratojugal does not contact squamosal; **142.1** Axial parapophyses reduced; **143.1** Axial diapophyses absent; **145.1** Axial pleurocoels absent; **151.1** Epipophyses on cervical vertebrae placed proximally; **234.1** Humeral torsion present; **235.1** Humeral shaft sigmoid; **308.1** Pubic fenestra ventral to obturator foramen

ACCTRAN: **27.1** Paired crescentic crests formed by nasal and lacrimal prominences; **127.1** Dentary teeth more numerous and smaller than maxillary teeth; **331.1** Femoral head transversely elongate

DELTRAN: **-317.0** Pubic boot absent; **-344.0** Ectocondylar tuber proximodistally short, proximally placed

As in ROWE (1989), NOVAS (1992), HOLTZ (1994), and SERENO (1997), a clade comprised of *Dilophosaurus* and the *Coelophysis*-*Syntarsus* clade (Coelophysidae) to the exclusion of other ceratosaurians was supported.

Paired crescentic crests formed by nasal and lacrimal prominences may be synapomorphic for Coelophysoidea (SERENO, 1997) as they are present in *Dilophosaurus* and *Syntarsus kayentakatae* ROWE 1989 (although not in *Coelophysis* nor in *Syntarsus rhodesiensis*). Such crests were the primary evidence for placing "*Dilophosaurus*" *sinensis* HU, 1993 in that genus: since these structures are found in other coelophysoids, and given certain other derived anatomical differences between these taxa (tooth row rostral to the orbit in *D. wetherilli*, five premaxillary teeth in "*D.*" *sinensis*, among others), it may be that the Chinese taxon does not share a more recent common ancestor with *Dilophosaurus*

than with some other coelophysoid genus. ROWE (1989) found evidence that *Liliensternus liliensterni* (HUENE, 1934) was a coelophysoid (see also RAUHUT & HUNGENBÜHLER, 1998), as did SERENO (1997), who also included *Procompsognathus* FRAAS, 1913 and *Segisaurus* CAMP, 1936 in this clade. CARPENTER (1997) has described a large Late Triassic North American coelophysoid *Gojirasaurus quayi*. These taxa were not included in this study: future analyses will hopefully clarify the relationships of these taxa to each other and to other ceratosaurians.

The Late Jurassic African *Elaphrosaurus bambergi* does share numerous derived features with coelophysoids in general, and coelophysids in particular (e.g., **154.1**, **160.1**, **165.1**, **376.2**). Unlike PAUL (1988) and NOVAS (1992), *Elaphrosaurus* was not found to be member of Coelophysoidea in this analysis, but rather was hypothesized to share a more recent common ancestry with abelisauroids and *Ceratosaurus*, as in HOLTZ (1994) and SERENO (1997). However, moving this taxon to a sister group position with node C or with Coelophysidae requires only one additional evolutionary step, and additional details may reveal that *Elaphrosaurus* was a late-surviving coelophysoid. (See also Discussion).

The newly discovered taxon *Genusaurus serus* ACCAIRE *et al.*, 1995 was considered by those authors to be a ceratosaur closer to *Coelophysis* than to *Ceratosaurus*. If such a position were confirmed, it would indicate the first known Cretaceous (middle Albian) coelophysoid. However, although this form demonstrates some ceratosaurian features (pelvic girdle sutures fused, proximal portion of pubic shaft approximately 30 degrees from the horizontal, trochanteric shelf well developed, sulcus along medial side of base of crista tibiofibularis), it does not show any unambiguously coelophysoid feature. In fact, a well-excavated proximal region of the fibular medial face is not known in coelophysoids, but is documented in the neoceratosaur *Carnotaurus*. Additional study may demonstrate *Genusaurus* to be a mid-Cretaceous European abelisauroid.

NODE D. NEOCERATOSAURIA

ALL: **149.1** Cervical epipophyses powerfully developed and prong-shaped; **185.4** Six sacrals.

ACCTRAN: **4.1** Premaxillary symphyseal region U-shaped in ventral view; **5.1** Premaxilla subnarily very deep, main body taller dorsoventrally than long rostrocaudally; **62.1** Infratemporal fenestra about twice as large as the area of the orbit in lateral view; **66.1** Quadrate-quadratojugal suture fused; **68.1** Quadrate dorsal ramus greater than height of orbit; **70.1** Quadrate articulation projects well caudal to

the caudal point of the occipital condyle; **83.1** Nuchal crest pronounced; **84.1** Supraoccipital with very pronounced, strongly demarcated median ridge on occipital surface; **103.1** Occipital condyle constricted neck; **116.1** Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle, prominent and extends laterally; **144.1** Axial epiphyses prominent; **181.2** Presacral pleurocoels camellate; **231.1** Ulna/femur length ratio less than 28%; **232.1** Radius/humerus length ratio less than 50%; **315.2** Pubic boot rounded, angle between shaft and caudal portion of boot acute; **355.1** Proximal region of fibular medial face shallow and not conspicuous.

DELTRAN: **189.1** Synsacrum present in adults; **285.1** Pelvic girdle sutures fused in adults; **366.1** Astragalocalcaneum (astragalus fused to calcaneum); **376.2** Metatarsal III dorsal surface dumbbell shaped (cranial and (especially) plantar surfaces expanded to slightly overlap surfaces of metatarsals II and IV).

NODE E.

ALL: **147.1** Cervical centra surfaces markedly opisthocoelous; **150.1** Cervical epiphyses directed dorsolaterally and taller than neural spine; **185.5** More than six sacrals; **186.1** Sacrals III-V transversely compressed; **302.1** Ilium about as long as femur; **334.1** Anterior trochanter present, separated from femoral head by cleft; **337.1** Fourth trochanter of femur present, but little developed.

ACCTRAN: **357.1** Cranial protuberance on fibula below expansion.

DELTRAN: **4.1** Premaxillary symphyseal region U-shaped in ventral view; **5.1** Premaxilla subnarily very deep, main body taller dorsoventrally than long rostrocaudally; **58.1** Jugal participates in internal antorbital fenestra; **62.1** Infratemporal fenestra about twice as large as the area of the orbit in lateral view; **68.1** Quadrate dorsal ramus greater than height of orbit; **70.1** Quadrate articulation projects well caudal to the caudal point of the occipital condyle; **83.1** Nuchal crest pronounced; **84.1** Supraoccipital with very pronounced, strongly demarcated median ridge on occipital surface; **103.1** Occipital condyle constricted neck; **116.1** Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle, prominent and extends laterally; **144.1** Axial epiphyses prominent; **160.2** Midcervical centra length less than twice diameter of cranial face; **315.2** Pubic boot rounded, angle between shaft and caudal portion of boot acute; **317.2** Pubic boot rounded, angle between shaft and caudal portion of boot acute; **339.1** Muscle scar in craniodistal region of femur present, non-elliptical in shape.

NODE F. ABELISAUROIDEA - ABELISAUROIDEA

ALL: **15.2** Maxillary antorbital fossa greatly reduced in size, not extending much beyond rim of the external antorbital fossa; **26.3** Narial prominences knobby rugosities across dorsal and lateral surface of nasals, extending onto dorsalmost surface of maxillae; **35.2** Lacrimal dorsal (= rostral) ramus absent; **37.1** Prefrontals reduced or absent; **41.1** Frontal-frontal suture fused; **42.2** Frontal-parietal suture on dorsal surface of skull fused, suture indistinguishable; **50.1** Postorbital-lacrimal contact broad; **53.1** Postorbital suborbital flange

ACCTRAN: **-117.0** Rostral prong of angular does not penetrate the dentary-splenic cavity; **161.1** Mid-cervical centra greater than 20% broader than tall; **176.1** Dorsal centrum transverse section wider than high; **188.1** Sacral neural spines fused to form lamina; **211.1** Scapular blade long, slender (four times or more longer than midshaft width) and strap-like; **212.1** Distal expansion of scapula reduced, less than width of proximal end of scapula; **213.1** Acromion in scapula reduced; **229.1** Humerus/scapula length ratio less than 65%; **-234.0** Humeral torsion absent; **237.1** Internal tuberosity on proximal end of humerus well differentiated and angular; **249.1** Ulnar facet for radius transversely expanded and concave; **269.1** Metacarpal-phalangeal joints not hyperextensible, extensor pits on metacarpals I-III reduced; **304.1** Iliac-ischial articulation smaller than iliac-pubic articulation; **-309.0** Pubis orientation propubic, shaft approximately 45 degrees from horizontal; **330.1** Femoral head approximately 90 degrees from shaft (head directed horizontally); **355.2** Proximal region of fibular medial face well excavated

DELTRAN: **16.1** Promaxillary fenestra present, visible in lateral view; **66.1** Quadrate-quadratojugal suture fused

As in NOVAS (1992), HOLTZ (1994), and SERENO (1997, 1998), a clade comprised of *Ceratosaurus* and abelisaurids was supported here. As in the studies by the latter two authors, *Elaphrosaurus* was found to be part of this clade. However, as noted above, support for a coelophysoid placement of this taxon is nearly as strong.

As HOLTZ (1994) noted, many features uniting neoceratosaurids are also found in tetanurines: under the most parsimonious distributions of derived character states, these are explainable either as convergences between Neoceratosauria and Tetanurae or as basal neotheropod characters subsequently lost in Coelophysoidea. Alternatively, *Ceratosaurus* and Abelisauridae may share a more recent common ancestor with tetanurines than with Coelophysoidea: however, such a phylogenetic scenario requires several additional steps given the present data base (see Discussion below).

Although this study did not examine various other neoceratosaurs, CORIA & SALGADO (1998) describe a new taxon assignable to this clade. That study details several forms that would belong to the stem-based taxon *Abelisauroida* (all taxa sharing a more recent common ancestor with *Carnotaurus* than with *Ceratops*) which were not included in this analysis, as well as additional character evidence for relationships within Neoceratosauria. SAMPSON *et al.* (1998) have described excellent, well-preserved remains of the abelisaurid *Majungatholus atopus* SUES & TAQUET, 1979, a form which they consider likely to be the sister taxon to *Carnotaurus* within Abelisauridae. This new material will greatly increase our knowledge of neoceratosaur osteology.

NOVAS (1997c) has suggested that *Carcharodontosaurus* and *Giganotosaurus* were abelisaurids or abelisaurid relatives. Such a relationship was not supported here, but is discussed below.

NODE G. TETANURAE

ALL: **13.1** Rostral ramus of maxilla present, dramatic change in curvature of rostradorsal surface of maxilla rostral to dorsal ramus forming concave surface; **14.2** Rostral ramus as long or longer rostrocaudally as dorsoventrally; **34.1** Slot in ventral process of lacrimal for jugal; **35.1** Lacrimal dorsal (rostral) ramus dorsoventrally pinched and narrow; **133.1** Caudalmost maxillary tooth position rostral to orbit; **147.1** Cervical centra surfaces opisthocoeleous; **211.1** Scapular blade long, slender (four times or more longer than midshaft width) and strap-like; **212.1** Distal expansion of scapula reduced, less than width of proximal end of scapula; **240.1** Humeral ends well expanded, greater than 150% midshaft diameter; **304.1** Iliac-ischial articulation smaller than iliac-pubic articulation; **305.1** Pubic peduncle of ilium more developed craniocaudally than mediolaterally; **341.1** Extensor groove in craniodistal region of femur present, but shallow and not conspicuous; **352.1** Tibia distal end expanded to back calcaneum; **362.1** Astragalar ascending process mediolaterally reduced, craniocaudally wide, and proximodistally low ("allosauroid condition")

ACCTRAN: **38.1** Prefrontal-frontal peg-in-socket suture; **48.1** Postorbital ventral process broader transversely than rostrocaudally with U-shaped cross-section; **61.1** Jugal recess; **64.2** Broad contact between dorsal ramus of quadratojugal and lateroventral ramus of squamosal; **76.1** Palatine tetrad; **78.1** Palatine recesses; **123.1** Retroarticular process of articular faces caudally; **197.2** Transition point in proximal half of tail; **215.1** Scapulacoracoid cranial margin with pronounced notch between acromial process and coracoid; **221.1** Sternal plates fused medially; **222.1** Sternum carina present; **223.2** Sternum wider mediolaterally

than long craniocaudally; **225.1** Furcula; **233.1** Manus/(humerus + radius) length ratio greater than 66%; **255.1** Semilunate carpal block fully developed with transverse trochlea; **257.2** Metacarpal IV present, without phalanges; **261.1** Articular surface between metacarpals I and II extends well into diaphysis of metacarpal I; **263.1** Metacarpal III clearly shorter than metacarpal II; **268.1** Metacarpal IV less than half length of metacarpal II; **279.1** Pollex ungual greater than three times longer than height of articular facet; **283.1** Manual ungual length extremely long; **334.1** Anterior trochanter present, separated from femoral head by cleft; **346.1** Cnemial process arises out of the lateral surface of tibial shaft; **351.1** Crista fibularis proximally placed; **353.1** Fibula closely appressed to tibia throughout main shaft; **360.1** Fibula distal end less than twice cranio-caudal width at midshaft, and consequently astragalar cup for fibula reduced; **364.1** Astragalar distal condyles oriented cranioventrally

DELTRAN: **16.1** Promaxillary fenestra present, visible in lateral view; **160.2** Midcervical centra length less than twice diameter of cranial face; **291.1** Brevis fossa distal end tapered; **338.2** Trochanteric shelf of femur absent; **339.1** Muscle scar in craniodistal region of femur present, non-elliptical in shape; **301.1** Crista fibularis present, not well developed; **344.1** Ectocondylar tuber proximodistally long, pronounced, and extends almost to distal end of femur.

NODE H.

ALL: **234.1** Humeral torsion present; **249.1** Ulnar facet for radius transversely expanded and concave; **330.1** Femoral head approximately 90 degrees from shaft (head directed horizontally).

ACCTRAN: **22.1** Pneumatic excavation without fenestra in cranial portion of maxillary antorbital fossa; **120.1** Splenial with notch for rostral margin of internal mandibular fenestra; **132.1** Premaxillary tooth crowns asymmetrical (strongly convex labially, relatively flattened lingually); **149.1** Cervical epiphyses powerfully developed and prong-shaped; **205.1** Paired caudal and cranial chevron bases; **315.2** Pubic boot shape rounded, angle between shaft and caudal portion of boot acute.

DELTRAN: **334.1** Anterior trochanter present, separated from femoral head by cleft; **335.2** Anterior trochanter of femur alariform; **346.1** Cnemial process arises out of the lateral surface of tibial shaft; **350.1** Crista fibularis present, not well developed; **351.1** Crista fibularis proximally placed; **376.1** Metatarsal III dorsal surface hourglass shaped.

NODE I.

ALL: **331.1** Femoral head transversely elongate.

ACCTRAN: None.

DELTRAN: **22.1** Pneumatic excavation without fenestra in cranial portion of maxillary antorbital fossa; **48.1** Postorbital ventral process broader transversely than rostrocaudally with U-shaped cross-section; **149.1** Cervical epiphyses powerfully developed and prong-shaped; **315.2** Pubic boot shape rounded, angle between shaft and caudal portion of boot acute; **317.1** Pubic boot present, less than 30% as long as pubic shaft; **341.1** Extensor groove in craniodistal region of femur shallow and not conspicuous; **353.1** Fibula closely appressed to tibia throughout main shaft; **360.1** Fibula distal end less than twice craniocaudal width at midshaft, and consequently astragalar cup for fibula reduced.

NODE J.

ALL: **31.2** Lacrimal prominences comprised of ridge continuous with raised surface of lateral edge of nasals; **336.2** Anterior trochanter of femur proximal most point above distal margin of femoral head; **355.1** Proximal region of fibular medial face slightly concave; **365.1** Pronounced horizontal groove across cranial face of astragalar condyles.

ACCTRAN: **-212.0** Distal expansion of scapula broad (subequal in width to proximal end of scapula); **339.1** Muscle scar in craniodistal region of femur present, non-elliptical in shape.

DELTRAN: **41.1** Orbit shorter than internal antorbital fenestra length; **61.1** Jugal recess; **64.2** Broad contact between dorsal ramus of quadratojugal and lateroventral ramus of squamosal; **205.1** Paired caudal and cranial chevron bases; **215.1** Scapulo-coracoid cranial margin with pronounced notch between acromial process and coracoid; **261.1** Articular surface between metacarpals I and II extends well into diaphysis of metacarpal I.

NODE K.

ALL: **139.1** Axial "spine table" (expanded distal end of neural spine); **146.1** Ventral keel on axial centrum absent; **155.1** Cervical zygapophyses displaced laterally away from centrum in dorsal view; **235.1** Humeral shaft sigmoid.

ACCTRAN: **4.1** Premaxillary symphyseal region U-shaped in ventral view; **-10.0** Premaxilla and nasal meet subnarily; **60.2** Jugal ventral quadratojugal process extends further caudally than dorsal quadratojugal process; **260.1** Metacarpal I one half to one third metacarpal II length; **264.1** Metacarpal III very much narrower (less than 50%) than metacarpal II; **266.1** Base of metacarpal III set on palmar surface of hand below base of metacarpal II; **267.1** Proximal articulation of metacarpal III triangular; **126.1** Cranial cervicals broader than deep on cranial

surface, with kidney-shaped articular surfaces that are taller laterally than at midline; **287.2** Anterior trochanter of femur proximalmost point above distal margin of femoral head.

DELTRAN: **319.1** Pubis and ischium proximal shafts narrow.

As in GAUTHIER (1986), NOVAS (1992), HOLTZ (1994), SERENO (1997), and most other recent studies of theropod phylogeny, a robustly supported clade of birds and theropods more closely related to birds than to *Ceratosaurus* was discovered. This clade, GAUTHIER's (1986) Tetanurae, comprises primarily the subdivisions Carnosauria and Coelurosauria, discussed below. However, there are several forms of theropod which (in the present analysis) lie outside the carnosaur-coelurosaur clade Avetheropoda, yet were found to share a more recent common ancestor with birds than with *Ceratosaurus*.

The relationships among the basal tetanurines, informally referred to as "megalosaurs" (in, for example, GAUTHIER (1986): p. 10) have been problematic in most recent studies (HOLTZ, 1994; SERENO *et al.*, 1994, 1996; SERENO, 1997). Unfortunately, the present analysis does not provide strong support for any particular scenario of "megalosaur" phylogeny. This uncertainty seems to stem from a number of sources, the most important being: a) the fairly large number of missing data from some of these taxa, representing our inadequate knowledge of the osteology of these forms at present; b) the lack of specializations in many of these taxa beyond those shared by all tetanurines, particularly in the case of the non-spinosaurid "megalosaurs"; and c) alternatively, the highly apomorphic nature of the skulls of spinosaurids (CHARIG & MILNER, 1997; SERENO *et al.*, 1998), in which the rostrum, dentition, palate, and basicranium are uniquely modified among theropods.

As previously noted, the fragmentary taxon "*Megalosaurus*" *hesperis* falls within this sector of the cladogram, but no particular sister group relationship was better supported than the others.

NOVAS (1992) proposed the name "Avipoda" for a clade comprised of *Eustreptospondylus*, *Piatnitzkysaurus*, and more advanced tetanurines. This corresponds to node I in this study. If additional work on theropod phylogenetics continues to support a subgroup excluding some basal tetanurines but uniting *Eustreptospondylus*, *Piatnitzkysaurus*, and more derived taxa, this name would serve as a useful label.

SERENO *et al.* (1994, 1996; 1998) and SERENO (1997) presented evidence that several of these basal tetanurines (in particular, *Torvosaurus*, *Eustreptospondylus*, and Spinosauridae) represented a

distinct clade of theropod, exclusive of other carnivorous dinosaurs. CHARIG & MILNER (1997) demonstrated that several of the "synapomorphies" for this postulated "Torvosauroida" (later changed to "Spinosauroidea") are absent in Spinosauridae. In the present study, some of the other characters suggested to support a monophyletic "Spinosauroidea" (**13.1**, **14.1**, **22.1**, **35.1**, and **279.1**) are explained in the most parsimonious distribution of states in this analysis to be basal tetanurine features lost in some or all avetheropod taxa.

Of particular note are conditions related to the rostral ramus ("anterior ramus" in BAKKER *et al.* (1992) and SERENO *et al.* (1994, 1996)) of the maxilla. The maxillae of basal tetanurines differ from those of ceratosaurs in the shape of the rostradorsal margin (Fig. 6). In ceratosaurs and herrerasaurids this line is a simple curve, convex dorsally, from the dorsal ramus to the tooth line. In tetanurines primitively this surface is a more complex curve, with a depression ventral to the external naris. This produces a rostral ramus to the maxilla, rostral to the dorsal ramus (**13.1**). The presence of this structure is found in all non-avetheropods for which skull material is known (although the condition in spinosaurids is distinct from the other taxa, given their elongate snouts: CHARIG & MILNER (1997)), and is also present in the skulls of most carnosaurids (the notable absences being *Sinraptor* and *Yangchuanosaurus*) and in basal coelurosaurids for which the skull is known (*Proceratosaurus* and *Ornitholestes*). As with sinraptorid carnosaurids, the clade of coelurosaurids comprised of *Scipionyx* and Maniraptoriformes have the primitive state with a simple dorsally convex curvature of the rostral portion of the maxilla. This distribution is most parsimoniously explained as independent reversals in Sinraptoridae and advanced Coelurosauria.

SERENO *et al.* (1994, 1996) specifically recognized a derived condition in which the rostral ramus was longer rostrocaudally than tall dorsoventrally. In the present study two different derived states were recognized to describe the relative proportions of the rostral ramus: those forms for which the structure is present, but shorter rostrocaudally than tall dorsoventrally (**14.1**) and the condition recognized by SERENO *et al.* (1994, 1996) (**14.2**). Rather than uniting Spinosauridae, *Torvosaurus*, *Eustreptospondylus*, and *Afrovenator* outside of other theropods, however, this condition was found to be the state at the base of Tetanurae, and subsequently shortened in various tetanurine taxa.

Curiously, all known basal tetanurines represent fairly large sized taxa (approximately 6 m or longer).

NODE L.

ALL: **17.1** Maxillary fenestra; **-22.0** Pneumatic excavation without fenestra in cranial portion of maxillary antorbital fossa absent; **322.1** Obturator process of ischium separate, trapezoidal; **323.1** Obturator process of ischium proximally placed; **341.2** Extensor groove in craniodistal region of femur deep and conspicuous

ACCTTRAN: **181.2** Presacral pleurocoels camelate; **217.1** Ventral coracoid process well developed; **355.2** Proximal region of fibular medial face well excavated

DELTRAN: **58.1** Jugal participates in internal antorbital fenestra; **197.2** Transition point in proximal half of tail; **253.1** Distal carpal I block does not overlap metacarpal II dorsally, but does so ventrally; **254.1** Distal carpal I fused to distal carpal II; **255.1** Semilunate carpal block fully developed with transverse trochlea; **260.1** Metacarpal I one half to one third metacarpal II length; **-279.0** Pollex ungual less than three times longer than height of articular facet; **-283.0** Manual ungual moderate length; **339.2** Muscle scar in craniodistal region of femur present, elliptical in shape; **364.1** Astragalar distal condyles oriented cranioventrally

NODE M. AVETHEROPODA

ALL: **-35.0** Lacrimal dorsal (rostral) ramus dorsoventrally deep; **-48.0** Postorbital ventral process broader rostrocaudally than transversely; **58.1** Squamosal constriction of lateral temporal fenestra; **169.1** Scars for interspinous ligaments terminate below apex of neural spine; **208.1** Middle chevron with dramatic bend in distal portion ("L-shaped"); **274.1** First phalanx of pollex greater than length of metacarpal II; **288.1** Iliac preacetabular fossa for M. cupperdicus

ACCTTRAN: **330.2** Femoral head greater than 90 degrees from shaft (head directed dorsally)

DELTRAN: **38.1** Prefrontal-frontal peg-in-socket suture; **76.1** Palatine tetraradiate; **78.1** Palatine recesses; **120.1** Splenial with notch for rostral margin of internal mandibular fenestra; **123.1** Retroarticular process of articular faces caudally; **132.1** Premaxillary tooth crowns asymmetrical (strongly convex labially, relatively flattened lingually); **212.1** Distal expansion of scapula reduced or absent; **217.1** Ventral coracoid process well developed; **225.1** Furcula; **233.1** Manus/(humerus + radius) length ratio greater than 66%; **-249.0** Ulnar facet for radius small and flat; **264.1** Metacarpal III very much narrower (less than 50%) than metacarpal II; **266.1** Base of metacarpal III set on palmar surface of hand below base of metacarpal II; **267.1** Proximal articulation of metacarpal III triangular; **268.1** Metacarpal IV less than half length of metacarpal II; **278.1** Pollex larger

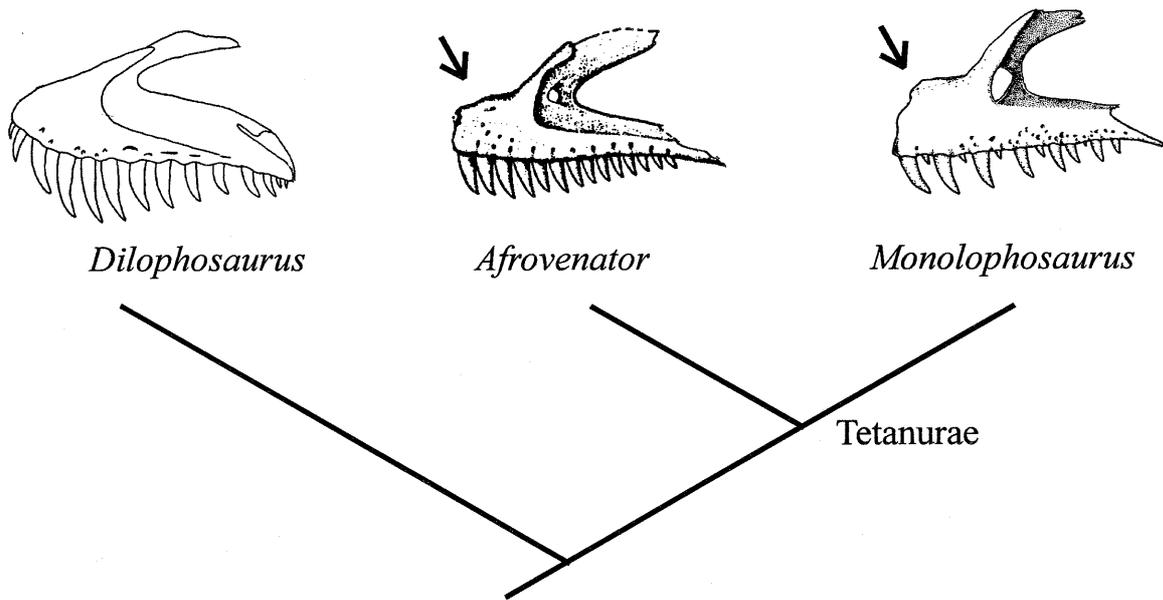


Fig. 6 - Cladogram comparing the left maxillae (in left lateral view) of the ceratosaur *Dilophosaurus* (modified from WELLES, 1984), the basal tetanurine *Afrovenator* (modified from SERENO *et al.*, 1994), and the avetheropod carnosaur *Monolophosaurus* (modified from ZHAO & CURRIE, 1993). Arrow indicates the presence of the rostral ramus of the maxilla, a tetanurine synapomorphy (character 13.1). Not to scale.

than other manual unguals; **355.2** Proximal region of fibular medial face well excavated

As in NOVAS (1992), HOLTZ (1994), SERENO *et al.* (1994, 1996), and SERENO (1997), a clade was recognized containing *Allosaurus* and those taxa closest to it as one branch, and Aves and those taxa closest to it as the other, outside of the more primitive tetanurines. Following HOLTZ (1994), and using a name for this clade first published in PAUL (1988), this clade comprised of all descendants of the most recent common ancestor of *Allosaurus* and Neornithes is termed Avetheropoda. SERENO *et al.* (1994, 1996) and SERENO (1997, 1998) suggested the alternative name "Neotetanurae": indeed, SERENO (1997, 1998) uses the same definition as the above, rendering this term a junior objective synonym of Avetheropoda (see also PADIAN, HUTCHINSON & HOLTZ (1999)). Perhaps the name "Neotetanurae" might be preserved as the name for a more inclusive taxon (for example, Neornithes and all taxa sharing a more recent common ancestor with Neornithes than with Spinosauridae).

The Early Cretaceous (?Barremian) *Afrovenator abakensis* was found to share several derived characters with Avetheropoda lacking in other basal tetanurines: in particular, unquestionable presence of a maxillary fenestra (**17.1**) and an obturator process on the ischium (**322.1**, **323.1**). Additionally, the semi-lunate carpal block (**255.1**) is present in *Afrovenator* as it is in avetheropods, but as the carpus is unknown in other non-avetheropod tetanurines, this

derived feature may be synapomorphic for a more inclusive group (see Discussion below).

The two divisions of Avetheropoda are termed Carnosauria (*Allosaurus* and all taxa sharing a more recent common ancestor with *Allosaurus* than with Neornithes) and Coelurosauria (Neornithes and all taxa sharing a more recent common ancestor with Neornithes than with *Allosaurus*): see PADIAN, HUTCHINSON & HOLTZ (1999) for discussion of the history of these terms. Both carnosaur and coelurosaur share the derived character state of fused clavicles (furculae): however, the lack of preservation of clavicles in more basal tetanurines allows for the possibility of this character state being synapomorphic for an even more inclusive group (see Discussion below). Twenty four other derived character states unite carnosaur and coelurosaur to the exclusion of other theropod clades, but sixteen of these cannot be fairly assessed at present in basal tetanurines, as the skeletal elements concerned are not recovered for these taxa at present.

NODE N. CARNOSAURIA

ALL: **23.1** Lateral surface of nasal participates in antorbital cavity, forming a nasal antorbital fossa; **29.1** Nasal recesses; **75.1** Palatines meet medially; **83.1** Nuchal crest pronounced; **97.1** Distance across basal tubera less than the transverse width of occipital condyle; **100.1** Basipterygoid processes short, but not fused to pterygoids; **166.1** Ventral pro-

cesses (hypapophyses) on cervicodorsal vertebrae present as small protrusions.

ACCTRAN: **67.2** Quadrate foramen small and enclosed within dorsal ramus of quadrate; **113.1** Rostral surangular foramen large, in rostrally-oriented depression; **229.1** Humerus/scapula length ratio less than 65%; **314.1** Pubic foramen perforating pubic apron in distal half of shaft; **350.2** Crista fibularis well developed; **382.1** Pedal digit I phalanges 1+2 subequal to pedal digit III phalanx 1.

DELTRAN: **24.1** Nasal participates in antorbital cavity; **60.2** Jugal ventral quadratojugal process extends further caudally than dorsal quadratojugal process; **70.1** Quadrate articulation projects well caudal to the caudalmost point of the occipital condyle.

NODE O. ALLOSAUROIDEA

ALL: **21.1** Pneumatic excavation of the ascending ramus of the maxilla; **26.2** Narial prominences comprised of paired ridges along lateral edges of nasals; **33.1** Lacrimal recess, single opening present; **47.1** Postorbital prominences present; **69.1** Quadrate articulation projects well ventral of the ventral surface of the maxilla; **116.2** Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle, prominent and pendant; **179.1** Caudal dorsal neural spines oriented cranially; **315.4** Pubic boot shape triangular (apex caudal) in ventral view and angle between shaft and caudal portion of boot acute.

ACCTRAN: **118.1** External mandibular fenestra reduced; **175.1** Dorsal centrum "hourglass" shaped, central section depth less than 60% height of cranial face; **307.1** Obturator foramen of pubis open ventrally to form obturator notch.

DELTRAN: **4.1** Premaxillary symphyseal region U-shaped in ventral view; **67.2** Quadrate foramen small and enclosed within dorsal ramus of quadrate; **77.1** Jugal process of palatine expanded; **81.1** Ventral ectopterygoid recess present and comma-shaped; **181.2** Presacral pleurocoels camellate; **257.2** Metacarpal IV present, without phalanges; **314.1** Pubic foramen perforating pubic apron in distal half of shaft; **316.1** Caudal portion of pubic boot longer than cranial portion, but latter present; **350.2** Crista fibularis well developed; **382.1** Pedal digit I phalanges 1+2 subequal to pedal digit III phalanx 1.

NODE P. SINRAPTORIDAE

ALL: **9.1** External nares with marked inset of the caudal margin; **-13.0** Rostral ramus of maxilla absent, rostradorsal surface of maxilla forms convex surface from dorsal ramus to ventral margin; **20.1** Promaxillary fenestra larger than maxillary fenestra;

56.1 Squamosal flange covering quadrate head in lateral view; **167.1** Neural spines of dorsals equal to twice centrum height; **357.1** Cranial protuberance on fibula below expansion.

ACCTRAN: **-57.0** Squamosal does not constrict lateral temporal fenestra.

DELTRAN: **-10.0** Premaxilla and nasal meet subnarily; **-14.0** Rostral ramus absent; **113.1** Rostral surangular foramen large, in rostrally-oriented depression; **175.1** Dorsal centrum "hourglass" shaped, central section thickness less than 60% height of cranial face; **-330.1** Femoral head approximately 90 degrees from shaft (head directed horizontally).

NODE Q. ALLOSAURIDAE

ALL: **-58.0** Jugal does not participate in internal antorbital fenestra; **103.1** Occipital condyle constricted neck; **115.1** Rostral ramus of surangular deep; **178.1** Dorsal column subequal to femur length; **257.3** Metacarpal IV absent; **317.2** Pubic boot present, greater than 30% as long as pubic shaft; **318.1** Pubic-ischial contact only narrow region; **349.1** Lateroproximal condyle of tibia with conspicuous waisting between body of condyle and main body of tibia in proximal view.

ACCTRAN: **16.2** Promaxillary fenestra present, obscured in lateral view by ascending ramus of maxilla; **87.2** Paroccipital process curving ventrally and pendant; **112.1** Dentary caudal depth 150-200% depth of dentary symphysis; **-170.0** Apices of dorsal neural spines unexpanded; **214.1** Caudal margin of acromial process of scapula forms abrupt change, perpendicular to blade.

DELTRAN: **-113.0** Rostral surangular foramen absent or very small pit; **118.1** External mandibular fenestra reduced; **229.1** Humerus/scapula length ratio less than 65%; **307.1** Obturator foramen of pubis open ventrally to form obturator notch; **330.2** Femoral head greater than 90 degrees from shaft (head directed dorsally).

NODE R.

ALL: **3.2** Five premaxillary teeth; **199.1** Distal caudal vertebrae with moderate interlocking, prezygapophyses extend more than one half, but less than one, centrum length; **-212.0** Distal expansion of scapula broad, subequal in width to proximal end.

ACCTRAN: **31.2** Lacrimal prominences triangular hornlets; **-78.0** Palatine recesses absent; **96.1** Basioccipital excluded from basal tuber; **195.1** Proximal caudal zygapophyses elongate.

DELTRAN: **10.1** Premaxilla and nasal do not meet subnarily; **87.2** Paroccipital process curving

ventrally and pendant; **-169.0** Scars for interspinous ligaments terminate at apex of neural spine; **214.1** Caudal margin of acromial process of scapula forms abrupt change, perpendicular to blade.

NODE S

ALL: **36.1** Lacrimal suborbital bar; **41.1** Frontal-frontal suture fused; **50.1** Postorbital-lacrimal contact broad; **53.1** Postorbital suborbital flange; **-100.0** Basipterygoid processes moderately long; **159.1** Elevation of cranial face of midcervical centra; **191.1** Caudal pleurocoels present in centra.

ACCTRAN: **-166.0** Ventral processes (hypapophyses) on cervicodorsal vertebrae absent; **183.1** Sacral pleurocoels; **236.1** Humeral head offset and emarginated ventrally by groove; **241.1** Deltapectoral crest on humerus expanded and offset from humeral shaft.

DELTRAN: **-14.1** Rostral ramus of maxilla shorter rostrocaudally than dorsoventrally.

NODE T.

ALL: **-10.0** Premaxilla and nasal meet subnarily; **15.2** Maxillary antorbital fossa greatly reduced in size, not extending much beyond rim of the external antorbital fossa; **-21.0** Pneumatic excavation of ascending ramus of maxilla absent; **26.3** Nasal prominences knobby rugosities across dorsal and lateral surface of nasals, extending onto dorsalmost surface of maxillae; **52.1** Postorbital bulbous rostrally projecting rugosity; **88.1** Basisphenoid, but not parasphenoid rostrum, strongly expanded and pneumatized; **131.1** Lateral surface of teeth with wrinkles in enamel internal to serrations.

ACCTRAN: **5.1** Premaxilla subnarily very deep, main body taller dorsoventrally than long rostrocaudally; **8.1** Maxillary process of premaxilla reduced, maxilla participates broadly in ventral surface of external naris; **-17.0** Maxillary fenestra absent; **37.1** Prefrontals reduced or absent; **42.2** Frontal-parietal suture on dorsal surface of skull fused, suture indistinguishable; **-57.0** Squamosal does not constrict lateral temporal fenestra; **-60.0** Jugal dorsal and ventral quadratojugal processes subequal in caudalmost extension; **62.1** Jugal recesses; **68.1** Quadrate dorsal ramus height greater than height of orbit; **105.1** Dentary end squared with expanded tip; **157.1** Cranial cervicals broader than deep on cranial surface, with reniform (kidney-shaped) articular surfaces that are taller laterally than at midline.

DELTRAN: **-87.0** Paroccipital process oriented more caudally than dorsally.

As argued by PADIAN, HUTCHINSON & HOLTZ (1999) (see also HOLTZ & BRETT-SURMAN, 1997),

the long established name Carnosauria HUENE, 1920 may be conserved as the clade comprised of *Allosaurus* and all taxa sharing a more recent common ancestor with this taxon than with Neornithes. In the present study, the oldest and most basal form in this clade is the Middle Jurassic *Monolophosaurus jiangi* ZHAO & CURRIE, 1993 of China. However, SERENO *et al.* (1994, 1996) and SERENO (1997) have proposed that *Cryolophosaurus ellioti* HAMMER & HICKERSON, 1994 is a member of this clade. If this hypothesis is correct, the age of this form would indicate not only a minimum Early Jurassic date for the origin of Carnosauria but also of the Coelurosauria (see also discussion of maniraptoriforms below), as well as such an early date for the origin of each of the various basal tetanurine lineages.

HARRIS (1998) observed that palatines that meet medially are present in both *Sinraptor* and *Allosaurus*. Such a geometry appears to be present in *Monolophosaurus* (ZHAO & CURRIE, 1993), but is absent in basal sauropodomorphs, *Herrerasaurus*, ceratosaurs, tyrannosaurids, ornithomimids, dromaeosaurids, and other coelurosaurs. In these taxa, the palatines remain separated medially by the rostral processes of the pterygoids.

Allosauroida CURRIE & ZHAO, 1993a has been proposed as the name for the clade comprised of all descendants of the most recent common ancestor of *Allosaurus* and *Sinraptor* (see also PADIAN, HUTCHINSON & HOLTZ, 1999). (SERENO (1997, 1998) uses the same name but with the definition employed here for Carnosauria). In the present study, this clade would contain all carnosaurs except for *Monolophosaurus*. HARRIS (1998) observed that allosauroids were characterized by caudal dorsal vertebrae in which the neural spines were oriented cranially rather than vertically (as in other theropods). This orientation is not present in *Monolophosaurus*, but is found in *Sinraptor*, *Allosaurus*, and *Acrocantiosaurus*. As such, it is supported here as a synapomorphy of Allosauroida.

Within the allosauroids, a sister group relationship for *Sinraptor* and *Yangchuanosaurus*, proposed in the first study of the former taxon (CURRIE & ZHAO, 1993a), is supported here. Similarly, HUTT, MARTILL & BARKER (1996) suggested that their newly described *Neovenator* (of the Wealden Group of the Isle of Wight) was closely related to the Late Jurassic North American genus *Allosaurus*, a position also retained in the present analysis.

The union of *Acrocantiosaurus*, *Giganotosaurus*, and *Carcharodontosaurus*, first proposed (with a different topology) by SERENO *et al.* (1996) was found in the present analysis. This clade of gigantic mid-Cretaceous (Aptian-Cenomanian) carnosaurs was called "Carcharodontosauridae" by SERENO *et*

al. (1996), although (under the phylogenetic taxonomy used here) this clade is part of Allosauridae (i.e., *Allosaurus* and all taxa sharing a more recent common ancestor with *Allosaurus* than with *Sinraptor*). Although the analysis of CURRIE & CARPENTER (in press) found that *Acrocanthosaurus* was more closely related to *Allosaurus* than to *Giganotosaurus* or *Carcharodontosaurus*, this study agrees with SERENO *et al.* (1996) and HARRIS (1998) in grouping the three giant mid-Cretaceous taxa exclusive of the Late Jurassic *Allosaurus*.

Examining the character states at node T reveals many derived features also demonstrated by abelisauroids. Indeed NOVAS (1997c) has suggested that *Giganotosaurus* and *Carcharodontosaurus* are closely related to the abelisauroid neoceratosaurs, a very different phylogenetic position from that found here. Although there are several cranial synapomorphies potentially uniting *Carcharodontosaurus* and Abelisauridae (in general) or *Abelisaurus* (in particular), additional features unite the African dinosaur with *Giganotosaurus*, while further cranial and postcranial character states group this South American dinosaur with the unquestioned tetanurine *Acrocanthosaurus* (see also the Discussion below).

In the current phylogeny, *Carcharodontosaurus* (of Cenomanian age) is the latest known carnosaur. No fossil evidence presently known indicates the survival of Carnosauria into the last twenty eight million years of the Cretaceous.

NODE U. COELUROSAURIA

ALL: **-147.0** Cervical centra surfaces amphiplatyan; **315.3** Pubic boot boat-shaped (pointed cranially and caudally) in ventral view and angle between shaft and caudal portion of boot acute; **354.1** Fibula proximal end 75% or more proximal width of tibia.

ACCTRAN: **15.1** Maxillary antorbital fossa greater than 40% of the rostrocaudal length of the antorbital cavity; **-31.0** Lacrimal prominences absent; **-45.0** Orbit shape round; **-54.0** Postorbital frontal process sharply upturned; **60.1** Jugal dorsal quadratojugal process extends further caudally than ventral quadratojugal process; **-61.0** Jugal recesses absent; **70.2** Quadrate articulation rostral to caudalmost point of occipital condyle; **80.1** Subsidiary fenestra between pterygoid and palatine; **82.1** Endocranial cavity enlarged relative to other dinosaurs, but temporal musculature extends onto frontals; **86.1** Paroccipital process with hollow proximal portion; **88.1** Basisphenoid, but not parasphenoid rostrum, strongly expanded and pneumatized; **90.1** Three tympanic recesses; **91.1** Branches of internal carotid artery enter hypoglossal fossa through single common foramen; **115.1** Rostral ramus of suran-

gular deep; **121.1** Coronoid extremely reduced or absent; **153.1** Cervical prezygapophyses flexed; **157.1** Cranial cervicals broader than deep on cranial surface, with kidney-shaped articular surfaces that are taller laterally than at midline; **-160.0** Midcervical centra length about twice diameter of cranial face; **190.1** Number of caudals between 30 and 44; **196.1** Caudal transverse processes only on caudals I-XV or fewer; **209.1** Distal chevrons with cranial and caudal projections, and more than twice as long cranio-caudally as tall dorsoventrally ("boat-shaped"); **-215.0** Scapulacoracoid cranial margin smooth; **226.1** Forelimb (humerus+radius+manus)/hindlimb (femur+tibia+pes) length ratio greater than 50% but less than 120%; **227.1** Forelimb/presacral vertebral series length ratio greater than 75% but much less than 200%; **232.2** Radius/humerus length ratio greater than 76%; **245.1** Ulnar shaft bowed caudally; **272.1** Length of phalanx 3 of manual digit III/(sum of lengths of phalanges 1+2 of digit III) greater than 100%; **330.2** Femoral head greater than 90 degrees from shaft (head directed dorsally); **332.1** Greater trochanter cleft from femoral head; **347.1** Incisura tibialis cranialis occupies more than 66% of medial surface of proximal tibia; **362.2** Astragalar ascending process cranio-caudally reduced and proximodistally tall, with dorsal margin sigmoid ("ornithomimoid/albertosauroid condition"); **-365.0** No pronounced horizontal groove across cranial face of astragalar condyles; **380.1** Metatarsal I plantar to medial side of metatarsal II; **386.1** Pedal ungual II significantly longer than pedal ungual III.

DELTRAN: None.

NODE V.

ALL: None

ACCTRAN: **307.1** Obturator foramen of pubis open ventrally to form obturator notch; **322.2** Obturator process of ischium separate, triangular shaped; **-341.1** Extensor groove in craniodistal region of femur present, but shallow and not conspicuous; **349.1** Lateroproximal condyle of tibia with conspicuous waisting between body of condyle and main body of tibia in proximal view.

DELTRAN: **4.1** Premaxillary symphyseal U-shaped in ventral view; **-10.0** Premaxilla and nasal meet subnarily; **15.1** Maxillary antorbital fossa greater than 40% of the rostrocaudal length of the antorbital cavity; **-45.0** Orbit shape round; **-61.0** Jugal recesses absent; **70.2** Quadrate articulation rostral to caudalmost point of occipital condyle.

NODE W.

ALL: None.

ACCTRAN: **7.1** Medial alae from premaxillae meet in front of vomera; **-44.0** Orbit longer than inter-

nal antorbital fenestra length; **116.1** Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle, prominent and extends laterally.

DELTRAN: **307.1** Obturator foramen of pubis open ventrally to form obturator notch; **318.1** Pubic-ischial contact only narrow region; **337.1** Fourth trochanter of femur little developed; **-341.1** Extensor groove in craniodistal region of femur present, but shallow and not conspicuous; **349.1** Lateroproximal condyle of tibia with conspicuous waisting between body of condyle and main body of tibia in proximal view; **362.2** Astragalar ascending process cranio-caudally reduced and proximodistally tall, with dorsal margin sigmoid ("ornithomimoid/albertosauroid condition"); **-365.0** No pronounced horizontal groove across cranial face of astragalar condyles.

NODE X.

ALL: **333.1** Femoral head transversely elongate.

ACCTRAN: **60.1** Jugal dorsal quadratojugal process extends further caudally than ventral quadratojugal process; **81.2** Ventral ectopterygoid recess present and subcircular; **277.1** Manual ungual region palmar to ungual groove subequal in width to region dorsal to ungual groove; **282.1** Manual ungual cross section blade-like, more than three times as deep as wide; **357.1** Cranial protuberance on fibula below expansion.

DELTRAN: **-31.0** Lacrimal prominences absent; **-44.0** Orbit longer than internal antorbital fenestra length; **82.1** Endocranial cavity enlarged relative to other dinosaurs, but temporal musculature extends onto frontals; **115.1** Rostral ramus of surangular deep; **-160.0** Midcervical centra length about twice diameter of cranial face; **181.2** Presacral pleurocoels camellate; **190.1** Number of caudals between 30 and 44; **196.1** Caudal transverse processes only on caudals I-XV or fewer; **209.1** Distal chevrons with cranial and caudal projections, and more than twice as long cranio-caudally as tall dorsoventrally ("boat-shaped"); **227.1** Forelimb/presacral vertebral series length ratio greater than 75% but much less than 200%; **322.2** Obturator process of ischium separate, triangular shaped; **332.1** Greater trochanter of femur cleft from femoral head.

NODE Y.

ALL: **-149.0** Cervical epipophyses rugosities on caudal zygapophyses; **154.1** Cervical neural spines low and cranio-caudally short; **186.2** Sacrals III-V dorsoventrally flattened.

ACCTRAN: **-13.0, -14.0** Rostral ramus of maxilla absent, rostradorsal surface of maxilla forms convex surface from dorsal ramus to ventral margin; -

26.0 Narial prominences absent; **71.1** Quadrate pneumaticity well developed; **72.1** Secondary palate well ossified from premaxilla through one-half the length of the ventral surface of the maxilla; **103.1** Occipital condyle constricted neck; **114.1** Caudal surangular foramen large opening; **369.1** Metatarsus proportions elongate relative to most other theropods of same femur length; **-376.0** Metatarsal III dorsal surface shape elliptical.

DELTRAN: **263.1** Metacarpal III clearly shorter than metacarpal II; **272.1** Length of phalanx 3 of manual digit III/(sum of lengths of phalanges 1 + 2 of digit III) greater than 100%; **277.1** Manual ungual palmar and dorsal regions subequal in width; **282.1** Manual ungual cross section blade-like, more than three times as deep as wide.

NODE Z.

ALL: **-235.0** Humeral shaft straight; **257.3** Metacarpal IV absent.

ACCTRAN: **157.1** Cranial cervicals broader than deep on cranial surface, with reniform (kidney-shaped) articular surfaces that are taller laterally than at midline.

DELTRAN: **-13.0, -14.0** Rostral ramus of maxilla absent, rostradorsal surface of maxilla forms convex surface from dorsal ramus to ventral margin; **-26.0** Narial prominences absent; **153.1** Cervical prezygapophyses flexed; **-215.0** Scapulacoracoid cranial margin smooth; **-221.0** Sternal plates unfused; **-222.0** Sternum carina absent; **-245.0** Ulnar shaft bowed caudally.

NODE aa.

ALL: **195.1** Proximal caudal zygapophyses elongate.

ACCTRAN: **8.1** Maxillary process of premaxilla reduced, maxilla participates broadly in ventral surface of external naris; **37.1** Prefrontals reduced or absent; **118.1** External mandibular fenestra reduced; **158.1** Cranial cervical centra extend beyond caudal extend of neural arch; **168.1** Apices of dorsal neural spines expanded transversely to form "spine table"; **188.1** Sacral neural spines fuse to form lamina; **-240.0** Humeral ends little or not expanded; **284.2** Manual unguals straight.

DELTRAN: **114.1** Caudal surangular foramen a large opening.

Coelurosauria is a well-supported clade of tetanurine dinosaurs. Most of the traditional coelurosaurians of previous studies (GAUTHIER, 1986; HOLTZ, 1994; SERENO, 1997; SUES, 1997), known from relatively complete material, comprise a clade of derived forms, the Maniraptoriformes HOLTZ, 1996b: these

taxa are discussed below. As in the case of basal Tetanurae, however, there exist a number of fragmentary forms which demonstrate some shared derived characters with Maniraptoriformes compared to other theropods, but which were found to lie outside that clade..

Among these, *Proceratosaurus bradleyi* is the oldest currently known (Bathonian age, Middle Jurassic). An alleged therizinosauroid maniraptoriform from the Sinemurian age (Early Jurassic) of the Lower Lufeng Formation, Yunnan, China (ZHAO & XU, 1998) is even older. If substantiated, this would indicate that Maniraptoriformes (and indeed, the various lineages of the oviraptorosaur-*Microvenator* clade, Paraves, Compsognathidae, and Arctometatarsalia, the ancestors of the basal coelurosaurs, and Carnosauria) would date back to at least the Sinemurian. However, the specimen in question is an isolated dentary, and given the resemblance of the dentary of therizinosauroids and basal sauropodomorphs (the latter common to the Early Jurassic dinosaurian fauna), this intriguing discovery is greeted with some caution.

Regardless of the phylogenetic identity of the Yunnan specimen, *Proceratosaurus* shares uniquely with other coelurosaurs several derived characteristics. The maxillary antorbital fossa (the wall of bone on the rostral portion of the antorbital fenestra: WITMER, 1997) forms 40% of the total rostrocaudal length of the antorbital fenestra, a derived condition first hypothesized as a coelurosaurian synapomorphy by SERENO *et al.* (1994, 1996) and supported here (Fig. 7). In carnosaurs, basal tetanurines, and ceratosaurs, the maxillary antorbital fossa represents a much smaller fraction of this length (and, correspondingly, the internal antorbital fenestra represents a larger fraction of the total structure). Furthermore, the articulation between the quadrates and the mandible lie rostral to the caudalmost point of the occipital condyle in *Proceratosaurus* and most other coelurosaurs. In contrast, the quadrate articulation lies at the same point or rostral to the caudalmost point of the occipital condyle in ceratosaurs, basal tetanurines, and carnosaurs. Even in the largest skulled of coelurosaurs, large tyrannosaurids such as *Tyrannosaurus rex* (MOLNAR, 1991) the articulation of the quadrates is slightly rostral to the end of the occipital condyle. Coupled with the flexion of the cervical prezygapophyses and the development of kidney-shaped articular surfaces in the cranial cervicals, the forward placement of the mandibular joint may indicate specializations towards greater lateral mobility in the necks of coelurosaurs relative to other theropods. In other theropods, the posterior placement of the mandibular joint may have interfered with lateral motion of the

neck. Unfortunately, the cervicals of *Proceratosaurus* are presently unknown.

The inclusion of *Gasosaurus constructus* in Coelurosauria is novel to this study. This poorly known Middle Jurassic Chinese form is admittedly fragmentary. Its pelvis retains several primitive features transformed in other, later coelurosaurs: the obturator foramen is present, the ischium is footed, and the obturator process appears to be trapezoidal. Nevertheless, the hindlimb possesses several coelurosaur characteristics: a femoral head at an angle greater than 90 degrees to the femoral shaft; a lesser trochanter cleft from the femoral head, and a fibula whose proximal portion is greater than 75% the proximal width of the tibia. Given the incomplete nature of this taxon, additional character evidence may reveal it does not belong to Coelurosauria. Pending such discovery, however, the current analysis suggests that this form does indeed share a more recent common ancestor with birds than with *Allosaurus*. (P. Currie, pers. comm. 1998, indicates that as yet undescribed specimens suggest that *Gasosaurus* is in fact a primitive carnosaur, perhaps a sinraptorid).

The Late Cretaceous (Campanian) North American taxon *Dryptosaurus*, previously suggested to be a coelurosaur by DENTON (1990), was found to be more derived than *Gasosaurus* in that it possesses a true obturator notch, a narrow proximal contact between the pubis and ischium, and a few other hindlimb characters. Unfortunately, this taxon too is incompletely known at present.

The Late Jurassic *Ornitholestes hermanni* OSBORN, 1903 is one of the most completely known basal coelurosaurs. As in HOLTZ (1994), SERENO *et al.* (1996), and SERENO (1998), but unlike GAUTHIER (1986) and MAKOVICKY & SUES (1998), this form was found to be more distantly related to birds than is Ornithomimosauria.

Sympatric with *Ornitholestes*, *Coelurus agilis* MARSH, 1879b was found to be somewhat more closely related to birds than the former taxon, as in MAKOVICKY & SUES (1998); however, unlike that study, *Coelurus* was here found to lie outside the clade comprised of all descendants of the most recent common ancestor of birds and ornithomimosaurians. Note that as in MAKOVICKY & SUES (1998), this study follows MILES, CARPENTER & CLOWARD (1998) in assigning the manual material AMNH 587 to *Coelurus* rather than *Ornitholestes*. New, more complete material of *Coelurus* currently under study by those latter authors will greatly aid our understanding of this coelurosaur and its phylogenetic position. Yet another small coelurosaur from the Late Jurassic Morrison Formation, known only from iso-

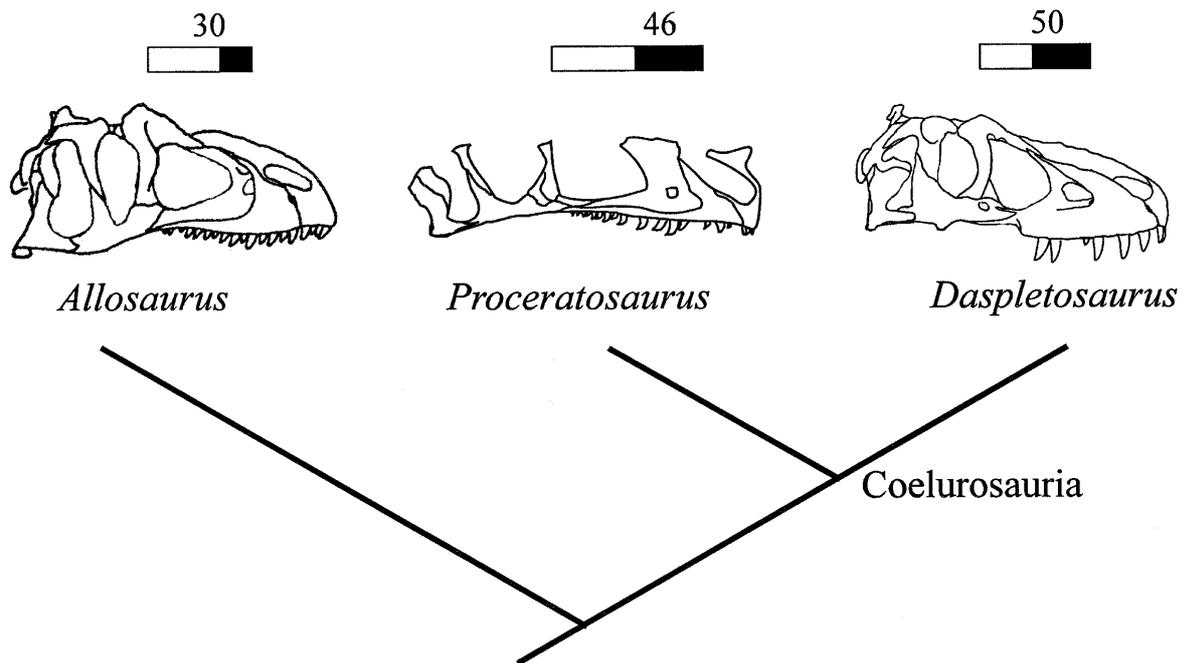


Fig. 7 - Cladogram comparing skulls (in right lateral view) of the carnosaur *Allosaurus* (modified from CURRIE, 1997), the basal coelurosaur *Proceratosaurus* (BMNH R4860, new reconstruction based on a photograph by the author), and the tyrannosaurid *Daspletosaurus* (modified from RUSSELL, 1970). Bar above skulls represent total length of antorbital fenestra; solid portion of bar and number above represents percentage of antorbital fenestra occupied by maxillary antorbital fossa (character 15). Not to scale.

lated vertebrae, was reported by MAKOVICKY (1997).

Scipionyx samniticus DAL SASSO & SIGNORE, 1998 is a recently described theropod taxon from the Albian of Italy. It is known from one of the most complete skeletons of any basal coelurosaur. The describers considered it to be a maniraptoriform of uncertain relationship. In the present analysis it was found to lie outside of Maniraptoriformes proper. However, as this specimen is likely a hatchling, it may be that an adult individual of *Scipionyx* may demonstrate maniraptoriform synapomorphies. At present, this taxon is potentially of great importance in determining the character distribution in basal members of the maniraptoriform clade.

It should be noted that, given the often marked difference between hatchling and adult dinosaur body size (CARPENTER, HIRSCH & HORNER, 1994), the small size of the type and only known specimen of *Scipionyx* (237 mm from tip of the premaxilla to the ninth caudal vertebra: DAL SASSO & SIGNORE, 1998) may not necessarily reflect a small adult size for this taxon.

Bagaraatan ostromi OSMÓLSKA, 1996 is known only from a fragmentary skeleton from the Nemegt Formation (Late Cretaceous, ?early Maastrichtian age) of Mongolia. In the present study its most parsimonious position is as the sister taxon of Maniraptoriformes. Like many maniraptoriform groups, this taxon demonstrates a greatly enlargement of the caudal surangular foramen (previously thought to also occur in the carnosaur *Acrocanthosaurus* (see STOVALL & LANGSTON, 1950; HOLTZ, 1994; new evidence demonstrates this condition is lacking in that carnosaur: CURRIE & CARPENTER, in press). *Bagaraatan* is noteworthy for sharing many features of the tibia and tarsus with ceratosaurian dinosaurs and with advanced ornithothoracine birds: these are best explained here by convergence.

NODE bb. MANIRAPTORIFORMES

ALL: **313.1** Pubic apron limited to distal half of pubic shaft; **336.3** Anterior trochanter of femur proximalmost point above proximal margin of femoral head.

ACCTRAN: None.

DELTRAN: **8.1** Maxillary process of premaxilla reduced, maxilla participates broadly in ventral surface of external naris; **-24.0** Nasal excluded from antorbital cavity; **71.1** Quadrate pneumaticity well developed; **80.1** Subsidiary fenestra between pterygoid and palatine; **76.1** Paroccipital process with hollow proximal portion; **90.1** Three tympanic recesses; **118.1** External mandibular fenestra re-

duced; **284.2** Manual unguals extremely curved; **347.1** Incisura tibialis occupies more than 66% of medial surface of proximal tibia; ; **-376.0** Metatarsal III dorsal surface shape elliptical; **380.1** Metatarsal I plantar to medial side of metatarsal II.

Following HOLTZ (1996b), the clade comprised of all descendants of the most recent common ancestor of *Ornithomimus* and Neornithes is named Maniraptoriformes. As well as ornithomimids and birds, HOLTZ (1994), SERENO (1997, 1998), and this study agree that Maniraptoriformes also includes tyrannosaurids, troodontids, therizinosauroids, oviraptorosaurs, and dromaeosaurids (although the arrangement of these taxa differ among these studies). In MAKOVICKY & SUES (1998), all of the above except for tyrannosaurids were included within this clade (there unnamed), as were *Ornitholestes* and *Coelurus*. HOLTZ (1996b) also clarified the phylogenetic definitions of the two main branches of maniraptoriform coelurosaurs: Maniraptora GAUTHIER 1986, Neornithes and all taxa sharing a more recent common ancestor with neornithines than with *Ornithomimus*; and its sister taxon by definition, Arctometatarsalia HOLTZ, 1994, *Ornithomimus* and all taxa sharing a more recent common ancestor with *Ornithomimus* than with Neornithes. Of note, nothing in these phylogenetic taxonomic definitions necessitates the presence of a particular derived character or suite of characters (e.g., grasping hands and pinched metatarsi, respectively) nor a particular combination of taxa. Instead, they simply describe two complimentary clades within the larger taxon Maniraptoriformes. As discussed below, some taxa with "maniraptor" hands may lie within Arctometatarsalia in the present analysis, while other taxa with arctometatarsi are found to be members of Maniraptora. See HOLTZ (1996b) and PADIAN, HUTCHINSON & HOLTZ (1999) for discussion.

A character complex of interesting distribution is the presence of a large ossified secondary palate formed by medial extensions of the maxillae (**72.1**) and by medial alae of the premaxillae contacting rostral to the vomers (**7.1**). Because the palate of several coelurosaurian taxa is unknown or unprepared, the precise distribution of these character states is unknown. Nevertheless, while therizinosauroids, oviraptorosaurs, dromaeosaurids, avialians, tyrannosaurids, troodontids, and ornithomimosaurids demonstrably possess these features, herrerasaurids, ceratosaurs, basal tetanurines, and carnosaurids do not. This pattern is complicated by the lack of a maxillary component to the secondary palate in Compsognathidae (*Sino-sauropteryx*, pers. observation 1998). An ossified secondary palate has been demonstrated to be biomechanically advantageous in resisting torsional forces in the skull (BUSBEY, 1995), which would be

consistent with the greater lateral flexibility possible in the cervical region of coelurosaurs compared to other theropods (see above). Additionally (and not mutually exclusive to torsional resistance), a large ossified secondary palate might allow continued breathing while the rostrum was occupied with food manipulation and processing.

In the most parsimonious trees in this analysis all but one of the maniraptoriform taxa unambiguously group as either arctometatarsalians or as maniraptorans. However, Troodontidae is equally parsimoniously placed as a paravian maniraptoran (the sister taxon to the dromaeosaurid-bird clade) or as a bullatosaurian arctometatarsalian (the sister taxon to Ornithomimosauria). The summary cladogram (Fig. 5) follows the first of these options, but character evidence for the second are discussed below. Furthermore, it requires only one additional evolutionary step to move Troodontidae to a sister group position to the oviraptorosaur-therizinosauroid clade within Maniraptora (see Discussion).

NODE cc. ARCTOMETATARSALIA

ALL: **25.1** Nasals narrow caudally behind external nares; **39.1** Rostral portion of frontals relatively triangular, suture with nasals forms a distinct acute angle; **55.1** Squamosal recess; **95.1** Three cranial nerve openings in acoustic fossa; **198.1** Midcaudal vertebrae with moderately long prezygapophyses, extending more than one half but less than one centrum length; **199.1** Distal caudal vertebrae with moderate interlocking, prezygapophyses extend more than one half, but less than one, centrum length; **206.1** Bridge of bone dorsal to haemal canal in distal chevrons; **-278.0** Pollex ungual subequal to unguals of digits II and III in size; **282.2** Manual ungual cross-section subtriangular, as wide or wider than deep; **287.1** Iliac blades dorsal surface meet along midline; **294.1** Preacetabular process of ilium cranial margin notched; **326.1** Semicircular scar on caudal surface of ischium, just distal to iliac process; **341.2** Extensor groove in craniodistal region of femur deep and conspicuous; **350.2** Crista fibularis well developed; **373.1** Metatarsals II and IV contact at midshaft on the plantar surface; **375.2** Metatarsal III dorsal surface area clearly smaller than metatarsals II and IV; **377.1** Arctometatarsus.

ACCTRAN: **251.1** Distal carpal shape flat and discoidal, no distinct articular surfaces; **283.2** Manual unguals relatively short; **363.1** Round external fossa at base of ascending process of astragalus; **379.2** Metatarsal I placed distally.

DELTRAN: **7.1** Medial alae from premaxillae meet in front of vomera; **60.1** Jugal quadratojugal dorsal process extends further caudally than ventral quadratojugal process; **72.1** Secondary palate well

ossified from premaxilla through one-half the length of the ventral surface of the maxilla; **132.2** Premaxillary tooth crowns incisiform and reduced in size; **188.1** Sacral neural spines fused to form lamina; - **240.0** Humeral ends little or not expanded; - **316.0** Caudal portion of pubic boot same length as cranial portion; **357.1** Cranial protuberance on fibula below expansion; **369.1** Metatarsus elongate relative to other theropods of same femoral length; **371.1** Metatarsal cross-section deeper craniocaudally than mediolaterally at midshaft; - **386.0** Pedal ungual II subequal to pedal ungual III.

As discussed above, Arctometatarsalia is defined as *Ornithomimus* and all taxa sharing a more recent common ancestor with *Ornithomimus* than with *Neornithes* (HOLTZ, 1996b). In half the most parsimonious trees found in this study (Fig. 3A, 4), Arctometatarsalia includes only Tyrannosauridae and Ornithomimosauria; in the other half, Troodontidae is included as well. As HOLTZ (1994) noted, many of the characters that unite tyrannosaurids and ornithomimosaurids (and troodontids) are found in the locomotory apparatus, particularly in the metatarsus but also in the pelvis and caudal region. Some of these characters are also found in various combinations in other taxa (e.g., *Elaphrosaurus*, *Coelurus*, Caenagnathidae, mononykine alvarezsaurids), but no other taxa demonstrate the possession of all of these features in the same animal (with the exception of Troodontidae). Thus, the majority of the characters uniting ornithomimosaurids and tyrannosaurids outside of other theropods are associated with higher cursorial ability (HOLTZ, 1995b) and might have been convergently acquired by these two different lineages near the base of Maniraptoriformes (as in SERENO, 1997; MAKOVICKY & SUES, 1998).

However, there are other features that unite tyrannosaurids and ornithomimosaurids in the present study. Some have to do with the forelimb, but could again be explained by the reduced (or at least altered) grasping ability in both tyrannosaurids and ornithomimosaurids relative to other coelurosaurs (HOLTZ, 1994). Unlike all other coelurosaurs (again, except for troodontids), the premaxillary teeth of tyrannosaurids and the basal ornithomimosaur *Pelecanimimus* are incisiform (**132.2**), with both carinae of each tooth being placed along the same plane perpendicular to the main axis of the skull (differing from typical avetheropods, in which the premaxillary teeth are asymmetrical). Furthermore, the morphology of the nasals and of rostral portion of the frontals (**25.1**, **39.1**) of basal tyrannosaurids and ornithomi-

mosaurids differs from that of other theropods (except for troodontids). Also, as WITMER (1997) noted, ornithomimosaurids and tyrannosaurids are the only two lineages of non-avian theropods known to possess squamosal recesses (**55.1**).

As noted by SERENO (1997), there are no possible phylogenetic positions for Troodontidae that do not result in some level of homoplasy (convergence or reversals) among maniraptoriform coelurosaurs. Indeed, as in HOLTZ (1994), troodontids were found to be arctometatarsalians closer to ornithomimosaurids than to tyrannosaurids in half of the most parsimonious trees in the present analyses. The following synapomorphies would support such a placement (only those in all trees or under delayed transformation are listed): **7.1**, **8.1**, **25.1**, **39.1**, **60.1**, **71.1**, **72.1**, **95.1**, **132.2**, **198.1**, **206.1**, **-278.0**, **287.1**, **-316.0**, **357.1**, **363.1**, **369.1**, **371.1**, **373.1**, **375.2**, **377.1**, **379.2**. Those characters not in this list but currently listed as occurring in all optimizations for node cc are found in Tyrannosauridae and one or both ornithomimosaur OTUs: these would be regarded as synapomorphies of the expanded Arctometatarsalia (including Troodontidae) under accelerated transformation. Additionally, tyrannosaurids and troodontids share a well-developed sagittal crest on the dorsal surface of the parietals (**43.1**), unlike ornithomimosaurids and indeed most other coelurosaurs.

Following HOLTZ (1994, 1996b), Bullatosauria is defined as all descendants of the most recent common ancestor of *Troodon* and *Ornithomimus*. Bullatosauria was supported on many (primarily cranial) characters. WITMER (1997) and MAKOVICKY & NORELL (1998) observed several additional cranial features shared by troodontids and ornithomimosaurids. THULBORN (1984) and PÉREZ-MORENO *et al.* (1994) found additional character support for a troodontid-ornithomimosaur clade. However, as discussed below, troodontids are supported here as basal paravian maniraptorans in half of the equally parsimonious trees in this study. Under this topology, the clade defined by all descendants of the most recent common ancestor of *Troodon* and *Ornithomimus* is exactly the same clade as that defined by the all descendants of the most recent common ancestor of *Neornithes* and *Ornithomimus*. Thus, Bullatosauria becomes a junior subjective synonym of Maniraptoriformes under this topology. Alternatively, when Troodontidae is placed as the sister group to Ornithomimosauria (and Bullatosauria is thus not the same clade as Maniraptoriformes), the following synapomorphies would support such a node (only those found under all optimizations and under delayed transformation are shown): **1.1**, **18.1**, **32.1**, **46.1**, **88.1**, **93.1**, **94.1**, **98.1**, **101.1**, **-116.0**,

126.1, 127.1, 130.1, 135.2, 157.1, 158.1, 163.1, -183.0, -195.0, 201.3, -264.0.

Thus, there is considerable support for a bullatosaurian arctometatarsalian position for Troodontidae. However, the manus of Troodontidae resembles those of non-tyrannosaurid, non-ornithomimosaurian coelurosaurs in several features, although these might be explainable as the retention of the primitive state, since lost in other arctometatarsalians. Similarly, the ischia of troodontids more closely resemble those of oviraptorosaurs, dromaeosaurids, and avialians in being less than two thirds the length of the pubis (**320.1**) and having a distally placed obturator process (**323.2**). This might plausibly be the basal condition for Maniraptoriformes, with the condition in Tyrannosauridae and Ornithomimidae representing novel extensions of the sub-process portion of the ischium, but this ad hoc explanation would require additional evidence (for example, discovery of the ischia of basal members of the tyrannosaurid and ornithomimosaur lineages).

It should be noted, however, that the most complete skeleton of Troodontidae currently described, that of the type specimen of *Sinornithoides youngi* RUSSELL & DONG, 1993b indicate that some troodontid features once thought to be similar to dromaeosaurids, avialians, and oviraptorosaurs are now known to resemble the condition in ornithomimosaurians. For example, unlike most other maniraptoriform coelurosaurs, metacarpal III is subequal in length to metacarpal II (rather than clearly shorter) in troodontids and ornithomimosaurians (**263.0**), and (as in non-maniraptorans) metacarpal III is unbowed (**265.0**). While the latter is most parsimoniously explained as the retention of a primitive trait, the former would best explained a single reversal in the common ancestor of all bullatosaurians if a troodontid-ornithomimosaur clade were supported.

Siamotyrannus isanensis BUFFETAUT, SUTETHORN & TONG, 1996 is a recently discovered form from the Early Cretaceous (?Barremian) of Thailand, purported to be an ancestral tyrannosaurid, as is the Late Jurassic North American species *Stokesosaurus clevelandi* MADSEN, 1976. These taxa were not included in the present analysis, pending completion of preparation of additional specimens and hitherto unreported skeletal elements of these species (E. BUFFETAUT, pers. commun. 1998; CHURE & MADSEN, 1998). The former taxon, as well as the fragmentary *Labocania anomala* MOLNAR, 1974 are the only theropods other than tyrannosaurids and ornithomimosaurians known to possess a pronounced semicircular scar on the caudal surface of the ischium, just distal to the iliac process (**326.1**): these taxa thus might be arctometatarsalians. *Itemirus medullaris* KURZANOV, 1976, known only from a

braincase, may be related to *Stokesosaurus* and/or tyrannosaurids (CHURE & MADSEN, 1998) or to dromaeosaurids (CURRIE & ZHAO, 1993b; CURRIE, 1995). Premaxillary teeth with the diagnostic U-shaped horizontal cross-section currently only known in Tyrannosauridae have been reported from the ?Aptian-Albian of Japan (M. MANABE, pers. comm. 1997).

NODE dd. ORNITHOMIMOSAURIA

ALL: **1.1** Skull shape elongate and platyrostral, with obtuse triangular paracoronar cross section; **6.1** Premaxilla long and pointed, with long nasal process; **8.2** Maxillary process of premaxilla extremely long, extends caudally from the caudal margin of the external naris for a distance greater than the rostrocaudal length of the external naris; **18.1** Maxillary fenestra long and low; **19.1** Promaxillary fenestra dorsal to maxillary fenestra; **32.1** Lacrimal caudal process at dorsal surface, lacrimal T-shaped; **46.1** Orbit margin with raised rim; **98.1** Parabasisphenoid bulbous capsule; **101.1** Occipital region directed ventrocaudally; **136.1** Neck length twice or more skull length; **141.1** Craniodorsal rim of axial neural spine convex curve in lateral view; **163.1** Caudal cervical postzygapophyses elongate; **201.3** Shaft of cervical ribs short (less than twice centrum length) and slender; **213.1** Acromion in scapula reduced; **250.1** Ulnar and radial ends closely joined, even by syndesmosis; **-255.0** Semilunate carpal block absent; **-263.0** Metacarpal III length subequal to metacarpal II; **-264.0** Metacarpal III width not very much narrower (greater than 50%) than metacarpal II; **269.1** Metacarpal-phalangeal joints not hyperextensible, extensor pits on metacarpals I-III reduced; **276.1** Flexor tubercle of unguals poorly developed and distally placed; **280.1** Pollex shape stout and robust, dorsoventrally compressed, with proximal articular surface quadrangular.

ACCTRAN: **3.3** Number of premaxillary teeth seven; **85.1** Orbitosphenoid absent; **93.1** Cranial tympanic recess invades basisphenoid; **94.1** Internal foramen of facial nerve cranioventral to vestibulocochlear nerve; **107.1** Symphyseal region of dentary medially recurved; **-114.0** Caudal surangular fenestra small pit; **126.1** Number of teeth greater than 100; **128.2** Tooth serrations absent; **127.1** Dentary teeth more numerous and smaller than maxillary teeth; **130.1** Tooth roots constricted; **135.2** Interdental plates absent in dentary; **-168.0** Apices of dorsal neural spines unexpanded; **182.1** Capitular facet of dorsal ribs situated dorsal to lamina, on prezygapophyseal base; **-195.0** Proximal caudal zygapophyses short; **260.2** Metacarpal I subequal to metacarpal II in length; **289.1** Fossa for origin of M. cuppediticus on ilium broad; **348.1** Lateroproximal

condyle (fibular condyle) on proximal end of tibia small and medially situated.

DELTRAN: **-37.0** Prefrontals well exposed on skull roof; **-54.0** Postorbital frontal process sharply upturned; **-116.0** Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle absent or faint ridge; **158.1** Cranial cervical centra extend beyond caudal extend of neural arch; **251.1** Distal carpal shape flat and discoidal, no distinct articular surfaces.

Following PADIAN, HUTCHINSON & HOLTZ (1999), Ornithomimosauria is defined as all descendants of the most recent common ancestor of *Pelecanimimus* and *Ornithomimus*.

The recently described *Pelecanimus polyodon* of the Early Cretaceous (Barremian) of Spain demonstrates many dental characteristics also found in troodontids, but lost in the (mostly) edentulous Ornithomimidae. The Early Cretaceous (?Aptian-Albian) *Harpymimus okladnikovi*, coded here within Ornithomimidae, is more primitive than *Pelecanimimus* in the retention of a metacarpal I much shorter than metacarpal II in length. This Asian taxon is being restudied by Osmólska and Pérez-Moreno, and may prove to lie outside the *Pelecanimimus*-Ornithomimidae (proper) clade in future analyses. Also of interest is the recent report of ornithomimosaurian material from the Aptian-Albian of Australia (RICH & VICKERS-RICH, 1994) and from the Barremian of Thailand (BUFFETAUT *et al.*, 1995; SUTEETHORN *et al.*, 1995).

NODE ee. MANIRAPTORA

ALL: **10.1** Premaxilla and nasal do not meet subnarily; **-57.0** Squamosal does not constrict lateral temporal fenestra; **172.1** Caudal edge of dorsal zygophyses overhangs centrum; **203.1** Medial gastral segment shorter than lateral segment; **298.1** Postacetabular process of ilium with concave caudal margin; **320.1** Ischium less than 66% length of pubis.

ACCTRAN: **89.1** Lateral depression surrounding opening to middle ear; **192.1** Caudal neural spines limited to caudals I-IX; **253.2** Distal carpal I block broadly overlaps metacarpal II dorsally and ventrally; **293.1** Preacetabular portion of ilium significantly longer than postacetabular portion; **381.1** Pedal digit IV larger than II and closer to III in length.

DELTRAN: **37.1** Prefrontals reduced or absent; **-54.0** Postorbital frontal process sharply upturned; **-116.0** Horizontal shelf on lateral surface of surangular rostral and ventral to the mandibular condyle absent; **158.1** Cranial cervical centra extend beyond caudal extent of neural arch; **-357.0** Cranial protuberance on fibula below expansion absent; **-371.0**

Metatarsals subequal or wider mediolaterally than craniocaudally at midshaft; **386.1** Pedal ungual II significantly longer than pedal ungual III.

In the present study, Maniraptora includes not only birds but also dromaeosaurids, oviraptorosaurs, therizinosauroids, and compsognathids (and troodontids in half of the equally parsimonious trees). This composition is similar to that found by GAUTHIER (1986) (although therizinosauroids, then called "segnosaurs", were at the time considered non-theropods). The conclusions here differ from HOLTZ (1994), where dromaeosaurids were the only non-avian theropod lineage considered closer to birds than to *Ornithomimus*. Unlike SERENO (1997), tyrannosaurids were not found here to share a more recent common ancestor with birds than with *Ornithomimus*.

Compsognathidae is here considered to comprise *Compsognathus longipes* WAGNER, 1861 and *Sinosauropteryx prima* JI & JI, 1996. These taxa share derived features in an enlarged phalanx 1 of manual digit I (with shaft diameter greater than that of the radius) and fan-shaped neural spines on the dorsal vertebrae (CHEN, DONG & ZHEN, 1998). Both these taxa are also characterized by tails with greater than 55 caudal vertebrae (more than those of all other coelurosaurs) (**190.0**) and by ischia with a slight expansion of the distal ischium (**327.0**). The former of these traits is most parsimoniously explained by a reversal, while the latter might be a retention of the primitive condition (if the pointed ischial tip is convergent in tyrannosaurids and advanced maniraptorans) or a reversal (if the condition in arctometatarsalians and maniraptorans represent a single evolutionary event): see Discussion below. As with *Scipionyx*, this taxon is unspecialized compared to most other advanced coelurosaurs, and so may be very informative with regard to the condition of the ancestral maniraptoriform and the ancestral maniraptoran.

MAKOVICKY & SUES (1998) considered the presence of medial gastral segments shorter than the lateral segments as synapomorphic of a troodontid-dromaeosaurid clade, not present in ornithomimosaurids, tyrannosaurids, and non-coelurosaurian theropods. However, compsognathids appear to demonstrate the same condition. As such, and given the current poor understanding of the gastralia in therizinosauroids, oviraptorosaurs, and basal birds, this feature (**203.1**) is most parsimoniously regarded here as a maniraptoran synapomorphy under the topology placing troodontids as paravians; if troodontids are bullatosaurians, the origin of this derived state is ambiguous.

NODE ff.

ALL: **130.1** Tooth roots constricted; **151.1** Epiphyses on cervical vertebrae placed proximally; **241.1** Deltapectoral crest on humerus expanded and offset from humeral shaft; **249.1** Ulnar facet for radius transversely expanded and concave; **296.1** Caudodorsal margin of ilium curves caudoventrally; **297.1** Postacetabular ala of ilium acuminate; **299.1** Supracetabular crest on ilium absent; **323.2** Obturator process of ischium distally placed; **327.1** Ischial foot absent; **374.1** Metatarsal IV longer than metatarsal II and closer to metatarsal III in length.

ACCTRAN: **32.1** Lacrimal caudal process at dorsal surface, lacrimal T-shaped; **126.1** Number of teeth greater than 100; **127.1** Dentary teeth more numerous and smaller than maxillary teeth; **128.1** Teeth with large denticles; **163.1** Caudal cervical postzygapophyses elongate; **166.1** Ventral process (hypapophyses) on cervicodorsal vertebrae present as small protrusions; **235.1** Humeral shaft sigmoid; **236.1** Humeral head offset and emarginated ventrally by groove; **243.1** Humeral entepicondyle prominent; **245.1** Ulnar shaft bowed caudally; **220.1** Metacarpal III bowed laterally; **281.1** Manual unguals II and III with small nubbin proximodistally; **284.1** Manual unguals with extreme curvature; **299.1** Supracetabular crest on ilium absent; **337.2** Fourth trochanter of femur absent; **384.1** Pedal unguals III and IV vertically oval in cross-section.

DELTRAN: **72.1** Secondary palate well ossified from premaxilla through one-half the length of the ventral surface of the maxilla; **103.1** Occipital condyle with constricted neck; **-223.0** Sternum shape relatively round; **240.1** Humeral ends well expanded, greater than 150% midshaft diameter; **253.2** Distal carpal I block broadly overlaps metacarpal II dorsally and ventrally.

This unnamed clade (comparable to the re-defined "Maniraptora" of SERENO (1997, 1998)) is very well supported based on character evidence (see also GAUTHIER, 1986). Although Troodontidae is only weakly supported within this clade in the present analysis, and Therizinosauoidea was placed outside it in the analysis of SERENO (1997, 1998), most recent workers have recovered a clade comprised of oviraptorosaurs, dromaeosaurids, and birds to the exclusion of ornithomimosaurs or tyrannosaurids: GAUTHIER (1986); SERENO (1997, 1998); SUES (1997); MAKOVICKY & SUES (1998); NOVAS & POL (in press).

Although the derived character state "tooth roots constricted" (130.1) was found to be synapomorphic for node ff, this condition is present only in some premaxillary teeth of one member of this clade, Dromaeosauridae (CURRIE & ZHAO, 1993b: fig. 6). Lateral (maxillary and dentary) teeth of dromaeosaurids do not show this condition. Additionally, the

tooth characters **126.1**, **127.1**, and **128.1**, optimized as present at node ff under accelerated transformation, represent the similarities in the teeth of therizinosauroids and troodontids. Dromaeosaurids lack these features, and retain the primitive state for these characters.

In the summary cladogram, the opisthopubic condition is considered to have evolved independently in therizinosauroids and eumaniraptorans (see Discussion below). However, if troodontids are moved to a bullatosaurian arctometatarsalian position (see above), opisthopuby (**309.3**) and an associated transformation of the ilium (**306.1**) become ambiguously polarized. These character states would be either synapomorphic for node ff, and secondarily lost in *Microvenator* plus Oviraptorosauria, or is independently evolved in the dromaeosaurid-bird clade and in therizinosauroids. MAKOVICKY & NORELL (1998) also noted the ambiguous nature of this character. It might be speculated that the convex curvature of the oviraptorosaurian pubis (**310.1**) might represent a "re-propubic" state derived from the opisthopubic condition: however, additional data would be needed to support this suggestion.

NODE gg.

ALL: **2.1** Premaxillary teeth absent, presumably covered with rhamphotheca; **6.1** Premaxilla long and pointed, with long nasal process; **-8.0** Maxillary process moderately long, premaxilla participates broadly in ventral surface of external naris; **-30.0** Lacrimal not exposed on skull roof; **40.1** Frontal very broadly exposed on skull roof, postorbital ramus does not project abruptly laterally from the orbital margin; **74.1** Vomer limited to rostral region; **79.1** Palatine fenestra (between ectopterygoid and palatine) closed; **100.2** Basipterygoid processes very short, fused to pterygoids; **107.1** Symphyseal region of dentary medially recurved; **-114.0** Caudal surangular foramen a small pit; **148.2** Postaxial cervical pleurocoels two pairs present; **-197.0** Transition point in tail absent; **200.2** Distal caudals markedly shorter than proximal caudals; **201.2** Shaft of cervical ribs short (less than twice centrum length) and broad; **-208.0** Middle chevron shape gentle curvature; **-209.0** Distal chevrons lacking cranial and caudal projections; **244.1** Ulnar facet on humerus expanded, merges with entepicondyle; **292.1** Preacetabular ala of ilium greatly expanded vertically; **335.3** Anterior trochanter of femur cylindrical in cross section; **367.1** Medial tuber on calcaneum enlarged

ACCTRAN: **-16.0** Promaxillary fenestra absent; **-17.0** Maxillary fenestra absent; **-81.0** Ventral ectopterygoid recess absent; **108.1** Rostral half of mandible concave; **-120.0** Splenial without notch for rostral margin of internal mandibular fenestra; **141.1**

Craniodorsal rim of axial neural spine convex curve in lateral view; **183.1** Sacral pleurocoels present; **187.1** Caudalmost sacral centrum markedly smaller than cranialmost sacral centrum; **222.1** Sternum earina present; **-272.0** Length of phalanx 3 of manual digit III (sum of lengths of phalanges 1 + 2 of digit III) greater than 100%; **275.1** Manual ungual, dorsal edge of articular facet with pronounced lip on dorsal edge; **289.1** Fossa for origin of *M. cuppedicus* on ilium broad

DELTRAN: **7.1** Medial alae from premaxillae meet in front of vomera; **121.1** Coronoid extremely reduced or absent; **-168.0** Apices of dorsal neural spines unexpanded; **-192.0** Caudal neural spines present beyond caudal X; **226.1** Forelimb (humerus+radius+manus)/hindlimb (femur+tibia+pes) length ratio greater than 50% but less than 120%; **243.1** Humeral entepicondyle prominent; **281.1** Manual unguals II and III with small nubbin proximodistally; **293.1** Preacetabular portion of ilium significantly longer than postacetabular portion; **299.1** Supracetabular crest on ilium absent; **-316.0** Caudal portion of pubic boot same length as cranial portion; **337.2** Fourth trochanter on femur absent; **384.1** Pedal unguals III and IV cross section vertically oval

As in RUSSELL & DONG (1993a), SUES (1997), and MAKOVICKY & SUES (1998) but unlike SERENO (1997), Therizinosauroida was found to be most closely related to the oviraptorosaurs among Theropoda. These taxa share numerous cranial and postcranial synapomorphies. Of note is the fact that many of these derived features are reversals: in some cases, such as the apparent loss of a transition point in the tail (**-159.0**) and related caudal transformations (**-192.0**, **200.2**, **-208.0**, **-209.0**) and the exclusion of the lacrimal from the skull roof (**-29.0**), are reversals to a pre-neotheropod state. Also as noted by MAKOVICKY & SUES (1998), the therizinosauroid-oviraptorosaur clade shares with Ceratosauria possession of two pleurocoels on the postaxial cervicals (**148.2**).

NODE hh.

ALL: **104.1** Dentary teeth absent; **-118.0** External mandibular fenestra large, horizontally oval; **156.1** Caudal cervical neural arch forms X-shape in dorsal view; **-169.0** Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae; **171.1** Dorsal transverse processes short, wide and only slightly inclined; **176.1** Dorsal centrum transverse section wider than high; **310.1** Pubic shaft with marked concave curvature cranially; **358.1** Fibular tubercle for *M. iliofibularis* ("anterolateral process") laterally projecting.

ACCTRAN: **5.1** Premaxilla subnarily very deep, main body taller dorsoventrally than long ros-

trocaudally; **-10.0** Premaxilla and nasal meet subnarily; **12.1** Maxillary teeth absent; **29.1** Nasal recesses present; **42.1** Frontals separated at medialmost point of suture by rostral process of parietals; **87.1** Paroccipital processes curving ventrally and pendant; **109.1** Dentary rami widely divergent caudally; **-110.0** Overlap of dentary onto postdentary bones; **-111.0** Intramandibular joint absent; **112.2** Dentary caudal depth greater than 220% depth of dentary symphysis; **-115.0** Rostral ramus of surangular shallow; **122.1** Articular facet for mandibular joint craniocaudally elongate and shallow; **124.1** Retroarticular process elongated and tapering; **178.1** Dorsal column subequal to femur length; **185.4** Number of sacrals six; **-195.0** Proximal caudal zygapophyses short; **-196.0** Caudal transverse processes present beyond caudal XV; **262.1** Metacarpal II length about 50% or greater humerus length; **265.1** Metacarpal III bowed laterally; **-386.0** Pedal ungual II subequal to pedal ungual III.

DELTRAN: **141.1** Craniodorsal rim of axial neural spine convex curve in lateral view; **157.1** Cranial cervicals broader than deep on cranial surface, with kidney-shaped articular surfaces that are taller laterally than at midline; **187.1** Caudalmost sacral centrum markedly smaller than cranialmost sacral centrum; **232.2** Radius greater than 76% length of humerus; **235.1** Humeral shaft sigmoid; **245.1** Ulnar shaft bowed caudally; **275.1** Manual ungual, dorsal edge of articular facet with pronounced lip on dorsal edge; **289.1** Fossa for *M. cuppedicus* on ilium broad.

NODE ii. OVIRAPTOROSAURIA

ALL: **106.1** Dentary symphysis fused; **191.2** Caudal pleurocoels present in centrum.

ACCTRAN: None.

DELTRAN: **12.1** Maxillary teeth absent; **87.2** Paroccipital process curving ventrally and pendant; **-88.0** Basicranium pneumatization minimal to moderate, but no expansion of basisphenoid; **-108.0** Rostral half of mandible ventrally convex or straight; **-110.0** Overlap of dentary onto postdentary bones; **-111.0** Intramandibular joint absent; **-115.0** Rostral ramus of surangular shallow; **122.1** Articular facet for mandibular joint craniocaudally elongate and shallow; **124.1** Retroarticular process elongated and tapering; **183.1** Sacral pleurocoels present; **185.4** Number of sacrals six; **186.2** Sacrals III-V dorsoventrally flattened; **188.1** Sacral neural spines fuse to form lamina; **-195.0** Proximal caudal zygapophyses short; **265.1** Metacarpal III bowed laterally.

Following the phylogenetic definitions in PADIAN, HUTCHINSON & HOLTZ (1999), Oviraptorosauria is defined as all descendants of the most recent common ancestor of *Oviraptor* and *Chirostenotes*. As such, *Microvenator* is excluded from Oviraptorosau-

ria proper in one out of the two topologies of maniraptoriform relationships in this study (Fig. 3C). Nevertheless, this small Early Cretaceous (?Aptian-Albian) taxon is clearly more closely related to Oviraptoridae and Caenagnathidae than to any other known taxon. As in SUES (1997) and MAKOVICKY & SUES (1998), this study found very strong support for uniting Oviraptoridae and Caenagnathidae to the exclusion of Therizinosauroidea. Note that this study agrees with CURRIE, GODFREY & NESSOV (1993), SUES (1997), MAKOVICKY & SUES (1998), and SERENO (1997), and disagrees with HOLTZ (1994) in recognizing the oviraptorosaurian nature of Caenagnathidae ("Elmisauridae" in the latter study), necessitating an independent evolution of the arctometatarsus in caenagnathid oviraptorosaurs and in true arctometatarsalians (and in troodontids, if they are not arctometatarsalians, and in mononykine alvarezsaurids: see also Discussion below).

NODE jj. PARAVES

ALL: **162.1** Carotid process on caudal cervical vertebrae; **194.1** Centra of caudals I-V box-like with increased flexural capability; **197.3** Transition point in caudals I-IX; **204.1** Chevron transition between caudal X and XVII; **-274.0** First phalanx of pollex less than or subequal to length of metacarpal II; **383.1** Pedal digit II hyperextensible; **385.1** Pedal ungual II sickle-shaped (blade-like cross section and highly recurved).

ACCTRAN: **92.1** Posttympanic recess confined to columnar process; **101.1** Occipital region directed ventrocaudally; **102.1** Foramen magnum taller than wide; **119.1** Splenial with extensive triangular exposure in lateral view between dentary and angular; **129.1** Posterior serrations much larger than anterior serrations in maxillary and dentary teeth; **135.2** Interdental plates absent in dentary; **198.1** Midcaudal vertebrae with moderately long prezygapophyses, extending more than one half but less than one centrum length; **200.1** Distal caudals more than 130% length of proximal caudals; **210.1** Distal chevron cranial and caudal bifurcations; **379.2** Metatarsal I placed distally.

DELTRAN: **32.1** Lacrimal caudal process at dorsal surface present, lacrimal T-shaped; **-67.0** Quadrate foramen large and situated between quadrate and quadratojugal; **81.2** Ventral ectopterygoid recess present and subcircular; **91.1** Branches of internal carotid artery enter hypoglosseal fossa through single common opening; **140.1** Axial neural spine compressed mediolaterally; **157.1** Cranial cervicals broader than deep on cranial surface, with reniform (kidney-shaped) articular surfaces that are taller laterally than at midline; **166.1** Ventral processes (hypapophyses) on cervicodorsal vertebrae

present as small protrusions; **192.1** Caudal neural spines limited to caudals I-IX; **235.1** Humeral shaft sigmoid; **236.1** Humeral head offset and emarginated ventrally by groove; **245.1** Ulnar shaft bowed laterally; **284.1** Manual unguals extremely curved; **381.1** Pedal digit IV larger than II and closer to III in length.

SERENO (1997) coined the term "Paraves" for birds and all theropods sharing a more recent common ancestor with birds than with oviraptorosaurs; in the present analysis this clade contains Dromaeosauridae (and Troodontidae in half the trees) as well as birds. A clade containing troodontids, dromaeosaurids, and birds has been recovered by a number of studies (GAUTHIER, 1986; SERENO, 1997, 1998; FORSTER *et al.*, 1998; MAKOVICKY & SUES, 1998; NOVAS & POL, in press). HOLTZ (1994) has been one of the few explicit analyses to discover a different relationship, with troodontids closer to ornithomimosaurids than to birds.

However, unlike previous studies supporting troodontid-dromaeosaurid-bird monophyly, this analysis did not support a troodontid-dromaeosaurid clade to the exclusion of birds (as in GAUTHIER, 1986 (where it was coded as such a priori); SERENO, 1997, 1998; MAKOVICKY & SUES, 1998; NOVAS & POL, in press) nor a troodontid-bird clade to the exclusion of dromaeosaurids (as in FORSTER *et al.*, 1998). Instead, troodontids were found to lie outside the dromaeosaurid-bird clade Eumaniraptora in all twenty most parsimonious trees (and indeed to lie outside Maniraptora in half the trees).

Nevertheless, several characters do support a troodontid-dromaeosaurid clade (**119.1**, **129.1**, **210.1**) while others support a troodontid-bird grouping (**92.1**, **101.1**, **102.1**, **135.2**, **198.1**, **379.2**). It should be noted here, however, that Troodontidae was incorrectly coded as possessing ischiadic terminal processes separate (**328.1** of this analysis) in the study of FORSTER *et al.* (1998), resulting in a basal avialian position for this clade. The terminal processes of the ischia of troodontids observed by the present author are indeed in contact, as attested by the flat articular surfaces in some specimens (e.g., *Troodon formosus*, RTMP 86.77.2) and fusion of the ischiadic symphyses in others (e.g., *Sauromithoides mongoliensis*, AMNH 6516) (see also NORELL & MAKOVICKY, 1997). Significantly, as discussed above, additional character evidence equally strongly supports a sister group relationship between ornithomimosaurids and troodontids outside of Maniraptora. Troodontids thus remain one of the most poorly resolved of maniraptoriform clades with regards to their phylogenetic position, despite the fact that this taxon is known from a number of excellent specimens.

Curiously, the presence of Troodontidae, Dromaeosauridae, and *Rahonavis* as serial sister taxa to Aves strongly supports the presence of a hyperextensible digit II (**383.1**) with a sickle-shaped claw (**385.1**) as the ancestral condition for birds. In trees where Troodontidae is considered an arctometatarsalian, however, the sickle claw is equally parsimoniously considered as basal to Eumaniraptora (under accelerated transformation) or as convergently acquired by dromaeosaurids and *Rahonavis* (under delayed transformation). A recently described fragmentary taxon, *Megaraptor namunhuaiquii* NOVAS, 1998, also possesses a sickle-shaped pedal digit II unguis. However, NOVAS (1998) noted that this form lacked derived features (such as the bowed ulna) that characterize dromaeosaurids and troodontids.

Related to this, as observed by PAUL (1988), SERENO (1997), and FORSTER *et al.* (1998) is the shared presence of a hyperextensible pedal digit II (**383.1**) in troodontids, dromaeosaurids, *Rahonavis*, *Archaeopteryx*, and some basal ornithothoracines. In the present study, this character state is considered synapomorphic for Paraves, and lost in Alvarezsauridae and advanced ornithothoracine birds. The presence of this structure in some forms (such as *Archaeopteryx*) which lack a trenchant sickle-claw suggests that the hyperextension of pedal digit II was employed for purposes other than predation (OSTROM, 1969a, b) in at least some paravians. Whether this structure may have originally served a predatory function, and was exapted into a scansorial function (or vice versa) lie beyond the scope of the present study.

Of minor note: NORELL & MAKOVICKY (1997) correctly identified a typographical error in the description of a character state uniting dromaeosaurids and birds used in HOLTZ (1994). They correctly observed that this character state (**381.1** in the present study) is in fact pedal digit IV is longer than pedal digit II. (The character state incorrectly written in HOLTZ (1994) as "pedal digit II longer than pedal digit IV" actually describes the condition in *Dilophosaurus* (WELLES, 1984)).

NODE kk. EUMANIRAPTORA

ALL: **63.1** Quadratojugal T-shaped; **87.1** Paracipital process with conspicuous twist in the distal end orienting distal surface more dorsally than proximal region; **125.1** Vertical columnar process on retroarticular process; **144.1** Axial epiphyses prominent; **207.1** Proximal chevron shape dorsoventrally depressed; **237.1** Internal tuberosity (= ventral tubercle) on proximal end of humerus well differentiated and angular; **238.1** Internal tuberosity on proximal end of humerus craniocaudally compressed and longitudinally elongate; **262.1** Metacar-

pal II about 50% or greater humerus length; **265.1** Metacarpal III bowed laterally; **306.1** Pubic peduncle of ilium extends more ventrally than ischiadic peduncle; **309.3** Opisthopubic; **334.2** Anterior (= lesser) trochanter nearly confluent with femoral head and greater trochanter; **343.1** Adductor fossa and associated caudodistal crest of distal femur reduced or absent; **348.1** Lateroproximal condyle (fibular condyle) on proximal end of tibia small and medially situated; **350.2** Crista fibularis well developed; **351.2** Crista fibularis distally placed.

ACCTRAN: **217.2** Coracoid subrectangular, dorsoventral depth more than 130% of craniocaudal width.

DELTRAN: **-89.0** Lateral depression surrounding opening to middle ear absent; **-126.0** Number of teeth less than 100; **-127.0** Dentary and maxillary teeth subequal in number and size; **226.1** Forelimb (humerus+radius+manus)/hindlimb (femur+tibia+pes) length ratio greater than 50% but less than 120%; **232.2** Radius length greater than 76% humerus length; **243.1** Humeral entepicondyle prominent; **316.2** Pubic boot cranial portion absent; **-384.0** Pedal unguis III and IV cross-section subtriangular.

PADIAN, HUTCHINSON & HOLTZ (1999) proposed "Eumaniraptora" for the clade comprised of all descendants of the most recent common ancestor of *Deinonychus* and Neornithes. Note that this term is not synonymous with SERENO's (1997) Paraves, which represents a more inclusive, stem-defined clade containing the node-defined Eumaniraptora. In the present study Troodontidae represents a paravian taxon that was not also a eumaniraptoran (in half the trees; in the other half, it is an arctometatarsalian clade).

In the phylogenetic taxonomy of PADIAN, HUTCHINSON & HOLTZ (1999), the two named branches of Eumaniraptora are Deinonychosauria COLBERT & RUSSELL, 1969 (*Deinonychus* and all taxa sharing a more recent common ancestor with *Deinonychus* than with Neornithes) and Avialae GAUTHIER, 1986 (Neornithes and all taxa sharing a more recent common ancestor with Neornithes than with *Deinonychus*). In the present study, as in HOLTZ (1994), but unlike SUES (1997), SERENO (1997), and MAKOVICKY & SUES (1998), Troodontidae was not found to be a member of Deinonychosauria: see above. The only OTU within Deinonychosauria in the present analysis is Dromaeosauridae.

Dromaeosaurids thus remain the closest known lineage of "traditional" theropod to birds. Placing troodontids as close or closer to birds than dromaeosaurids would require the shared derived characters described above to have been either a) convergently acquired in Dromaeosauridae and Avialae or

b) present in basal Paraves and subsequently lost in Troodontidae. (See Discussion below)

Of additional note, several character state reversals listed in the DELTRAN category for this clade (**-89.0**, **-126.0**, **-127.0**) are required in this topology as the derived state is present in both troodontids on one branch and therizinosauroids and/or oviraptorosaurs on the other. Thus, under some optimizations these characters were hypothesized to be present ancestrally in Paraves, and would then have to be reversed in Eumaniraptora. However, these conditions might alternatively support a sister group relationship between troodontids and the therizinosauroid-oviraptorosaur clade to the exclusion of Paraves (see Discussion).

NODE II. AVIALAE

ALL: **173.1** Vertebral foramen/cranial articular facet ratio (vertical diameters) of dorsals 0.4 or greater; **190.2** Number of caudals less than 25; **216.1** Glenoid oriented laterally; **246.1** Proximal ulnar shaft arched; **293.1** Preacetabular portion of ilium significantly longer than postacetabular portion; **325.1** Ischial proximodorsal process just distal to iliac process; **328.1** Ischiadic terminal processes separate; **-355.0** Proximal region of fibular medial face flat; **-374.0** Metatarsal IV subequal in length to metatarsal II; **380.2** Metatarsal I completely reverted

ACCTRAN: **1.2** Skull shortened and platyrostral, with acute triangular paracoronar cross-section; **-4.0** Premaxillary symphyseal region V-shaped in ventral view; **6.1** Premaxilla long and pointed with long nasal process; **51.1** Postorbital-jugal contact absent; **55.1** Squamosal recess; **-64.1** Dorsal ramus of quadratojugal does not contact squamosal; **74.1** Vomer extends caudally to basicranium; **76.2** Palatine triradiate (no jugal process); **82.2** Endocranial cavity greatly enlarged, temporal musculature fails to extend origin onto frontals; **-103.0** Occipital condyle constricted neck absent; **-114.0** Caudal surangular foramen small pit; **124.1** Retroarticular process elongated and tapering; **141.1** Craniodorsal rim of axial neural spine convex curve in lateral view; **-152.0** Caudal cervical epiphyses short; **-169.0** Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae; **184.1** First sacral procoelous; **218.1** Coracoid caudoventral process length more than twice glenoid diameter; **220.1** Coracoid angle with scapula at level of glenoid cavity sharp; **221.1** Sternal plates fused; **227.2** Forelimb/presacral vertebral series length ratio about 200% or more; **230.1** Humerus/ulna length ratio less than or equal to 100%; **247.1** Diameter of ulnar shaft much thicker than that of radius; **-263.0** Metacarpal III length subequal to metacarpal II; **269.1** Metacarpal-phalangeal joints not hyperextensible, extensor pits on metacarpals I-III reduced; **273.1**

Pollex ends at level of mid-length of phalanx 1 of digit II; **-277.0** Manual ungual, region palmar to ungual groove wider than region dorsal to ungual groove; **335.4** Anterior trochanter of femur forms trochanteric crest (fusion of greater and anterior trochanters); **360.2** Fibular distal end pinches out less than half way down tibia length

DELTRAN: **163.1** Caudal cervical postzygapophyses elongate; **-168.0** Apices of dorsal neural spines unexpanded; **-198.0** Midcaudal vertebrae with short prezygapophyses, extending less than one half centrum length; **-210.0** Distal chevron cranial and caudal bifurcations absent; **293.1** Preacetabular portion of ilium significantly longer than postacetabular portion; **-369.0** Metatarsus proportions moderate; **379.2** Metatarsal I placed at distal end of metatarsal II

NODE mm. AVES

ALL: **178.1** Dorsal column subequal to femur length; **-195.0** Proximal caudal zygapophyses short; **313.2** Pubic apron strongly reduced transversely and restricted to distal 25% or less of pubic length; **323.3** Obturator process absent, caudoventral margin of ischium smooth from obturator notch to tip; **-385.0** Pedal ungual II same shape as other pedal unguals

ACCTRAN: **171.1** Dorsal transverse processes short, wide and only slightly inclined; **174.1** Dorsal hyposphene-hypantrum accessory articulations absent; **177.1** Dorsal centrum ends biconvex

DELTRAN: **1.2** Skull shortened and platyrostral, with acute triangular paracoronar cross-section; **-4.0** Premaxillary symphyseal V-shaped in ventral view; **6.1** Premaxilla long and pointed with long nasal process; **51.1** Postorbital-jugal contact absent; **55.1** Squamosal recess; **-64.1** Dorsal ramus of quadratojugal does not contact squamosal; **74.1** Vomer extends caudally to basicranium; **76.2** Palatine triradiate (no jugal process); **92.1** Posttympanic recess confined to columnar process; **101.1** Occipital region directed ventrocaudally; **102.1** Foramen magnum taller than wide; **-103.0** Occipital condyle constricted neck absent; **-114.0** Caudal surangular foramen small pit; **121.1** Coronoid extremely reduced or absent; **-119.0** Splenial obscured or only slightly visible in lateral view; **-120.0** Splenial without notch on rostral margin for internal mandibular fenestra; **128.2** Serrations absent; **-132.0** Premaxillary tooth crowns conical; **141.1** Craniodorsal rim of axial neural spine convex curve in lateral view; **-169.0** Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae; **218.1** Coracoid caudoventral process length more than twice glenoid diameter; **220.1** Coracoid angle with scapula at level of glenoid cavity sharp; **221.1** Sternal plates

fused; **-263.0** Metacarpal III length subequal to metacarpal II; **273.1** Pollex ends at level of mid-length of phalanx 1 of digit II; **299.1** Supracetabular crest on ilium absent; **-386.0** Pedal unguis II subequal in length to pedal unguis III

GAUTHIER (1986) explicitly gave his new taxon Avialae a stem-based definition (p. 36), although some authors (NOVAS & PUERTA, 1997; Ji *et al.*, 1998) have subsequently used this term as a node-defined taxon (all descendants of the most recent common ancestor of *Archaeopteryx* and modern birds). In this study, one taxon was found to share a more recent common ancestor with neornithine birds than with *Deinonychus*, but which were found to lie outside the clade of *Archaeopteryx* plus Neornithes. This is the recently discovered species *Rahonavis ostromi* (FORSTER *et al.*, 1998) of the ?Campanian of Madagascar. Similarly, the fragmentary form *Unenlagia comahuensis* NOVAS & PUERTA, 1997 (of the Turonian of Argentina) was also found to lie within Avialae but outside of Aves in some of the most parsimonious trees in which it was included. If future studies support this topology, or those which place *Unenlagia* closer to modern birds than to *Rahonavis*, this would support an hypothesis of secondary (rather than primary) flightlessness in the large-bodied *Unenlagia*. However, there is no phylogenetic evidence found here for hypotheses of secondary flightlessness in non-avian maniraptorans (dromaeosaurids, troodontids, oviraptorosaurs, etc.) or other non-avian coelurosaurs (as suggested by THULBORN (1984) and PAUL (1988)).

As mentioned previously, the pes of *Rahonavis* resembles that of troodontids and dromaeosaurids in the possession of a hyperextensible pedal digit II terminating in a sickle claw. The pes of *Unenlagia* is, regrettably, unknown. Sickle clawed *Megaraptor* occurs in the same deposits as *Unenlagia*, but what little is known of the anatomy of *Megaraptor* suggests that it is more distantly related to birds than are dromaeosaurids (NOVAS, 1998), while *Unenlagia* appears to be a basal bird in this analysis and those of NOVAS & PUERTA (1997) and FORSTER *et al.* (1998).

Because *Rahonavis* is incompletely known (e.g., neither cranial nor manual material has been recovered), there are many characteristics shared by *Archaeopteryx* and more advanced birds that may at a later date be found to be synapomorphic for a more inclusive clade.

Unenlagia and *Rahonavis* share one potential synapomorphy (vertically oriented pubis, **263.3**), although this character state is known in at least one specimen of *Archaeopteryx* (WELLNHOFER, 1993; FORSTER *et al.*, 1998).

The recently described Early Cretaceous taxa *Protarchaeopteryx robusta* Ji & Ji, 1997 and *Caudip-*

teryx zoui Ji *et al.*, 1998 were not included in the present analysis (but these spectacularly preserved taxa are included in work in preparation by the present author). The preliminary phylogenetic analysis of Ji *et al.* (1998) placed *Caudipteryx* as a non-avian avialian (following the taxonomy here), and *Protarchaeopteryx* as either a non-avian avialian, a deinonychosaur, or as the sister group to Eumaniraptora.

NODE hh. METORNITHES

ALL: **-34.0** Slot in ventral process of lacrimal for jugal absent; **59.1** Jugal postorbital process absent; **65.1** Quadrate articulates with both prootic and squamosal, and the later contacts neither the quadratojugal nor the postorbital; **222.1** Sternum carina present; **223.1** Sternum longer craniocaudally than wide mediolaterally; **224.1** Sternum much greater than coracoid length; **239.2** Internal tuberosity (=ventral tubercle) of humerus projected caudally, separated from humeral head by deep capital incision; **242.1** Humeral distal condyle with only cranial aspect; **248.1** Ulnar distal condyle subtriangular shaped in distal view, with a dorsomedial condyle, and twisted more than 54 degrees with respect to the proximal end; **252.1** Carpometacarpus (distal carpals fused to each other and to metacarpus); **258.1** Metacarpal III present, without unguis; **-350.1** Crista fibularis present, not well developed; **358.1** Fibular tubercle for M. iliofibularis (= "anterolateral process") laterally projecting

ACCTRAN: **134.1** Dentary tooth implantation set in paradental groove; **166.2** Ventral processes (hypapophyses) on cervicodorsal vertebrae very well developed; **189.1** Synsacrum present in adults; **259.1** Metacarpal II absent; **-284.0** Manual unguis curvature straight; **-288.0** Iliac preacetabular fossa for M. cuppedicus absent; **-320.0** Ischium greater than 75% length of pubis; **366.1** Astragalocalcaneum (astragalus fused to calcaneum); **368.1** Tibiotarsus (astragalocalcaneum fused to tibia); **-383.0** Pedal digit II not hyperextensible

DELTRAN: **177.1** Dorsal centrum ends biconvex; **184.1** First sacral procoelous

Following SERENO (1997, 1998), PADIAN & CHIAPPE (1998), and PADIAN, HUTCHINSON & HOLTZ (1999), and contra GAUTHIER (1986), the term Aves is used for the clade comprised of all descendants of the most recent common ancestor of *Archaeopteryx* and Neornithes (see the first four papers for justification). Unlike PAUL (1988), this analysis did not support the hypothesis that dromaeosaurids were more closely related to *Archaeopteryx* than either are to modern birds, nor the hypothesis that ornithomimosaurs, oviraptorosaurs, and troodontids shared a more recent common ancestor with Neornithes than did *Archaeopteryx*.

As in the analyses of PERLE *et al.* (1993, 1994), CHIAPPE, NORELL & CLARK (1996, 1998), NOVAS (1996, 1997a), and FORSTER *et al.* (1998), the highly apomorphic Alvarezsauridae were found to be birds more closely related to Neornithes than is *Archaeopteryx* (a result surprising to the present author). As discussed in those previous works, and shown in the character state lists above, alvarezsaurids were found to share more derived characters with Ornithothoraces (all descendants of the most recent common ancestor of *Iberomesornis* and Neornithes: see PADIAN, HUTCHINSON & HOLTZ, 1999). It did not support the conclusion of MARTIN (1997), whose phylogenetic analysis (itself methodologically problematic, as the all-zero outgroup was used as an OTU in that study) recovered an ornithomimosaurian position for the alvarezsaurid *Mononykus olecranus* PERLE *et al.*, 1993. Following PERLE *et al.* (1993), the term Metornithes is used for the clade comprised of all descendants of the most recent common ancestor of *Mononykus* and Neornithes.

As NOVAS (1996, 1997a), NOVAS & POL (in press), and SERENO (1997) observed, primitive alvarezsaurids (*Alvarezsaurus calvoi* BONAPARTE, 1991 and *Patagonykus puertai* NOVAS, 1996) lack some derived features found in both Ornithothoraces and the derived mononykine alvarezsaurids *Mononykus*, *Parvicursor remotus* KARHU & RAUTIAN, 1996, and *Shuvuuia deserti* CHIAPPE, NORELL & CLARK, 1998: these character states, previously proposed as synapomorphies of *Mononykus* and Ornithothoraces (e.g., PERLE *et al.*, 1993), are best explained as convergences between advanced alvarezsaurids and ornithothoracines. The present analysis agrees with NOVAS (1996, 1997a) and disagrees with SERENO (1997) and NOVAS & POL (in press), however, in proposing that the lack of some derived features of the postcranium found in *Archaeopteryx* and Ornithothoraces are reversals to a pre-avian condition, rather than evidence of a non-avian phylogenetic position of Alvarezsauridae.

The presence of an arctometatarsus even more specialized than that found in Caenagnathidae or Arctometatarsalia in *Mononykus* and *Parvicursor* (377.2; see HOLTZ (1995b): p. 511) is interpreted as convergence with the former two taxa, an hypothesis strongly supported by the lack of this condition in the more basal alvarezsaurids *Patagonykus* and *Alvarezsaurus* or in other eumaniraptorans.

DISCUSSION

Although many attributes of theropod phylogenetic history can be examined given the new hypothesis proposed here, three main aspects will be discussed. These are: new distributions for derived character states previously hypothesized as synapomorphies of various theropod subclades; alterna-

tive combinations of various theropod taxa, in light of the character evidence presented here; and the implications for the present new phylogeny of theropod dinosaurs when mapped onto stratigraphic time.

REVISED DISTRIBUTION OF PREVIOUS SYNAPOMORPHIES OF THEROPOD SUBCLADES

The inclusion of many new characters and taxa in the present analysis results, not surprisingly, in new distributions for character states previously hypothesized to characterize various subclades of theropods. Some of these characters are discussed below.

Prior to the extensive revision of archosaur facial pneumaticity by WITMER (1997), it was hypothesized that the small opening in the rostral region of the antorbital fossa of non-coelophysid ceratosaurids was homologous to the maxillary fenestra of tetanurines (GAUTHIER, 1986; HOLTZ, 1994). However, as WITMER has cogently argued, this structure might be more appropriately homologized with the promaxillary fenestra, a structure previously thought to have arisen only among more advanced tetanurines (HOLTZ, 1994; SERENO *et al.*, 1994, 1996). The promaxillary fenestra (16.1) is present in Spinosauridae, *Eustreptospondylus*, *Piatnitzkysaurus*, *Afrovenator*, and most avetheropods, but is not found in *Torvosaurus*. As such, the most parsimonious set of trees for basal tetanurines suggest that this condition was present in the ancestor of all tetanurines studied here, and that its lack in *Torvosaurus* (and in the derived caenagnathid and therizinosauroid coelurosaurids) are secondary reversals.

Given that the promaxillary fenestra is not present in *Ceratosaurus* and in Coelophysidae (although both these forms exhibit a small dimple which does not perforate the maxilla in approximately the same location, condition 16.3), but is present in Abelisauridae and *Dilophosaurus*, this character has an uncertain distribution among Ceratosauria as a whole. As the most parsimonious trees in the current study resolve this character as present in basal tetanurines, it is considered to be present in Neotheropoda ancestrally under accelerated transformation, and thus the absence of this structure in *Ceratosaurus* and Coelophysidae is explained by convergence. However, under delayed transformation it is optimized as absent in Ceratosauria ancestral, and thus evolving independently in tetanurines, abelisaurids, and *Dilophosaurus*.

The origin of the maxillary fenestra (17.1) is likewise ambiguous, although it is not present in any known ceratosaurian. This structure can clearly be identified if the promaxillary fenestra itself can also be demonstrated in the same specimen, as the opening between the promaxillary fenestra and the

internal antorbital fenestra. This is clearly the case in *Afrovenator* and most carnosaur and coelurosaur. In "*Megalosaurus*" *hesperis* (BMNH R332) the lateral aspect of the maxilla is not exposed, so it is uncertain whether the large opening visible from the medial side is a maxillary fenestra or a promaxillary fenestra (WITMER, 1997). The very large openings in the rostral part of the antorbital fossa of *Monolophosaurus* and *Giganotosaurus* are difficult to homologize with other tetanurines: they might be very large promaxillary fenestrae, true maxillary fenestrae (in which case the promaxillary fenestrae have been lost), or structures representing the fusion of these two openings (a possibility suggested by WITMER, 1997). In *Carcharodontosaurus* only a single, smaller fenestra is present in the rostral portion of the antorbital fossa: again, it is uncertain if this is the promaxillary fenestra or the maxillary fenestra. In this genus (as in the abelisaurids), the maxillary antorbital fossa as a whole is reduced (**15.2**), resulting in a very large internal antorbital fenestra.

In any case, the lack of both promaxillary and maxillary fenestrae in caenagnathid oviraptorosaurs and therizinosauroids are considered reversals. The absence of both fenestrae in these coelurosaur might conceivably be synapomorphic for the oviraptorosaur-therizinosauroid clade, but this would require the redevelopment of these same structures in oviraptorid oviraptorosaurs.

In the analysis of HOLTZ (1994), the presence of the jugal participating in the margin of the internal antorbital fenestra (**58.1**) was hypothesized to be synapomorphic of "Maniraptora" (properly *Ornitholestes* plus Maniraptoriformes: HOLTZ, 1996b). It was also noted to be present in the coelophysoid *Dilophosaurus* and the abelisaurid *Carnotaurus* (resulting in a coding of "(0,1)" for this feature, Character 86, for Abelisauridae in HOLTZ, 1994). Subsequent to that study, this condition has been observed in various other non-maniraptoriform taxa, including *Monolophosaurus* (ZHAO & CURRIE, 1993), *Sinraptor* (CURRIE & ZHAO, 1993a), and *Afrovenator* (SERENO *et al.*, 1994). It is also present in *Herrerasaurus* (SERENO & NOVAS, 1994), a form that may be the sister taxon to the ceratosaur-tetanurine clade Neotheropoda. Because of the greater distribution of this feature than previously recognized, the current analysis considers it potentially a neotheropod, or even a herrerasaurid plus neotheropod, synapomorphy under accelerated transformation.

The furcula (**225.1**) was once known only in derived coelurosaur (BARSBOLD, 1983; GAUTHIER, 1986). Its discovery in taxa more distantly related to birds (CHURE & MADSEN, 1996; MAKOVICKY & CURRIE, 1998) indicates it has a much broader distribution than previously realized. The clavicles are fused

to form a furcula in allosaurids and an unnamed "carcharodontosaurid" (ALCOBER *et al.*, 1998) (neither separate clavicles nor fused furculae have been reported for other carnosaurian taxa) and various coelurosaurian clades, but are apparently unfused where known among ceratosaurs (the neoceratosaur *Carnotaurus* (BONAPARTE, NOVAS & CORIA, 1990); *Segisaurus* (CAMP, 1936)). This indicates that, minimally, the clavicles were fused into a furcula in the basalmost avetheropod (i.e., the most recent common ancestor of carnosaur and coelurosaur). However, as neither separate clavicles nor furculae have been reported among the non-avetheropod tetanurines, it may be that this structure arose even more basally among theropods (see also SERENO, 1997).

The development of the sternum in theropod phylogeny has a rather perplexing distribution. It seems to be poorly preserved in many taxa (being recovered in only one specimen of *Archaeopteryx*, for example, despite the excellent preservation of several of the other specimens: WELLNHOFER, 1993). In birds and in some oviraptorids (BARSBOLD, 1983) the sternal plates are fused into a single medial element, while in dromaeosaurids (NORELL & MAKOVICKY, 1997), tyrannosaurids (LAMBE, 1917), ornithomimosaur (PÉREZ-MORENO *et al.*, 1994), *Scipionyx* (DAL SASSO & SIGNORE, 1998), and abelisaurids (BONAPARTE, NOVAS & CORIA, 1990) there is a pair of unfused elements. The recent discovery of sternal plates fused into a single median element (**221.1**) with a ventral ridge (**222.1**) in spinosaurids (CHARIG & MILNER, 1997) and sinraptorid carnosaur (CURRIE & ZHAO, 1993a), similar to the condition found in oviraptorids and birds, may be convergent with these coelurosaur. Alternatively, however, such fusion might be ontogenetically controlled (CURRIE & ZHAO, 1993a; CHARIG & MILNER, 1997), in which case the specimens of theropods with unfused sternals represent subadult or juvenile individuals (an hypothesis already proposed for the type of *Scipionyx*: DAL SASSO & SIGNORE, 1998).

There has been much discussion of the semilunate carpal block (**255.1**) and its significance in theropod phylogeny (OSTROM, 1969b, 1975a, 1975b, 1976, 1995, 1997; BARSBOLD, 1983; GAUTHIER & PADIAN, 1985; GAUTHIER, 1986; CHATTERJEE, 1988, 1997; FEDUCCIA, 1996; PADIAN & CHIAPPE, 1997, 1998; CURRIE & CARPENTER, in press). Although OSTROM (1969a, b) identified this structure as the radiale, PADIAN & CHIAPPE (1997, 1998) and CURRIE & CARPENTER (in press) argue that this block is homologous to the fusion of distal carpals 1 and 2, a view accepted here. Indeed, in therizinosauroids (BARSBOLD, 1983; RUSSELL & DONG, 1993a) these bones are incompletely fused, demonstrating that this block is composed of two elements.

Previously known only from relatively derived coelurosaurian forms (GAUTHIER, 1986; HOLTZ, 1994; OSTROM, 1997), this structure is now identified in carnosaurs (*Allosaurus* sp., Tate Museum unpublished material; *Acrocanthosaurus atokensis*, CURRIE & CARPENTER, in press) and the basal tetanurine *Afrovenator* (SERENO *et al.*, 1994). Based on the distribution of derived character states found in this analysis, the sequence of transformations of the theropod wrist can be summarized as: 1) fusion of distal carpals 1 & 2 among basal neotheropods, as documented in some (but not all) specimens of coelophysids (COLBERT, 1989; RAATH, 1990) and all adult tetanurine carpi except for therizinosauroids; 2) development of well developed trochlea and the semilunate shape (255.1) but the element does not completely cap the proximal surfaces of metacarpals I and II, among tetanurines, as demonstrated in *Afrovenator*, carnosaurs, *Coelurus*, *Scipionyx*, and tyrannosaurids; 3) expansion of the semilunate carpal block to cap the entire proximal surfaces of metacarpals (253.2), as demonstrated in maniraptoran coelurosaur (and separately in troodontids, if they are arctometatarsalians); and 4) fusion of the semilunate carpal block and the metacarpals to form a carpometacarpus (252.1), as demonstrated in meornithine birds. Unfortunately, the wrist of many theropods is incompletely known, even for otherwise well preserved and articulated specimens such as the types of *Ceratosaurus* (GILMORE, 1920) and *Compsognathus* (OSTROM, 1978), so that it is uncertain exactly precisely where within the phylogeny these transformations took place. For example, the carpus is currently unknown or undescribed for all non-avetheropod tetanurines other than *Afrovenator*, and is only partly known in any neoceratosaur (*Carnotaurus*: BONAPARTE, NOVAS & CORIA, 1990).

Some specimens of tyrannosaurids and all ornithomimosaurids lack well developed trochlear surfaces on any of their carpals (251.1), but the most complete wrists known for these taxa (e.g., *Tyrannosaurus* (PIN 552-1), *Albertosaurus* (ROM 807; CMN 11315), *Gorgosaurus* (CMN 2120); *Struthiomimus* (UCMZ(VP) 1980.1), *Pelecanimimus* (LH 7777)) demonstrate that they possessed a single large carpal element which did not completely cap metacarpals I and II. This most likely represents modifications of the stage 2 of the evolution of the theropod carpus mentioned above, and may well be associated with the loss or modification of more typical advanced tetanurine manual function in these two derived taxa, rather than derived from a "maniraptoran"-like condition as previously hypothesized (HOLTZ, 1994). Indeed, the carpus of a subadult specimen of the tyrannosaurid *Albertosaurus sarcophagus* (CMN 11315) quite clearly demonstrates a semilunate carpal block comparable in relative size and shape to those of *Afrovenator*, carnosaurs,

and basal coelurosaurids rather than the condition in oviraptorosaurs, troodontids, dromaeosaurids, or basal birds. However, if troodontids are indeed the sister taxon to ornithomimosaurids, the distribution becomes more problematic: either the ancestral maniraptoriform had a large semilunate carpal block, subsequently reduced in tyrannosaurids and lost in ornithomimosaurids, or troodontids developed an expanded semilunate carpal independently of true maniraptorans.

Tyrannosaurids and ornithomimosaurids also pose a problem with regards to the distribution of several other manual characters shared by Maniraptora or its subclades and troodontids (as well as other postcranial features discussed above). These might have been present in the ancestral maniraptoriforms, and subsequently lost in the derived manus of tyrannosaurids and ornithomimosaurids (HOLTZ, 1994); they might have been independently derived in maniraptorans and troodontids; or they might indicate a closer relationship between troodontids and the maniraptoran taxa here rather than with tyrannosaurids and ornithomimosaurids. However, this last hypothesis would require that the various cranial, pelvic, and hindlimb features shared by troodontids, ornithomimosaurids, and/or tyrannosaurids to have evolved more than once, or to have been lost in Maniraptora (other than Troodontidae).

GAUTHIER (1986) proposed that the absence of a fourth manual digit beyond embryonic stages (257.3) was synapomorphic for Tetanurae. This hypothesis was supported in additional analyses (e.g., HOLTZ, 1994). However, as Gauthier observed, a fragment of bone at the proximal end of metacarpal III in *Coelurus* (AMNH 619; at the time considered assignable to *Ornitholestes*; see also OSBORN, 1916; OSTROM, 1969b) may be a remnant of metacarpal IV. This suggested that the fourth metacarpal (although not necessarily the fourth digit) was present in some tetanurines. The presence of metacarpal IV in tetanurines (indeed, in avetheropods) is supported by the discovery of a probable metacarpal IV in the sinraptorid carnosaur *Sinraptor* (CURRIE & ZHAO, 1993a). The relatively flattened distal end of this element suggests no phalanges were present (212.2). Nevertheless, if Currie & Zhao have correctly identified this bone (a homology accepted by the present author), the absence of this element in allosaurid carnosaurs and maniraptoriform coelurosaurids is best explained by convergence. Unfortunately, the manus of basal carnosaurs (e.g., *Monolophosaurus*) and basal coelurosaurids (*Gosaurus*, *Proceratosaurus*, *Dryptosaurus*) is unknown or incompletely known at present.

The obturator notch on the pubis (307.1) has previously been used to diagnose Avetheropoda (HOLTZ, 1994). This structure is present in allo-

saurids, *Dryptosaurus*, *Ornitholestes*, *Coelurus*, *Scipionyx*, *Bagaraatan*, and all the various maniraptoriform subclades, thus including all the tetanurine taxa employed by GAUTHIER (1986) and all avetheropod taxa used by HOLTZ (1994). If the phylogenetic hypothesis presented here is correct, however, it would indicate that this opening is not a synapomorphy of Tetanurae or Avetheropoda, but was instead independently derived in allosaurids and advanced coelurosaurs (SERENO *et al.*, 1994, 1996). The basal carnosaur *Monolophosaurus* retains an obturator foramen (307.0) (and thus lacks an obturator notch) (ZHAO & CURRIE, 1993), as do the sinraptorids *Yangchuanosaurus* (DONG, ZHOU & ZHANG, 1983) and *Sinraptor hepingensis* (GAO, 1992). It is not apparent whether the lack of contact between bone ventral to the obturator foramen of *Sinraptor dongi* (CURRIE & ZHAO, 1993a) represents an incipient obturator notch, a pathological condition, or simply a matter of post-mortem damage. Furthermore, the pubis of the basalmost coelurosaurian taxon in this analysis, *Gasosaurus*, retains the obturator foramen and thus lacks an obturator notch. The most parsimonious explanation of the distribution of this character state in the present analysis is that it evolved independently in allosaurid carnosaurs and in advanced coelurosaurs.

As mentioned above, opisthopuby (309.3) is minimally synapomorphic for Eumaniraptora (dromaeosaurids plus birds). Curiously, although articulated dromaeosaurid remains indicate that these forms were fully opisthopubic (NORELL & MAKOVICKY, 1997) like metornithine birds, basal avialians such as some specimens of *Archaeopteryx* (WELLENHOFER, 1993), and the type and only specimens of *Unenlagia* (NOVAS & PUERTA, 1997) and *Rahonavis* (FORSTER *et al.*, 1998) had pubes which were vertically oriented rather than fully retroverted (309.2). Thus, either full retroversion occurred independently in dromaeosaurids and metornithines, or non-metornithine avialians experienced a partial "de-retroversion" from a fully opisthopubic state. A third alternative, that dromaeosaurids share a more recent common ancestor with metornithine birds than either does with *Archaeopteryx*, *Rahonavis*, and *Unenlagia*, is not supported by abundant derived character states possessed by these latter three taxa and later birds which are not present in Dromaeosauridae.

In those trees where Troodontidae is considered an arctometatarsalian, the sister clade to eumaniraptorans contains one taxon (Therizinosauroida), which also possesses a fully retroverted pubis. It is thus possible (under accelerated transformation) that opisthopuby is ancestral for the oviraptorosaur-therizinosauroid-eumaniraptoran clade. If this were the case, the propubic condition in *Microvenator* and

oviraptorosaurs would represent a "de-retroversion".

The obturator process of the ischium (322.1-2, 323.1-2) had been hypothesized by GAUTHIER (1986) to be synapomorphic for Tetanurae, and by HOLTZ (1994) to be synapomorphic for Avetheropoda. Additionally, HOLTZ (1994) found a triangular (rather than trapezoidal) shaped obturator process (323.2) to be synapomorphic for Coelurosauria. In the present analysis, the distribution of these character states is revised. Although the basalmost carnosaur *Monolophosaurus* and the sinraptorid *Yangchuanosaurus* lacks an obturator process (retaining, instead, the primitive state of an obturator flange: CHARIG & MILNER, 1997), the sister group to Avetheropoda in this analysis, *Afrovenator*, clearly demonstrates this condition (SERENO *et al.*, 1994). The basalmost coelurosaur in the present study for which pelvic material is known, *Gasosaurus*, has a carnosaur- or *Afrovenator*-like trapezoidal obturator process (323.1) (DONG & TANG, 1985), but all more derived coelurosaurs have triangular structures (except for some derived birds, which lack the structure altogether).

HOLTZ (1994) hypothesized that the loss of the ischial foot (327.1) was a synapomorphy of Coelurosauria. This was in part due to inaccurate coding of the condition in *Compsognathus*: re-inspection of this taxon (and its sister taxon, *Sinosauroptryx*, coded together here as Compsognathidae) indicates that a small expansion of the distal tip of the ischium is present (327.0). A similar termination of the ischium is present in *Scipionyx* (hypothesized here as the sister taxon to Maniraptoriformes), while *Gasosaurus* has a more primitive large expansion of the distal ischiadic tip. The distal part of the ischium is not preserved in *Dryptosaurus*, *Proceratosaurus*, or *Deltadromeus*, while in *Ornitholestes* the ischium does terminate in the point.

As discussed by HOLTZ (1994), the distal end of the ischium in ornithomimids also ends in a small expansion, but as in those trees in this analysis where troodontids are considered arctometatarsalians, it is most parsimoniously explained here as a reversal, as the immediate outgroups to this clade (Troodontidae and Tyrannosauridae) both possess a pointed tip. When troodontids are considered paravian maniraptorans, however, the ornithomimid condition is equally parsimoniously regarded as a reversal (if the tyrannosaurid condition is synapomorphic with that in non-compsognathid maniraptorans) or a retention of the primitive condition (if the tyrannosaurid condition is independently acquired from advanced maniraptorans). SERENO (1997) postulated that an ischium terminating in a point was synapomorphic for a clade comprised of Tyrannosauridae and "Maniraptora" (oviraptorosaurs, deinonycho-

saur (including troodontids), and birds: in fact, by the definition of the term, tyrannosaurids would be within Maniraptora in his phylogeny; see PADIAN, HUTCHINSON & HOLTZ, 1999), and that this clade was sister taxon to an ornithomimosaur-therizinosauroid clade which retained a primitive ischiadic expansion. The condition in therizinosauroids is variable, however. RUSSELL & DONG (1993a) considered the Early Cretaceous therizinosauroid *Alxasaurus* to lack a distal ischiadic point (based on two flattened strap-like elements they considered to be the ischia), whereas other therizinosauroids show a number of different conditions: a terminal point in *Enigmosaurus mongoliensis* and a very slight expansion in *Segnosaurus galbinensis* (BARSBOLD, 1983) to a greatly expanded flange in *Nanshiungosaurus brevispinus* DONG, 1979. For this reason, this character is coded as multistate (both present and absent) for therizinosauroids. Depending on the optimization chosen, an ischium ending in a point is either basal for Maniraptoriformes (and thus reversed in those therizinosauroids lacking this condition) or is derived independently in oviraptorosaurs and paravians, in which case therizinosauroids retained the primitive distal ischiadic expansion primitively, and those forms ending in a tip represent yet another independent derivation of this structure.

HOLTZ (1994) postulated that all taxa possessing the arctometatarsalian condition (**377.1**) (the pinched third metatarsal, possibly a specialization for enhanced cursorial ability: HOLTZ, 1995b) formed a single clade, and thus this structure was hypothesized to have arisen only a single time in theropod history. New data requires that this hypothesis be rejected. Abundant character evidence supports the hypothesis that caenagnathids ("elmsaurids" in HOLTZ, 1994) are nested in a clade of theropods lacking the arctometatarsalian condition (see also SUES (1997) and MAKOVICKY & SUES (1998)). Although possessing a pinched metatarsal III, caenagnathid metatarsi differ from those found in tyrannosaurids and bullatosaurids in that metatarsals II and IV do not contact each other on the plantar surface (**373.0**) (whereas these elements do contact on the plantar surface in ornithomimids, troodontids, and tyrannosaurids, **373.1**). Furthermore, the alvarezsaurid birds *Mononykus*, *Shuvuuia*, and *Parvicursor* possesses an arctometatarsalian pes even more "pinched" than that found in Arctometatarsalia proper: the proximal shaft of metatarsal III is entirely lost, reducing this bone to simply the distal wedge (**377.2**). However, other alvarezsaurids (such as *Patagonykus* and *Alvarezsaurus*) lack a pinched third metatarsal (**377.0**). The current phylogenetic hypothesis requires at least three origins of this structure: in caenagnathid oviraptorosaurs, in advanced alvarezsaurids, and in true arctometatarsali-

ans. In trees where troodontids are considered the sister taxon to eumaniraptorans, a fourth origin of the pinched metatarsus is required. Other metatarsal features shared by Caenagnathidae, mononykine alvarezsaurids, and Arctometatarsalia, such as an elongated metatarsus (**369.1**) and metatarsals which have a midshaft cross section deeper cranio-caudally than wide mediolaterally (**371.1**), are also found in the coelophysoid *Elaphrosaurus* and the basal coelurosaur *Coelurus*.

ALTERNATIVE RELATIONSHIPS BETWEEN THEROPOD CLADES

As has been noted in previous studies (HOLTZ, 1994; SERENO, 1997), there can be no phylogenetic solution for theropod interrelationships that does not result in some homoplasy. Some of this homoplasy suggests alternative relationships to those found in the most parsimonious trees in the present study.

Bremer support values or "decay indices" (BREMER, 1988; DONOGHUE *et al.*, 1992), although of limited utility in comparison between data matrices due to their dependence on data set size (SANDERSON & DONOGHUE, 1996), were calculated for this study using the AutoDecay program (ERIKSSON, 1998). The results are plotted on Fig. 8. A large number of nodes have Bremer support values of 1 or 0: this is due in part to the insecure phylogenetic position of taxa known only from very incomplete fossils or with a high number of plesiomorphic character states (which can thus assume many alternative positions on the tree without greatly affecting tree metrics). For example, the highly incomplete *Rahonavis* can assume many positions among Avialae without greatly increasing tree length.

Nevertheless several topologies were found to be better supported. In order of increasing support, these are: monophyly of dromaeosaurids and avialians to the exclusion of other theropods, the inclusion of tyrannosaurids in Arctometatarsalia, the inclusion of compsognathids in Maniraptora, the union of the oviraptorosaur-therizinosauroid and paravian clades to the exclusion of all other coelurosaurids, and the sister group position of Troodontidae to Eumaniraptora (the latter four topologies not reflected on Fig. 8 as drawn); Abelisauridae and the *Ceratosaurus*-abelisaurid clades to the exclusion of other ceratosaurs; Coelurosauria as composed here and the union of *Microvenator*, Oviraptoridae, and Caenagnathidae to the exclusion of other theropods; the union of coelophysoids and neoceratosaurs to the exclusion of other theropods; and the composition of Tetanurae, Ornithomimosauria, the therizinosauroid-oviraptorosaur clade, and Avialae as found here.

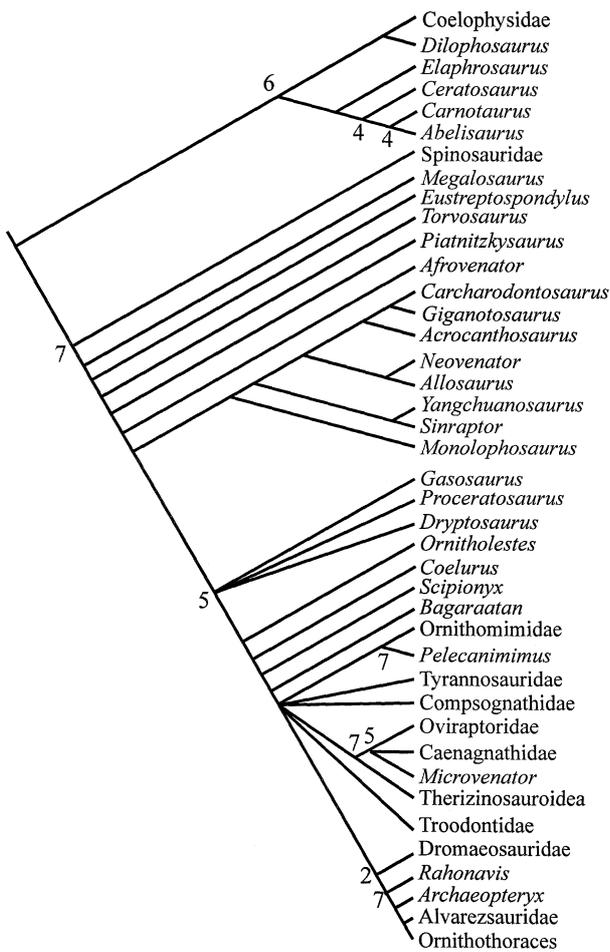


Fig. 8 - Bremer support ("decay indices") for the most parsimonious trees found in this analysis. Only values greater than one are shown. Calculations made using AutoDecay (ERIKSSON, 1998), employing the summary cladogram (Fig. 5), but shown here on the strict consensus of all twenty most parsimonious trees (Fig. 3). Not shown here due to polytomies on the consensus are a score of two each for nodes V, W, cc, ee, ff, and jj.

An additional method of comparing different tree topologies is also employed here. Using MacClade, the differences in tree length (i.e., the number of additional evolutionary steps necessary to explain that topology compared to the most parsimonious found here) were evaluated for some previously suggested phylogenies. Although this method lacks some of the utility of more explicit search methods (such as calculations of Bremer support indices), it may shed some insight on the relative strength of support for various additional tree topologies.

For these calculations, the summary tree (Fig. 5) was used, and (in most cases) only a single OTU was moved to the new position.

Elaphrosaurus was found here to be a basal neoceratosaur, closer to *Ceratosaurus* than to *Coelo-*

physis. However, placing it as a basal coelophysoid (i.e., as the sister taxon to node C) or as the sister taxon to Coelophysidae require only one additional step (tree length 1405). Although *Elaphrosaurus* was once considered an ornithomimosaur (e.g., GAUTHIER, 1986; OSMÓLSKA & BARSBOLD, 1990), it requires fifty one additional steps (tree length 1455) to place this taxon as the sister group to *Pelecanimimus*+*Ornithomimidae*.

As noted above, Neoceratosauria shares some features with tetanurines not found in coelophysoid ceratosaurids. BAKKER (1986) and PAUL (1988) proposed phylogenies (which were not, it must be noted, the result of numerical cladistic analyses) in which these taxa shared a more recent common ancestor with birds than with *Coelophysis*. Moving Neoceratosauria to a sister group position to node G requires eleven additional steps (tree length of 1415). As a taxonomic note, the clade comprised of the traditional "neoceratosaurids" and Tetanurae would be properly called "Neoceratosauria", as it would be comprised of *Ceratosaurus* and all taxa sharing a more recent common ancestor with that genus than with *Coelophysis* (see TABLE II). "Ceratosaurs" (i.e., *Ceratosaurus* and all taxa sharing a more recent common ancestor with it than with Neornithes) would be comprised solely of *Ceratosaurus* and Abelisauridae, and thus Coelophysoidea would not be considered ceratosaurids. Furthermore, the node-defined taxon Neotheropoda (i.e., all descendants of the most recent common ancestor of *Ceratosaurus* and Neornithes) would become a subgroup of the stem-defined Neoceratosauria, and the coelophysoids would not be considered neotheropods.

NOVAS (1997b) proposed that the "carcharodontosaurs" *Carcharodontosaurus* and *Giganotosaurus* were closely related to Abelisauridae. SAMPSON *et al.* (1998) also recognized several potential synapomorphies between abelisaurids and "carcharodontosaurids", without proposing a sister group relationship between the two. As noted previously there are abundant cranial similarities between abelisaurids and carcharodontosaurs as a whole, and between *Carcharodontosaurus* and *Abelisaurus* in particular. Placing *Carcharodontosaurus* as the sister taxon to Abelisauridae requires thirty eight additional steps (tree length 1442), and placing it as the sister taxon to *Abelisaurus* requires thirty five additional steps (tree length 1439). Moving *Carcharodontosaurus*+*Giganotosaurus* to a sister group relationship with either Abelisauridae as a whole or *Abelisaurus* in particular both require forty nine more steps than the most parsimonious tree (tree length 1453).

SERENO *et al.* (1994) proposed "Torvosauroidae" (later emended to "Spinosauroidea": OLSHEVSKY,

1995; SERENO *et al.* (1996, 1998)) in which the "torvosaurids" (*Torvosaurus* and *Eustreptospondylus*) and spinosaurids formed their own clade outside of all other theropods. CHARIG & MILNER (1997) examined several of the alleged synapomorphies of this taxon, and found them to be wanting in *Baryonyx* and other spinosaurids. Other features proposed for this grouping were discovered, in the present analysis, to be basal tetanurine characters lost in some advanced subclades. Restoring Spinosauroida with the ingroup topology as in SERENO *et al.* (1998) to a sister group relationship to *Piatnitzkysaurus*+(*Afrovenator*+Avetheropoda) requires only seven additional steps (tree length 1411). As the anatomy of some of these taxa (such as *Eustreptospondylus*) becomes better known, new support for this clade might be found.

Although the relatively unspecialized "megalosaur"-grade tetanurines were found to lie outside of Avetheropoda in this study, it requires only five additional steps to place *Afrovenator* as a basal carnosaur (tree length 1409) and only six to place *Megalosaurus* in that position (tree length 1410).

ELZANOWSKI & WELLNHOFER (1993) and MARTHILL *et al.* (1996) suggested that spinosaurid dinosaurs (or some member taxon thereof) were closely related to bullatosaurian coelurosaurs, primarily on cranial and dental features. Moving Spinosauridae to a sister group position with Bullatosauria requires thirty three additional steps (tree length 1437); for trees where troodontids are considered paravians, it requires thirty four additional steps to place spinosaurids as the sister taxon to Ornithomimosauria (tree length 1438). Although the highly apomorphic spinosaurids were found to be the basalmost branch of Tetanurae in this study, this position is not strongly supported. Alternative topologies including Spinosauridae within Avetheropoda as either a basal coelurosaur (sister taxon to node U) or a basal carnosaur (sister taxon to node O) require only seven or six extra steps (tree lengths 1412 and 1411, respectively). Similarly, placing Spinosauridae as the sister group to Avetheropoda requires seven additional steps (tree length 1412), and as the sister group to the *Afrovenator*-avetheropod clade requires only six additional steps (tree length 1411). As with most Cretaceous theropod lineages, spinosaurids are highly specialized and as-yet undiscovered basal members of this taxon would greatly aid in more strongly establishing their relationship.

Because its skeletal material is so abundant, and the osteology is well known, *Allosaurus* has served as an outgroup for studies of coelurosaurian relationships (e.g., PÉREZ-MORENO *et al.*, 1994; FORSTER *et al.*, 1998; MAKOVICKY & SUES, 1998). However, as discussed above, many of the characters previously used as synapomorphies between

Allosaurus and coelurosaurs (such as the obturator notch or the loss of metacarpal IV) are shown here to be convergent between advanced allosaurid carnosaurs and advanced coelurosaurs. Placing Allosauridae (node Q) as the sister group to the more advanced coelurosaurs (all those closer to birds than to *Gasosaurus*) requires fourteen additional steps (tree length 1418). Osteological data from *Allosaurus* alone should therefore be used with some caution as an outgroup for coelurosaurian studies: data from the better described of the more primitive carnosaurs (e.g., *Sinraptor* and *Monolophosaurus*) should also be considered in future analyses.

In those studies in which Tyrannosauridae is coded as its own OTU, it has been found to share a more recent common ancestor with birds and other typical coelurosaurs than with *Allosaurus* (Fig. 1). However, tyrannosaurids were found to occupy several possibly different positions within Coelurosauria in these different studies. PÉREZ-MORENO *et al.* (1994) and MAKOVICKY & SUES (1998) placed tyrannosaurids as the sister group to Maniraptoriformes. This topology is eleven steps longer than the most parsimonious trees (tree length 1415). Although no post-Gauthier study has found tyrannosaurids to share a more recent common ancestor with *Allosaurus* than with birds, placing the tyrant dinosaurs as the sister taxon to Allosauridae requires forty six additional steps (1450), as the sister to the *Acrocantinosaurus* plus (*Carcharodontosaurus*+*Giganotosaurus*) clade requires forty eight additional steps (tree length 1452), and as the sister taxon to *Acrocantinosaurus* requires fifty one extra steps (tree lengths 1455).

Although troodontids have been universally regarded as coelurosaurs (Fig. 1), the position of this clade, too, has varied from analysis to analysis. In particular, troodontids share many derived features with avialians, dromaeosaurids, therizinosauroids, oviraptorosaurs, and various combinations thereof not present in Tyrannosauridae or Ornithomimosauria. GAUTHIER (1986) considered troodontids a priori to be the sister taxon of Dromaeosauridae within Deinonychosauria, a position found in the studies of SERENO (1997) and MAKOVICKY & SUES (1998). This requires ten extra steps (tree length 1414). FORSTER *et al.* (1998) found troodontids to be basal avialians (i.e., closer to *Archaeopteryx* and later birds than to Dromaeosauridae), a position requiring only nine steps more than the most parsimonious (tree length 1413).

Troodontids also share numerous characters with Therizinosauroidea and Oviraptorosauria (as mentioned in RUSSELL & DONG, 1993a). Placing Troodontidae as the sister group to the therizinosauroid-oviraptorosaur clade (node gg) requires only one additional steps more than the most

parsimonious (tree length 1405), and is thus a very serious candidate for a potential position for this taxon in future studies. Placing troodontids as the sister group to node ff (the clade comprised of oviraptorosaurs, therizinosauroids, and eumaniraptorans) requires only three additional steps (tree length 1407), and again might well be supported in future analyses.

Therizinosauroidea has also been a problematic coelurosaurian taxon. The study here agrees with the conclusions of SUES (1997) and MAKOVICKY & SUES (1998) in which oviraptorosaurs are the sister taxon to these long necked theropods. However, CLARK, NORELL & PERLE (1994) discussed features shared with therizinosauroids, troodontids, and ornithomimosauria. Moving Therizinosauroidea to a position as the sister taxon to Bullatosauria requires thirty one extra steps (tree length 1435). SERENO (1997) proposed a clade comprised of Ornithomimosauria and Therizinosauroidea. Placing therizinosauroids as the sister taxon to ornithomimosauria in a configuration using troodontids as maniraptorans requires thirty four additional steps (tree length 1438).

HOLTZ (1994) considered Oviraptoridae and Caenagnathidae ("Elmisauridae" in that study) to be more closely related to *Ornithomimus* than to birds, and thus arctometatarsalians under the revised taxonomy of HOLTZ (1996b). As SUES (1997) and MAKOVICKY & SUES (1998) have firmly established, a sister group relationship between Oviraptoridae and Caenagnathidae is well supported by character evidence, as is a therizinosauroid-oviraptorosaur clade (node gg in this study). Moving the whole clade Therizinosauroidea+(*Microvenator*+Oviraptorosauria) to a sister taxon position with node cc (Tyrannosauridae+Ornithomimosauria) requires twelve additional steps (tree length 1416).

Although the taxa and characters employed in this study and that of MAKOVICKY & SUES (1998) do not wholly overlap, a new arrangement using the present data matrix was employed to reconstruct a similar topology among the advanced coelurosaurs (for their trees, see Fig. 1K). Leaving all other taxa in the positions of the summary cladogram, the advanced coelurosaurs were rearranged for the following topology: Compsognathidae, Tyrannosauridae, *Pelecanimimus*+Ornithomimididae, *Ornitholestes*, and *Coelurus* were progressively closer outgroups to node ff, and Troodontidae was placed as the sister group to Dromaeosauridae within Deinonychosauria. This topology is twenty eight steps (tree length 1432) than the most parsimonious arrangements found in this analysis.

Similarly, the coelurosaurian arrangement of the tree of SERENO (1997) (Fig. 1I) was also recon-

structed by similar methods. In this case, Compsognathidae was the sister group to a clade comprised of an ornithomimosaur-therizinosauroid branch and a branch with tyrannosaurids and oviraptorosaurs as progressively closer sister taxa to a clade containing Deinonychosauria (Dromaeosauridae+Troodontidae) and Avialae. This arrangement is forty two steps longer (tree length 1446) than the most parsimonious trees found in this study.

HISTORICAL DISTRIBUTION OF THEROPOD CLADES

Mapping the summary cladogram (Fig. 5) onto the stratigraphic time scale (Fig. 9, 10) demonstrates that there remain long durations in the geologic record where, according to the present analysis, certain taxa should be present but have yet to be discovered or recognized. For example, no tetanurines nor neoceratosaurs have been described from the Late Triassic, although the existence of coelophysoid ceratosaurs requires that both those former taxa must have already diverged from Ceratosauria and Coelophysoidea, respectively. Similarly, the presence of *Allosaurus* in the Late Jurassic requires that the divergence between the *Allosaurus-Neovenator* and the "carcharodontosaur" lineages must have occurred by this point in time, despite the fact that no members of the latter clade have been identified from units older than the Aptian (although RAUHUT (1995) suggested that some isolated teeth from the Upper Jurassic Tendaguru Group of Tanzania may be from this lineage).

Of particular importance is the recent discovery of an alleged therizinosauroid dentary from the Sinemurian age Lower Lufeng Formation of Yunnan, China (ZHAO & XU, 1998). If confirmed, this would indicate that the divergence between therizinosauroids and oviraptorosaurs, between the therizinosauroid-oviraptorosaur clade and the paravian lineage, between advanced maniraptorans and Compsognathidae, between Maniraptora and Arctometatarsalia, and all further divergences within coelurosaurian lines would necessarily have occurred by the Sinemurian (Fig. 10), if the summary cladogram of the present analysis is supported. *Siamotyrannus* may document the presence of Tyrannosauridae in the Barremian (the probable sister taxon to this clade, Ornithomimosauria, is already known from that interval in the form of *Pelecanimimus*). The tooth taxon *Koparion* CHURE, 1994 may record the presence of Troodontidae in the Kimmeridgian Morrison Formation of Utah, extending the range of this taxon to the Late Jurassic. Presence of possible maniraptoriforms in the Middle Jurassic had previously been suggested by the discovery of isolated dromaeosaurid- and troodontid-like teeth from the Bathonian of England

A NEW PHYLOGENY OF THE CARNIVOROUS DINOSAURS

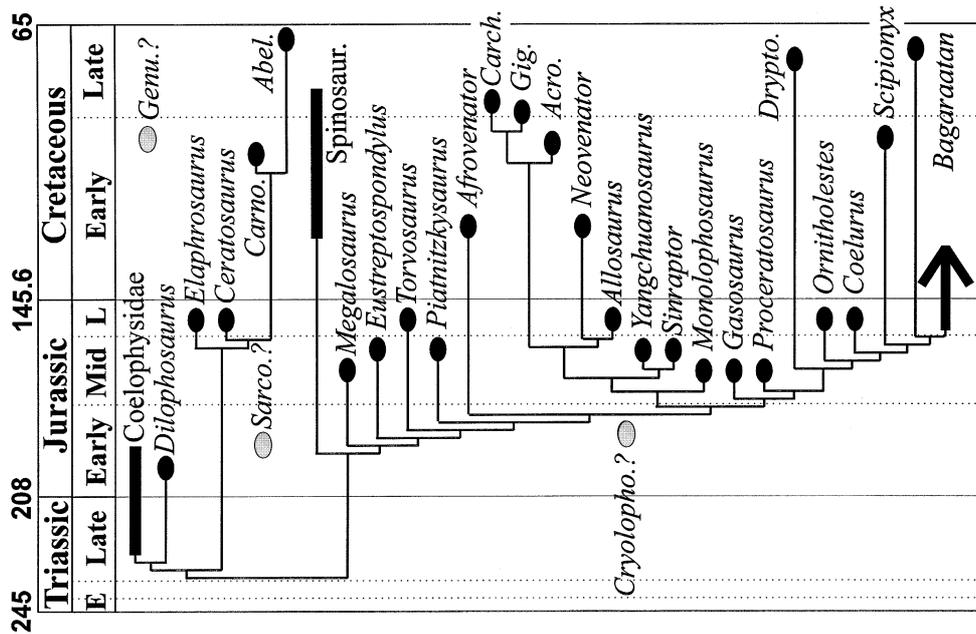


Fig. 9 - Summary cladogram (Fig. 5) superimposed on the geochronologic time scale I: non-maniraptoriform neotheropods. Geochronology follows GRADSTEIN *et al.* (1995). Solid bars, maximum known duration of suprageneric OTUs; solid ovals, approximate geochronologic position for generic or specific OTUs; arrow indicates Maniraptoriformes (Fig. 10). *Genusaurus* and *Sarcosaurus* are probable ceratosaurs not used in this analysis; *Cryolophosaurus* is a possible Early Jurassic carnosaur not used in this analysis: see text for discussion. Abbreviations: *Abel.*, *Abelisaurus*; *Acro.*, *Acrocantanosaurus*; *Carch.*, *Carcharodontosaurus*; *Carno.*, *Carnotaurus*; *Cryolopho.*, *Cryolophosaurus*; *Drypto.*, *Dryptosaurus*; *Genu.*, *Genusaurus*; *Gig.*, *Giganotosaurus*; "*M.*", "*Megalosaurus*"; *Sarco.*, *Sarcosaurus*; *Spinosaur.*, *Spinosauridae*.

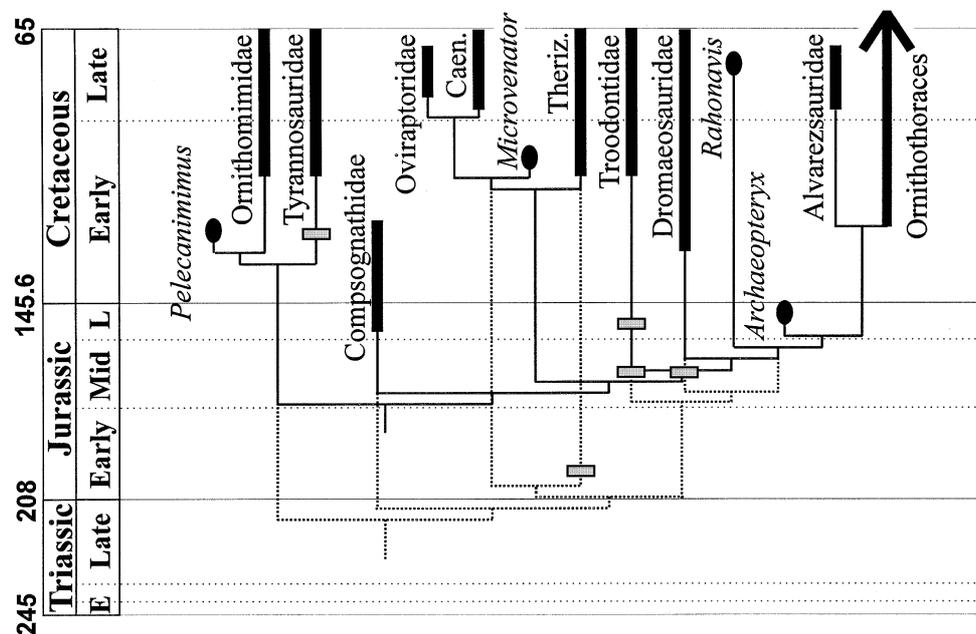


Fig. 10 - Summary cladogram (Fig. 5) superimposed on the geochronologic time scale II: maniraptoriform coelurosaurs. Geochronology follows GRADSTEIN *et al.* (1995). Solid bars, maximum known duration of suprageneric OTUs; solid ovals, approximate geochronologic position for generic or specific OTUs; gray horizontal bars, approximate geochronologic position for material referred to the OTU immediately above. Solid lines, divergence pattern sufficient to explain branching event without early problematic specimens; dotted lines, divergence pattern necessary to accommodate problematic early occurrences referable to the OTU. Barremian tyrannosaurid, *Siamotyrannus*; Sinemurian therizinosaurid, ZHAO & XU (1998); Kimmeridgian troodontid, *Koparion*; Bathonian troodontid and dromaeosaurid teeth, EVANS & MILNER, 1994; METCALF & WALKER, 1994. Abbreviations: *Caen.*, *Caenagnathidae*; *Theriz.*, *Therizinosaurioidea*.

sult in any phylogenetic position requires some degree of homoplasy. Identification of Middle Jurassic carnosaurs and coelurosaurs indicate that the divergence between these lineages was earlier than previously suggested, and renewed search for pre-Late Jurassic theropod fossils (both in the field and in collections) may prove among the most fruitful discoveries for resolving the phylogeny of the carnivorous dinosaurs.

ACKNOWLEDGMENTS

Many thanks are offered to the numerous people who have aided me in my on-going research in theropod systematics. This text was greatly improved by the comments and corrections by the numerous individuals, both official referees and other interested parties, who read and reviewed this manuscript: in particular, I wish to thank Ralph Molnar (Queensland Museum), Phil Currie (Royal Tyrrell Museum of Palaeontology), Hans-Dieter Sues (Royal Ontario Museum), Scott Sampson (State University of New York - Stony Brook), and Bernardino Pérez-Moreno (Universidad Autónoma, Madrid) for their helpful comments. The author is solely responsible for any errors (and original concepts) presented herein.

ABBREVIATIONS

AMNH - American Museum of Natural History, New York City; BMNH - Natural History Museum, London; CMN - Canadian Museum of Nature, Ottawa, Alberta; LH - Las Hoyas collection, Museo de Cuenca, Cuenca (housed in the Unidad de Paleontología, Universidad Autónoma de Madrid); MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; PIN - Palaeontological Institute, Moscow; ROM - Royal Ontario Museum, Toronto, Ontario; RTMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UCMZ(VP) - Museum of Zoology, University of Calgary, Calgary, Alberta.

APPENDIX I

Morphological characters used in the present study. Multistate characters are considered unordered unless otherwise noted. Character polarity based on outgroup comparison: see text for explanation. Scoring: 0 = primitive state; 1, 2, 3, 4, or 5 = derived character states.

1. Skull shape: 0, oreinirostral; 1, elongate and platyrostral, with obtuse triangular paracoronar cross-section; 2, shortened and platyrostral, with acute triangular paracoronar cross-section. **UO**

2. Premaxillary teeth: 0, present; 1, absent, presumably covered with a rhamphotheca. (RUSSELL & DONG, 1993a)

3. Number of premaxillary teeth: 0, four; 1, three; 2, five; 3, seven; 4, six. **UO**

4. Premaxillary symphyseal region: 0, V-shaped in ventral view; 1, U-shaped in ventral view; 2, Y-shaped in ventral view. **UO** (HOLTZ, 1994)

(EVANS & MILNER, 1994; METCALF & WALKER, 1994).

The data from this new analysis indicates that the chronological conclusions of HOLTZ (1994), among others, were premature, and that the primary divergences within Avetheropoda and Coelurosauria may have been considerably earlier than the Late Jurassic. Instead, presence of *Monolophosaurus*, *Proceratosaurus*, and *Gasosaurus* indicate a minimal Middle Jurassic divergence of Carnosauria and Coelurosauria. Furthermore, Early Jurassic taxa possibly referable to these clades (*Cryolophosaurus* and the Yunnan "therizinosauroid", respectively) not included in the present analysis may indicate that the primary avetheropod divergence occurred tens of millions of years early than this study indicates. As such, this predicts that a greater diversity of theropods (including early members of more typical Late Jurassic and Cretaceous lineages) should be present in Lower and Middle Jurassic formations than have currently been recognized.

CONCLUSION

The present study supports many of the previously discovered phylogenetic relationships among neotheropod dinosaurs. Due to the fragmentary and/or plesiomorphic nature of non-avetheropod tetanurines and non-maniraptoriform coelurosaur fossil material, however, these regions of the phylogenetic tree remain poorly resolved. Even for taxa for whom the anatomy is relatively well-known, such as Troodontidae, the mosaic of derived features re-

5. Premaxilla subnarial depth: **0**, shallow to moderately deep, main body as long or longer rostrocaudally than high dorsoventrally; **1**, very deep, main body taller dorsoventrally than long rostrocaudally. (HOLTZ, 1994).
6. Premaxilla shape: **0**, short and rounded, with short nasal process; **1**, long and pointed, with long nasal process. (GAUTHIER, 1986)
7. Medial alae from premaxilla: **0**, absent or separate; **1**, meet in front of vomers. (RUSSELL & DONG, 1993a)
8. Maxillary process of premaxilla: **0**, moderately long, premaxilla participates broadly in ventral surface of external naris; **1**, reduced, maxilla participates broadly in ventral surface of external naris; **2**, extremely long, extends caudally from the caudal margin of the external naris for a distance greater than the rostrocaudal length of the external naris. **UO**
9. External nares: **0**, without marked inset of the caudal margin; **1**, with marked inset of the caudal margin. (SERENO *et al.*, 1994)
10. Premaxilla/nasal contact: **0**, premaxilla and nasal meet subnarily; **1**, premaxilla and nasal do not meet subnarily.
11. Subnarial gap: **0**, absent; **1**, present. (GAUTHIER, 1986)
12. Maxillary teeth: **0**, present; **1**, absent.
13. Rostral ramus of maxilla: **0**, absent, rostradorsal surface of maxilla forms convex surface from dorsal ramus to ventral margin; **1**, present, dramatic change in curvature of rostradorsal surface of maxilla rostral to dorsal ramus forming concave surface
14. Rostral ramus size: **0**, absent; **1**, shorter rostrocaudally than dorsoventrally; **2**, as long or longer rostrocaudally as dorsoventrally. **UO** (SERENO *et al.*, 1996)
15. Maxillary antorbital fossa: **0**, approximately 10-25% of the rostrocaudal length of the antorbital cavity; **1**, greater than 40% of the rostrocaudal length of the antorbital cavity; **2**, greatly reduced in size, not extending much beyond the rim of the external antorbital fenestra. (SERENO *et al.*, 1994)
16. Promaxillary fenestra: **0**, absent; **1**, present, visible in lateral view; **2**, present, obscured in lateral view by ascending ramus of maxilla; **3**, small depression in same anatomical position which does not perforate the maxilla. **UO** (HOLTZ, 1994)
17. Maxillary fenestra: **0**, absent; **1**, present. (GAUTHIER, 1986)
18. Maxillary fenestra shape: **0**, round; **1**, long and low. (WITMER, 1997)
19. Position of the maxillary and promaxillary fenestrae: **0**, promaxillary rostral to maxillary; **1**, promaxillary dorsal to maxillary. (WITMER, 1997)
20. Relative size of promaxillary and maxillary fenestrae: **0**, maxillary fenestra larger; **1**, promaxillary fenestra larger. (WITMER, 1997)
21. Pneumatic excavation of the ascending ramus of the maxilla: **0**, absent; **1**, present. (SERENO *et al.*, 1996)
22. Pneumatic excavation without fenestra in cranial portion of maxillary antorbital fossa: **0**, absent; **1**, present. (SERENO *et al.*, 1998)
23. Nasal antorbital fossa: **0**, lateral surface of nasal excluded from antorbital cavity; **1**, lateral surface of nasal participates in antorbital cavity, forming a nasal antorbital fossa. (WITMER, 1997)
24. Nasal participation in antorbital cavity: **0**, nasal excluded from antorbital cavity; **1**, nasal participates in antorbital cavity.
25. Nasal expansion behind external nares: **0**, broadly expanded; **1**, narrow caudally. (HOLTZ, 1994)
26. Narial prominences: **0**, absent; **1**, median horn or crest; **2**, paired ridges along lateral edges of nasals; **3**, knobby rugosities across dorsal and lateral surface of nasals, extending onto dorsal-most surface of maxillae; **4**, "bark-like" rugosities, including concave pits separated by crests. **UO** (CURRIE & CARPENTER, in press)
27. Paired crescentic crests formed by nasal and lacrimal prominences: **0**, absent; **1**, present. (ROWE, 1989)
28. Nasal fusion: **0**, absent, nasals separate; **1**, present, nasals fused together.
29. Nasal recesses: **0**, absent; **1**, present. (WITMER, 1997)
30. Lacrimal: **0**, not exposed on skull roof; **1**, broadly exposed on skull roof. (GAUTHIER, 1986)
31. Lacrimal prominence: **0**, absent; **1**, triangular hornlets; **2**, ridge continuous with raised surface of lateral edge of nasals.
32. Lacrimal caudal process at dorsal surface: **0**, absent, lacrimal L-shaped or simple shaft; **1**, present, lacrimal T-shaped. (MAKOVICKY & SUES, 1998)
33. Lacrimal recess: **0**, absent; **1**, single opening present; **2**, multiple openings present. **O** (WITMER, 1997)
34. Slot in ventral process of lacrimal for jugal: **0**, absent; **1**, present. (SERENO *et al.*, 1996)
35. Lacrimal dorsal (= rostral) ramus: **0**, dorsoventrally thick; **1**, dorsoventrally pinched and narrow; **2**, absent. **O** (SERENO *et al.*, 1996)
36. Lacrimal suborbital bar: **0**, absent; **1**, present. (CURRIE & CARPENTER, in press)
37. Prefrontals: **0**, well exposed on skull roof; **1**, reduced or absent. (GAUTHIER, 1986)
38. Prefrontal-frontal peg-in-socket suture: **0**, absent; **1**, present. (SERENO *et al.*, 1994)
39. Rostral portion of frontals: **0**, relatively square, suture with nasals forms a relatively obtuse angle or W; **1**, triangular, suture with nasals form a distinctly acute angle. (HOLTZ, 1994)
40. Frontal shape: **0**, narrow or truncated rostrally, postorbital ramus projects laterally from orbital margin of frontal; **1**, very broadly exposed on skull roof, postorbital ramus does not project abruptly laterally from the orbital margin. (HOLTZ, 1994)
41. Frontal-frontal suture: **0**, unfused; **1**, fused.
42. Frontal-parietal suture on dorsal surface of skull: **0**, forms a relatively straight line transversely; **1**, frontals separated at medialmost point of suture by rostral process of parietals; **2**, frontals and parietals fused, suture indistinguishable. **UO**
43. Dorsal surface of parietals: **0**, flat, ridge borders supratemporal fenestra; **1**, sagittal crest along midline.
44. Orbit length: **0**, subequal to or longer than internal antorbital fenestra length; **1**, shorter than internal antorbital fenestra length.
45. Orbit shape: **0**, round; **1**, oval or key-shaped, rounded dorsally, constricted ventrally. (GAUTHIER, 1986)
46. Orbit margin: **0**, smooth; **1**, raised rim. (HOLTZ, 1994)
47. Postorbital prominences: **0**, absent; **1**, present. (RUSSELL & DONG, 1993a)
48. Postorbital ventral process: **0**, broader rostrocaudally than transversely; **1**, broader transversely than rostrocaudally with U-shaped cross-section. (SERENO *et al.*, 1996)
49. Postorbital ventral process ventralmost extension: **0**, dorsal to ventral margin of orbit; **1**, ventral to ventral margin of orbit. (CURRIE & CARPENTER, in press)
50. Postorbital-lacrimal contact: **0**, postorbital does not contact lacrimal; **1**, broad.
51. Postorbital-jugal contact: **0**, present; **1**, absent. (CHIAPPE, NORELL & CLARK, 1998)
52. Postorbital bulbous rostrally projecting rugosity: **0**, absent; **1**, present. (SERENO *et al.*, 1996)
53. Postorbital suborbital flange: **0**, absent; **1**, present.
54. Postorbital frontal process: **0**, sharply upturned; **1**, about same level or slightly higher than squamosal process, producing T-shaped postorbital. (CURRIE, 1995)
55. Squamosal recess: **0**, absent; **1**, present. (WITMER, 1997)

56. Squamosal flange covering quadrate head in lateral view: **0**, absent; **1**, present. (SERENO *et al.*, 1994)
57. Squamosal constriction of lateral temporal fenestra: **0**, absent; **1**, present. (CURRIE & CARPENTER, in press)
58. Jugal: **0**, does not participate in margin of internal antorbital fenestra; **1**, participates in internal antorbital fenestra. (HOLTZ, 1994)
59. Jugal postorbital process: **0**, present; **1**, absent. (CURRIE & CARPENTER, in press)
60. Jugal quadratojugal processes caudalmost extensions: **0**, dorsal and ventral processes subequal in caudalmost extension; **1**, dorsal extends further caudally; **2**, ventral extends further caudally. **UO**. (CURRIE & CARPENTER, in press)
61. Jugal recesses: **0**, absent; **1**, present. (WITMER, 1997)
62. Infratemporal fenestra: **0**, subequal or less in area of orbit in lateral view; **1**, about twice as large as the area of the orbit in lateral view. (HOLTZ, 1994)
63. Quadratojugal: **0**, L-shaped; **1**, T-shaped. (CURRIE, 1995)
64. Quadratojugal-squamosal contact: **0**, tip of dorsal ramus of quadratojugal contacts tip of lateroventral ramus of squamosal; **1**, dorsal ramus of quadratojugal does not contact squamosal; **2**, broad contact between dorsal ramus of quadratojugal and lateroventral ramus of squamosal. **UO**
65. Articulations of quadrate and squamosal: **0**, quadrate articulates only with squamosal and the latter bone contacting both the quadratojugal and postorbital; **1**, quadrate articulates with both prootic and squamosal, and the latter contacting neither the quadratojugal nor the postorbital. (CHIAPPE, NORELL & CLARK, 1996)
66. Quadrate-quadratojugal suture: **0**, unfused; **1**, fused.
67. Quadrate foramen: **0**, large and situated between quadrate and quadratojugal; **1**, reduced or absent; **2**, small and enclosed within dorsal ramus of quadrate. **UO**
68. Quadrate dorsal ramus: **0**, less than height of orbit; **1**, greater than height of orbit.
69. Depth of quadrate articulation: **0**, level with ventral surface of maxilla in lateral view; **1**, projects well ventral of the ventral surface of the maxilla. (HOLTZ, 1994)
70. Length of quadrate articulation: **0**, only slightly caudal to the caudal point of occipital condyle in dorsal view; **1**, projects well caudal to the caudal point of the occipital condyle; **2**, rostral to caudal point of occipital condyle. **UO**
71. Quadrate pneumaticity: **0**, absent or poorly developed; **1** well developed.
72. Secondary palate: **0**, primarily soft; **1**, well ossified from premaxilla through one-half the length of the ventral surface of the maxilla.
73. Vomera: **0**, separate rostrally; **1**, fused rostrally. (GAUTHIER, 1986)
74. Vomer length: **0**, limited to rostral region; **1**, extends caudally to basicranium. (RUSSELL & DONG, 1993a)
75. Palatines meet medially: **0**, absent, separated by vomera and/or pterygoids; **1**, present. (HARRIS, 1998)
76. Palatine shape: **0**, subrectangular or trapezoidal; **1**, tetra-radiate; **2**, triradiate (no jugal processes). **UO** (HARRIS, 1998)
77. Jugal process of palatine expanded distally: **0**, absent; **1**, present. (HARRIS, 1998)
78. Palatine recesses: **0**, absent; **1**, present. (WITMER, 1997)
79. Palatine fenestra (between ectopterygoid and palatine): **0**, open; **1**, closed. (RUSSELL & DONG, 1993a)
80. Subsidiary fenestra between pterygoid and palatine: **0**, absent; **1**, present. (GAUTHIER, 1986)
81. Ventral ectopterygoid recess: **0**, absent; **1**, present and comma-shaped; **2**, present and subcircular. **UO** (SERENO *et al.*, 1996)
82. Endocranial cavity: **0**, typical size of other bipedal dinosaurs; **1**, enlarged relative to other dinosaurs, but temporal musculature extends origin onto frontals; **2**, greatly enlarged, temporal musculature fails to extend origin onto frontals. **O** (GAUTHIER, 1986)
83. Nuchal crest: **0**, small or absent; **1**, pronounced. (HOLTZ, 1994)
84. Supraoccipital with very pronounced, strongly demarcated median ridge: **0**, absent; **1**, present.
85. Orbitosphenoid: **0**, present; **1**, absent. (HOLTZ, 1994)
86. Paroccipital process pneumatization: **0**, solid proximal portion; **1**, hollow proximal portion.
87. Paroccipital process orientation: **0**, occipital surface of distal end oriented more caudally than dorsally; **1**, conspicuous twist in the distal end orients distal surface more dorsally than proximal region; **2**, curving ventrally and pendant. **UO** (CURRIE, 1995)
88. Basicranium pneumatization: **0**, minimal to moderate, but no expansion of basisphenoid; **1**, basisphenoid, but not parasphenoid rostrum, strongly expanded and pneumatized. (RUSSELL & DONG, 1993a)
89. Lateral depression surrounding opening to middle ear: **0**, absent; **1**, present. (MAKOVICKY & SUES, 1998)
90. Number of tympanic recesses: **0**, two or fewer; **1**, three. (MAKOVICKY & SUES, 1998)
91. Branches of internal carotid artery entering hypoglossal fossa: **0**, enter separately; **1**, enter through single common foramen. (MAKOVICKY & SUES, 1998)
92. Posttympanic recess: **0**, invades paroccipital process; **1**, confined to columnar process. (MAKOVICKY & NORELL, 1998)
93. Cranial tympanic recess: **0**, excluded from basisphenoid; **1**, invades basisphenoid. (MAKOVICKY & NORELL, 1998)
94. Internal foramen of facial nerve: **0**, ventral to vestiblocochlear nerve; **1**, cranioventral to vestiblocochlear nerve. (MAKOVICKY & NORELL, 1998)
95. Number of cranial nerve openings in acoustic fossa: **0**, two; **1**, three. (MAKOVICKY & NORELL, 1998)
96. Basisoccipital: **0**, not excluded from basal tuber; **1**, excluded from basal tuber. (SERENO *et al.*, 1996)
97. Distance across basal tubera: **0**, greater than transverse width of occipital condyle; **1**, less than the transverse width of occipital condyle.
98. Parabasisphenoid bulbous capsule: **0**, absent; **1**, present. (HOLTZ, 1994)
99. Exoccipital-opisthonic caudoventral limit of contact with basisphenoid separated from basal tubera by notch: **0**, absent; **1**, present. (CURRIE & CARPENTER, in press)
100. Basipterygoid processes: **0**, moderately long, not fused to pterygoids; **1**, very short, not fused to pterygoids; **2**, very short, fused to pterygoids. **UO** (RUSSELL & DONG, 1993a)
101. Occipital region: **0**, directed caudally; **1**, directed ventro-caudally. (HOLTZ, 1994)
102. Foramen magnum dimensions: **0**, subcircular or wider than tall; **1**, taller than wide. (MAKOVICKY & SUES, 1998)
103. Occipital condyle constricted neck: **0**, absent; **1**, present. (MAKOVICKY & SUES, 1998)
104. Dentary teeth: **0**, present; **1**, absent.
105. Dentary end: **0**, rounded; **1**, squared with expanded tip. (SERENO *et al.*, 1996)
106. Dentary symphysis: **0**, dentaries separate; **1**, dentaries fused.
107. Symphyseal region of dentary: **0**, straight; **1**, medially recurved. (CLARK, PERLE & NORELL, 1994)
108. Rostral half of mandible: **0**, ventrally convex or straight; **1**, concave. (RUSSELL & DONG, 1993a)

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109. Dentary rami: **0**, subparallel; **1**, widely divergent caudally. (MAKOVICKY & SUES, 1998)
110. Reduced overlap of dentary onto postdentary bones: **0**, absent; **1**, present. (GAUTHIER, 1986)
111. Intramandibular joint: **0**, absent; **1**, present. (SERENO & NOVAS, 1992)
112. Dentary caudal depth: **0**, subequal to 120% depth of dentary symphysis; **1**, 150-200% depth of dentary symphysis; **2**, greater than 220% depth of dentary symphysis.
113. Rostral surangular foramen: **0**, absent or very small pit; **1**, larger, in rostrally-oriented depression.
114. Caudal surangular foramen: **0**, small pit; **1**, large opening. (HOLTZ, 1994)
115. Rostral ramus of surangular: **0**, shallow; **1**, deep. (GAUTHIER, 1986)
116. Horizontal shelf on lateral surface of surangular, rostral and ventral to the mandibular condyle: **0**, absent or faint ridge; **1**, prominent and extends laterally; **2**, prominent and pendant. **UO**
117. Rostral prong of angular: **0**, does not penetrate the dentary-splenic cavity; **1**, penetrates the dentary-splenic cavity. (BAKKER, WILLIAMS & CURRIE, 1988)
118. External mandibular fenestra: **0**, large, horizontally oval; **1**, reduced. (GAUTHIER, 1986)
119. Splenic: **0**, obscured or only slightly visible in lateral view; **1**, extensive triangular exposure in lateral view between dentary and angular. (CURRIE, 1995)
120. Splenic with notch on rostral margin of internal mandibular fenestra: **0**, absent; **1**, present. (SERENO *et al.*, 1996)
121. Coronoid: **0**, present; **1**, extremely reduced or absent. (RUSSELL & DONG, 1993a)
122. Articular facet for mandibular joint: **0**, deeply concave; **1**, craniocaudally elongate and shallow. (MAKOVICKY & SUES, 1998)
123. Retroarticular process of articular: **0**, faces dorsocaudally; **1**, faces caudally. (SERENO *et al.*, 1994)
124. Retroarticular process shape: **0**, short and deep; **1**, elongated and tapering. (CURRIE, GODFREY & NESSOV, 1993)
125. Vertical columnar process on retroarticular process: **0**, absent; **1**, present. (CURRIE, 1995)
126. Number of teeth: **0**, less than 100; **1**, greater than 100. (PÉREZ-MORENO *et al.*, 1994)
127. Dentary and maxillary teeth: **0**, subequal in number and size; **1**, dentary teeth more numerous and smaller than maxillary teeth. (RUSSELL & DONG, 1993a)
128. Serrations: **0**, small serrations; **1**, large denticles; **2**, absent. **UO**
129. Relative serration (or denticle) size of anterior and posterior carinae of maxillary and dentary teeth: **0**, subequal; **1**, posterior serrations much larger than anterior serrations.
130. Tooth roots: **0**, unstricted; **1**, constricted.
131. Lateral surface of teeth: **0**, smooth; **1**, with wrinkles in enamel internal to serrations. (CURRIE & CARPENTER, in press)
132. Premaxillary tooth crowns: **0**, conical; **1**, asymmetrical (strongly convex labially, relatively flattened lingually); **2**, incisiform and reduced in size. **UO**
133. Caudalmost maxillary tooth position: **0**, beneath midpoint of orbit; **1**, rostral to orbit. (GAUTHIER, 1986)
134. Dentary tooth implantation: **0**, set in sockets; **1**, set in paradental groove. (CHIAPPE, NORELL & CLARK, 1996)
135. Interdental plates: **0**, present and separate; **1**, fused together; **2**, absent in dentary. **UO**
136. Neck length: **0**, less than twice the length of skull; **1**, twice or more the length of skull.
137. First intercentrum: **0**, small occipital fossa (three times as wide as tall) and large odontoid notch; **1**, large occipital fossa (two or less times as wide as tall) and small odontoid notch. (GAUTHIER, 1986)
138. Second intercentrum cranial articulation with first intercentrum: **0**, slight concavity; **1**, broad crescentic fossa. (GAUTHIER, 1986)
139. Axial "spine table" (expanded distal end of neural spine): **0**, absent; **1**, present. (GAUTHIER, 1986)
140. Axial neural spine shape: **0**, flared transversely; **1**, compressed mediolaterally. (MAKOVICKY & SUES, 1998)
141. Craniodorsal rim of axial neural spine: **0**, concave in lateral view; **1**, convex curve in lateral view. (MAKOVICKY & SUES, 1998)
142. Axial parapophyses: **0**, prominent; **1**, reduced. (ROWE, 1989)
143. Axial diapophyses: **0**, present; **1**, absent. (ROWE, 1989)
144. Axial epipophyses: **0**, moderately developed; **1**, prominent. (GAUTHIER, 1986)
145. Axial pleurocoels: **0**, present; **1**, absent. (ROWE, 1989)
146. Ventral keel on axial centrum: **0**, present; **1**, absent. (MAKOVICKY & SUES, 1998)
147. Cervical centra surfaces: **0**, amphiplatyan or mildly opisthocelous; **1**, markedly opisthocelous.
148. Postaxial cervical pleurocoels: **0**, absent; **1**, one pair present; **2**, two pairs present. **O**
149. Cervical epipophyseal shape: **0**, rugosity on caudal zygapophyses; **1**, powerfully developed and prong shaped. (RUSSELL & DONG, 1993a)
150. Cervical epipophyseal height and orientation: **0**, directed caudolaterally and shorter than neural spine; **1**, directed dorsolaterally and taller than neural spine. (HOLTZ, 1994)
151. Epipophyses on cervical vertebrae: **0**, placed distally on postzygapophyses; **1**, placed proximally. (MAKOVICKY & SUES, 1998)
152. Caudal cervical epipophyses size: **0**, short; **1**, elongate.
153. Cervical prezygapophyses: **0**, planar; **1**, flexed. (GAUTHIER, 1986)
154. Cervical neural spines: **0**, tall; **1**, low and craniocaudally short. (RUSSELL & DONG, 1993a)
155. Cervical zygapophyses direction: **0**, overhang centrum parasagittally; **1**, displaced laterally away from centrum in dorsal view. (MAKOVICKY & SUES, 1998)
156. Caudal cervical neural arch forms X-shape in dorsal view: **0**, absent; **1**, present. (MAKOVICKY & SUES, 1998)
157. Cranial cervicals: **0**, subcircular in cranial view; **1**, broader than deep on cranial surface, with reniform (kidney-shaped) articular surfaces that are taller laterally than at midline. (GAUTHIER, 1986)
158. Cranial cervical centra caudal extent: **0**, level with or shorter than caudal extent of neural arch; **1**, extend beyond caudal extent of neural arch. (MAKOVICKY & SUES, 1998)
159. Elevation of cranial face of midcervical centra: **0**, present; **1**, absent. (SERENO *et al.*, 1996)
160. Midcervical centra length: **0**, around twice diameter of cranial face; **1**, four times or more diameter of cranial face; **2**, less than twice diameter of cranial face. **UO**
161. Midcervical centra breadth: **0**, less than 20% broader than tall; **1**, greater than 20% broader than tall. (SERENO *et al.*, 1996)
162. Carotid process on caudal cervical vertebrae: **0**, absent; **1**, present. (MAKOVICKY & SUES, 1998)
163. Caudal cervical postzygapophyses: **0**, short; **1**, elongate. (MAKOVICKY & SUES, 1998)
164. Longest postaxial cervicals: **0**, III-V; **1**, VI-IX. (NOVAS, 1994)

165. Cervical ribs: **0**, unfused to centra in adults; **1**, fused to centra in adults. (GAUTHIER, 1986)
166. Ventral processes (hypapophyses) on cervicodorsal vertebrae: **0**, absent; **1**, present as small protrusion; **2**, very well developed. **O** (GAUTHIER, 1986)
167. Neural spines of dorsals: **0**, less than or equal to centrum height; **1**, equal to twice centrum height; **2**, more than twice centrum height. **O**
168. Apices of dorsal neural spines: **0**, unexpanded; **1**, expanded transversely to form "spine table". (MAKOVICKY & SUES, 1998)
169. Scars for interspinous ligaments: **0**, terminate at apex of neural spine in dorsal vertebrae; **1**, terminate below apex of neural spine. (MAKOVICKY & SUES, 1998)
170. Dorsal transverse processes: **0**, laterally directed and subrectangular in dorsal view; **1**, strongly backturned caudally and triangular in dorsal view. (HOLTZ, 1994)
171. Dorsal transverse processes direction: **0**, long and caudodorsally inclined; **1**, short, wide and only slightly inclined. (MAKOVICKY & SUES, 1998)
172. Caudal edge of dorsal postzygapophyses: **0**, level with caudal intracentral articulation; **1**, overhangs centrum. (MAKOVICKY & SUES, 1998)
173. Vertebral foramen/cranial articular facet ratio (vertical diameters) of dorsals: **0**, around 0.1-0.3; **1**, 0.4 or greater. (CHIAPPE, NORELL & CLARK, 1996)
174. Dorsal hyosphene-hypantrum accessory articulations: **0**, present; **1**, absent. (CHIAPPE, NORELL & CLARK, 1996)
175. Dorsal centrum shape: **0**, cylindrical, central section thickness greater than 60% height of cranial face; **1**, "hourglass" shaped, central section thickness less than 60% height of cranial face. (HOLTZ, 1994)
176. Dorsal centrum transverse section: **0**, subcircular or oval; **1**, wider than high. (MAKOVICKY & SUES, 1998)
177. Dorsal centrum ends: **0**, amphiplatyan; **1**, biconvex. (CHIAPPE, NORELL & CLARK, 1996)
178. Dorsal column: **0**, much longer than femur length; **1**, subequal to femur length.
179. Caudal dorsal neural spines: **0**, oriented vertically or caudally; **1**, oriented cranially. (HARRIS, 1998)
180. Cranial and median dorsal pleurocoels: **0**, absent; **1**, one pair present; **2**, two pairs present. **O**
181. Presacral pleurocoel structure: **0**, absent; **1**, camerate; **2**, camellate. **O**
182. Caputular facet of dorsal ribs: **0**, lies on cranioventral lamina from transverse process; **1**, situated dorsal to lamina, on prezygapophyseal base. (RUSSELL & DONG, 1993a)
183. Sacral pleurocoels: **0**, absent; **1**, present.
184. First sacral: **0**, amphiplatyan; **1**, procoelous. (CHIAPPE, NORELL & CLARK, 1996)
185. Number of sacrals (as determined by number of vertebrae which attach to pelvic girdle): **0**, two; **1**, three; **2**, four; **3**, five; **4**, six; **5**, more than six. **O**
186. Sacrals III-V: **0**, moderately or uncompressed; **1**, transversely compressed; **2**, dorsoventrally flattened. **UO**
187. Caudalmost sacral centrum size: **0**, subequal in width with cranialmost sacral centrum; **1**, markedly smaller than cranialmost sacral centrum. (MAKOVICKY & SUES, 1998)
188. Sacral neural spines fuse to form lamina: **0**, absent; **1**, present.
189. Synsacrum (fusion of sacral centra, neural arches, neural spines, transverse processes, and sacral ribs to ilia): **0**, absent; **1**, present in adults.
190. Number of caudals: **0**, 45 or more; **1**, 30-44; **2**, less than 25. **O** (HOLTZ, 1994)
191. Caudal pleurocoels: **0**, absent; **1**, present in centrum; **2**, present in neural arch. **UO**
192. Caudal neural spines: **0**, present beyond caudal X; **1**, limited to caudals I-IX. (GAUTHIER, 1986)
193. Ventral groove in cranial caudals: **0**, absent; **1**, present. (ROWE & GAUTHIER, 1990)
194. Centra of caudals I-V: **0**, spool-shaped; **1**, box-like with increased flexural capability. (GAUTHIER, 1986)
195. Proximal caudal zygapophyses: **0**, short; **1**, elongate.
196. Caudal transverse processes: **0**, present beyond caudal XV; **1**, only on caudals I-XV or fewer. (HOLTZ, 1994)
197. Transition point: **0**, absent; **1**, in distal half of tail; **2**, in proximal half of tail; **3**, in caudals I-IX. **O** (GAUTHIER, 1986)
198. Midcaudal vertebrae: **0**, short prezygapophyses, extend less than one half centrum length; **1**, moderate prezygapophyses, extend more than one half but less than one centrum length; **2**, extremely long prezygapophyses, extend more than one centrum length. **O**
199. Distal caudal vertebrae: **0**, only slight interlocking, prezygapophyses extend less than one half centrum length; **1**, moderately interlocking, prezygapophyses extend more than one half, but less than one, centrum length; **2**, strong interlocking, non-ossified structures (cartilaginous extensions of prezygapophyses?) producing rigidity in caudals VII and distal; **3**, extremely strong interlocking, bony extensions of prezygapophyses extending up to 12 centrum lengths; **4**, pygostyle. **UO**
200. Distal caudal length: **0**, as long as proximal caudals; **1**, more than 130% length of proximal caudals; **2**, markedly shorter than proximal caudals. **UO**
201. Shaft of cervical ribs: **0**, moderately long (two to three times centrum length) and slender; **1**, extremely long (four or more times centrum length) and slender; **2**, short (less than twice centrum length) and broad; **3**, short (less than twice centrum length) and slender. **UO**
202. Uncinate processes: **0**, absent or unossified; **1**, ossified.
203. Medial gastral segment: **0**, longer than lateral segment; **1**, shorter than lateral segment (NORELL & MAKOVICKY, 1997)
204. Chevron transition: **0**, beyond caudal XVII; **1**, between caudal X and XVII. (GAUTHIER, 1986)
205. Paired caudal and cranial chevron bases: **0**, absent; **1**, present. (SERENO *et al.*, 1994)
206. Bridge of bone dorsal to haemal canal in distal chevrons: **0**, absent; **1**, present.
207. Proximal chevron shape: **0**, dorsoventrally elongate; **1**, dorsoventrally depressed. (GAUTHIER, 1986)
208. Middle chevron shape: **0**, gentle curvature; **1**, dramatic bend in distal portion ("L-shaped"). (SERENO *et al.*, 1994)
209. Distal chevrons with cranial and caudal projections, and more than twice as long craniocaudally as tall dorsoventrally ("boat-shaped"): **0**, absent; **1**, present. (HOLTZ, 1994)
210. Distal chevron cranial and caudal bifurcations: **0**, absent; **1**, present. (SERENO, 1997)
211. Scapular blade: **0**, short and broad; **1**, long, slender (four times or more longer than midshaft width) and strap-like. (GAUTHIER, 1986)
212. Distal expansion of scapula: **0**, broad (subequal in width to proximal end of scapula); **1**, reduced or absent. (CURRIE & ZHAO, 1993a)
213. Acromion on scapula: **0**, prominent; **1**, reduced or absent.
214. Caudal margin of acromial process of scapula: **0**, gentle slope; **1**, abrupt change, perpendicular to blade.
215. Scapulacoracoid cranial margin: **0**, smooth; **1**, pronounced notch between acromial process and coracoid. (CURRIE & CARPENTER, in press)

216. Glenoid orientation: **0**, caudolateral; **1**, lateral. (NOVAS & PUERTA, 1997)
217. Coracoid shape: **0**, craniocaudally elongate to subcircular; **1**, ventral coracoidal process well developed; **2**, subrectangular, dorsoventral depth more than 130% of craniocaudal width; **3**, strut-like. **UO** (GAUTHIER, 1986)
218. Coracoid caudoventral process length: **0**, less than twice glenoid diameter; **1**, more than twice glenoid diameter. (CHIAPPE, NORELL & CLARK, 1996)
219. Coracoid biceps tubercle: **0**, absent or poorly developed; **1**, conspicuous and well developed. (PÉREZ-MORENO *et al.*, 1993)
220. Coracoid angle with scapula at level of glenoid cavity: **0**, moderate; **1**, sharp. (CHIAPPE, NORELL & CLARK, 1996)
221. Sternal plates: **0**, separate; **1**, fused.
222. Sternum carina: **0**, absent; **1**, present.
223. Sternum shape: **0**, relatively round; **1**, longer craniocaudally than wide mediolaterally; **2**, wider mediolaterally than long craniocaudally. **UO**
224. Sternum size: **0**, craniocaudal length similar to coracoid length; **1**, much greater than coracoid length.
225. Furcula: **0**, absent, clavicles unfused; **1**, present.
226. Forelimb (humerus + radius + manus)/hindlimb (femur + tibia + pes) length ratio: **0**, less than 50%; **1**, greater than 50% but less than 120%; **2**, greater than 120%. **O** (GAUTHIER, 1986)
227. Forelimb/presacral vertebral series length ratio: **0**, less than 75%; **1**, greater than 75% but much less than 200%; **2**, about 200% or more. **O** (GAUTHIER, 1986)
228. Manus/pes length ratio: **0**, much less than 100%; **1**, greater than 100%.
229. Humerus/scapula length ratio: **0**, greater than 65%; **1**, less than 65%. (PÉREZ-MORENO *et al.*, 1993)
230. Humerus/ulna length ratio: **0**, greater than 100%; **1**, less than or equal to 100%.
231. Ulna/femur length ratio: **0**, greater than 27%; **1**, less than 27%. (SERENO *et al.*, 1996)
232. Radius/humerus length ratio: **0**, less than 75% but greater than 50%; **1**, less than 50%; **2**, greater than 76%. **UO**
233. Manus/(humerus + radius) length ratio: **0**, less than 66%; **1**, greater than 66%. (GAUTHIER, 1986)
234. Humeral torsion: **0**, absent; **1**, present. (PÉREZ-MORENO *et al.*, 1993)
235. Humeral shaft: **0**, straight; **1**, sigmoid. (HOLTZ, 1994)
236. Humeral head: **0**, low and confluent with deltapectoral and bicipital crests; **1**, offset and emarginated ventrally by groove. (MAKOVICKY & SUES, 1998)
237. Internal tuberosity (= ventral tubercle) on proximal end of humerus development: **0**, not well differentiated; **1**, well differentiated and angular. (RUSSELL & DONG, 1993a)
238. Internal tuberosity (= ventral tubercle) of humerus shape: **0**, conical; **1**, craniocaudally compressed and longitudinally elongate.
239. Internal tuberosity (= ventral tubercle) of humerus direction: **0**, projected ventrally; **1**, projected proximally; **2**, projected caudally, separated from humeral head by deep capital incision. **UO** (CHIAPPE, NORELL & CLARK, 1996)
240. Humeral ends: **0**, little or not expanded; **1**, well expanded, greater than 150% midshaft diameter. (PÉREZ-MORENO *et al.*, 1993)
241. Deltapectoral crest on humerus: **0**, low; **1**, expanded and offset from humeral shaft. (MAKOVICKY & SUES, 1998)
242. Humeral distal condyle: **0**, mainly on distal aspect; **1**, cranial aspect. (NOVAS, 1996)
243. Humeral entepicondyle: **0**, small; **1**, prominent. (MAKOVICKY & SUES, 1998)
244. Ulnar facet on humerus: **0**, small or absent; **1**, expanded, merges with entepicondyle. (RUSSELL & DONG, 1993a)
245. Ulnar shaft: **0**, straight; **1**, bowed caudally. (GAUTHIER, 1986)
246. Shape of proximal ulnar shaft: **0**, straight; **1**, arched.
247. Diameter of ulnar shaft: **0**, equal to or slightly thicker than that of radius; **1**, much thicker than that of radius.
248. Ulnar distal condyle: **0**, transversely compressed and craniocaudally extended approximately at same plane of humero-ulnar flexion-extension movement; **1**, subtriangular shaped in distal view, with a dorsomedial condyle, and twisted more than 54 degrees with respect to the proximal end. (NOVAS, 1996)
249. Ulnar facet for radius: **0**, small and flat; **1**, transversely expanded and concave. (MAKOVICKY & SUES, 1998)
250. Ulnar and radial distal ends: **0**, loosely joined; **1**, closely joined, even with syndesmosis. (PÉREZ-MORENO *et al.*, 1994)
251. Distal carpal shape: **0**, cubic and well formed, with obvious articular surfaces; **1**, flat and discoidal, no distinct articular surfaces. (HOLTZ, 1994)
252. Carpometacarpus: **0**, absent, carpals distinct units; **1**, present, carpals fused to each other and to metacarpus.
253. Distal carpal I block: **0**, only overlaps base of metacarpal I; **1**, does not overlap metacarpal II dorsally (does so ventrally); **2**, broadly overlaps metacarpal II dorsally and ventrally. **O**
254. Distal carpal I: **0**, unfused to distal carpal II; **1**, fused to distal carpal II.
255. Semilunate carpal block fully developed with transverse trochlea: **0**, absent; **1**, present. (GAUTHIER, 1986)
256. Metacarpal V: **0**, present, with digit; **1**, present, without ungual; **2**, present, without phalanges; **3**, absent. **O**
257. Metacarpal IV: **0**, present, with digit; **1**, present, without ungual; **2**, present, without phalanges; **3**, absent. **O**
258. Metacarpal III: **0**, present, with digit; **1**, present, without ungual; **2**, present, without phalanges; **3**, absent. **O**
259. Metacarpal II: **0**, present, with digit; **1**, absent.
260. Metacarpal I size: **0**, greater than one half of metacarpal II length, but less than metacarpal II length; **1**, one half to one third metacarpal II length; **2**, subequal to metacarpal II length. **UO**
261. Articular surface between metacarpals I and II: **0**, placed just at proximal end of metacarpal I; **1**, extends well into diaphysis of metacarpal I. (GAUTHIER, 1986)
262. Metacarpal II length: **0**, much less than humerus length; **1**, about 50% or greater humerus length.
263. Metacarpal III length: **0**, subequal to metacarpal II; **1**, clearly shorter than metacarpal II; **2**, clearly longer than metacarpal II. **UO** (PÉREZ-MORENO *et al.*, 1993)
264. Metacarpal III width: **0**, not very much narrower (greater than 50%) than metacarpal II; **1**, very much narrower (less than 50%) than metacarpal II. (GAUTHIER, 1986)
265. Metacarpal III shape: **0**, straight; **1**, bowed laterally. (GAUTHIER, 1986)
266. Base of metacarpal III: **0**, along same plane as metacarpals I and II; **1**, set on palmar surface of hand below base of metacarpal II. (GAUTHIER, 1986)
267. Proximal articulation of metacarpal III: **0**, subquadrilateral; **1**, triangular. (RUSSELL & DONG, 1993a)
268. Metacarpal IV length: **0**, more than half length of metacarpal II; **1**, less than half length of metacarpal II.
269. Metacarpal-phalangeal joints: **0**, hyperextensible, deep extensor pits on metacarpals I-III; **1**, not hyperextensible, extensor pits on metacarpals I-III reduced. (PÉREZ-MORENO *et al.*, 1994)
270. Longest digit in manus: **0**, digit III; **1**, digit II; **2**, digit I. **UO**
271. Penultimate phalanx: **0**, not longest of nonungual phalanges; **1**, longest nonungual phalanx. (SERENO & NOVAS, 1992)

272. Length of phalanx 3 of manual digit III (sum of lengths of phalanges 1 + 2 of digit III): **0**, less than 100%; **1**, greater than 100%. (GAUTHIER, 1986)
273. Pollex: **0**, ends at level of mid-length of phalanx 2 of digit II; **1**, ends at level of mid-length of phalanx 1 of digit II.
274. First phalanx of pollex: **0**, Less than or subequal to length of metacarpal II; **1**, greater than length of metacarpal II.
275. Manual ungual, dorsal edge of articular facet: **0**, relatively smooth; **1**, pronounced lip on dorsal edge. (RUSSELL & DONG, 1993a)
276. Flexor tubercle of unguals: **0**, well developed and proximally placed; **1**, poorly developed and distally placed. (PÉREZ-MORENO *et al.*, 1994)
277. Manual ungual, region palmar to ungual groove: **0**, wider than region dorsal to ungual groove; **1**, palmar and dorsal regions subequal in width. (RUSSELL & DONG, 1993a)
278. Pollex ungual size: **0**, subequal to unguals of digits II and III in size; **1**, larger than other manual unguals.
279. Pollex ungual length: **0**, less than three times longer than height of articular facet; **1**, greater than three times longer than height of articular facet. (SERENO *et al.*, 1996)
280. Pollex ungual shape: **0**, trenchant, dorsoventrally deep, with proximal articular surface elliptical; **1**, stout and robust, dorsoventrally compressed, with proximal articular surface quadrangular. (NOVAS, 1996)
281. Manual unguals II and III: **0**, smooth proximodistal surface; **1**, small nubbin proximodistally. (RUSSELL & DONG, 1993a)
282. Manual ungual cross section: **0**, generally oval, two to three times as deep as wide; **1**, blade-like, more than three times as deep as wide; **2**, subtriangular, as wide or wider than deep. **UO**
283. Manual ungual length: **0**, moderate; **1**, extremely long; **2**, relatively short. **UO**
284. Manual ungual curvature: **0**, moderate; **1**, extremely curved; **2**, straight. **UO**
285. Pelvic girdle sutures: **0**, unfused in adults; **1**, fused in adults. (ROWE & GAUTHIER, 1986)
286. Ilium shape: **0**, brachyliac; **1**, dolichoiliac. (GAUTHIER, 1986)
287. Iliac blades dorsal surface: **0**, do not meet along midline; **1**, meet along midline. (HOLTZ, 1994)
288. Iliac preacetabular fossa for *M. cuppedicus*: **0**, absent; **1**, present. (GAUTHIER, 1986)
289. Fossa for origin of *M. cuppedicus* on ilium: **0**, narrow or absent; **1**, broad. (MAKOVICKY & SUES, 1998)
290. Brevis fossa (for *M. caudofemoralis brevis*) depth: **0**, absent or poorly developed; **1**, pronounced. (GAUTHIER, 1986)
291. Brevis fossa distal end: **0**, brevis fossa absent; **1**, distal tapered; **2**, broad distal end. **UO** (SERENO *et al.*, 1996)
292. Preacetabular ala of ilium: **0**, not greatly expanded vertically; **1**, greatly expanded vertically. (RUSSELL & DONG, 1993a)
293. Preacetabular portion of ilium: **0**, subequal in length to postacetabular portion; **1**, significantly longer than postacetabular portion.
294. Preacetabular process of ilium: **0**, cranial margin smooth; **1**, cranial margin notched. (SERENO *et al.*, 1996)
295. Median vertical ridge on external surface of ilium: **0**, absent; **1**, present. (RUSSELL & DONG, 1993a)
296. Caudodorsal margin of ilium: **0**, gently arched; **1**, curves caudoventrally. (GAUTHIER, 1986)
297. Postacetabular ala of ilium: **0**, squared caudally; **1**, acuminate. (RUSSELL & DONG, 1993a)
298. Postacetabular process of ilium: **0**, straight caudal margin; **1**, concave caudal margin.
299. Supracetabular crest on ilium: **0**, present; **1**, absent. (RUSSELL & DONG, 1993a)
300. Supracetabular shelf on ilium: **0**, absent; **1**, present. (ROWE & GAUTHIER, 1990)
301. Acetabular height/craniocaudal length: **0**, 27-33%; **1**, about 50%. (SERENO & NOVAS, 1992)
302. Ilium length: **0**, clearly shorter than femur; **1**, about as long as femur.
303. Prominent antitrochanter on ilium: **0**, absent; **1**, present.
304. Iliac-ischial articulation: **0**, larger than iliac-pubic articulation; **1**, smaller than iliac-pubic articulation. (SERENO *et al.*, 1994)
305. Pubic peduncle of ilium proportions: **0**, more developed mediolaterally than craniocaudally; **1**, more developed craniocaudally than mediolaterally. (SERENO *et al.*, 1994)
306. Pubic peduncle of ilium depth: **0**, extends ventrally to the same level as ischiadic peduncle; **1**, extends more ventrally than ischiadic peduncle. (GAUTHIER, 1986)
307. Obturator foramen of pubis: **0**, present; **1**, open ventrally to form obturator notch. (GAUTHIER, 1986)
308. Pubic fenestra ventral to obturator foramen: **0**, absent; **1**, present. (ROWE, 1989)
309. Pubis orientation: **0**, propubic, shaft approximately 45 degrees from horizontal; **1**, propubic, proximal portion of shaft approximately 30 degrees from horizontal; **2**, vertical; **3**, opisthopic; **4**, caudoventrally directed with twisted proximal region. **UO**
310. Pubic shaft: **0**, straight; **1**, marked concave curvature cranially; **2**, marked convex curvature cranially. **UO** (MAKOVICKY & SUES, 1998)
311. Pubic apices: **0**, in contact; **1**, separate. (CHIAPPE, NORELL & CLARK, 1996)
312. Pubic blade: **0**, five or less times as long as broad; **1**, at least six times as long as broad.
313. Pubic apron: **0**, transversely wide and proximodistally long, extending more than 50% of pubis length; **1**, limited to distal half of pubis length; **2**, strongly reduced transversely and restricted to distal 25% or less of pubic length. (NOVAS, 1996)
314. Pubic foramen perforating pubic apron in distal half of pubic shaft: **0**, absent; **1**, present. (HARRIS, 1998)
315. Pubic boot shape: **0**, absent; **1**, broad triangle, angle between shaft and caudal portion of boot obtuse; **2**, rounded, angle between shaft and caudal portion of boot acute; **3**, boat-shaped (pointed cranially and caudally) in ventral view and angle between shaft and caudal portion of boot acute; **4**, triangular (apex caudal) in ventral view and angle between shaft and caudal portion of boot acute. **UO** (HOLTZ, 1994)
316. Pubic boot proportions: **0**, caudal portion same length as cranial portion; **1**, caudal portion longer than cranial portion, but latter present; **2**, cranial portion absent. **UO** (GAUTHIER, 1986)
317. Pubic boot size: **0**, absent; **1**, less than 30% as long as pubic shaft; **2**, greater than 30% as long as pubic shaft. **O** (SERENO *et al.*, 1996)
318. Pubic-ischial contact: **0**, dorsoventrally deep shelf; **1**, only narrow region. (SERENO *et al.*, 1994)
319. Pubis and ischium proximal shafts: **0**, broad; **1**, narrow. (SERENO *et al.*, 1994)
320. Ischium/pubis length ratio: **0**, greater than 75%; **1**, less than 66%. (GAUTHIER, 1986)
321. Ischial antitrochanter: **0**, small or absent; **1**, large. (ROWE & GAUTHIER, 1990)
322. Obturator process shape: **0**, joined to pubic articular process; **1**, separate, trapezoidal; **2**, separate, triangular. **UO** (HOLTZ, 1994)
323. Obturator process position: **0**, joined to pubic articular process ("obturator flange" of CHARIG & MILNER (1997)); **1**, separate, proximally placed; **2**, separate, distally placed; **3**, absent, caudoventral margin of ischium smooth from obturator notch to tip. **O**

324. Ischium obturator process or flange: **0**, not perforated by foramen; **1**, perforated by foramen.
325. Ischial proximodorsal process just distal to iliac process: **0**, absent; **1**, present. (NOVAS & PUERTA, 1997)
326. Semicircular scar on caudolateral surface of ischium, just distal to iliac process: **0**, absent; **1**, present. (HOLTZ, 1994)
327. Ischial foot: **0**, present; **1**, absent. (HOLTZ, 1994)
328. Ischiadic terminal processes: **0**, in contact; **1**, separate. (CHIAPPE, NORELL & CLARK, 1996)
329. Femur shape: **0**, prominent sigmoid curvature (S-shaped in two planes); **1**, bowed in convex arc with less pronounced sigmoidality. (GAUTHIER, 1986)
330. Femoral head angle to shaft: **0**, less than 90 degrees (head directed ventrally); **1**, approximately 90 degrees (head directed horizontally); **2**, greater than 90 degrees (head directed dorsally). **O** (HARRIS, 1998)
331. Femoral head shape: **0**, bulky; **1**, transversely elongate; **2**, rounded. **UO**
332. Greater trochanter of femur position: **0**, confluent with femoral head; **1**, cleft from femoral head. (HOLTZ, 1994)
333. Greater trochanter of femur shape: **0**, rugosity; **1**, moundlike eminence. (GAUTHIER, 1986)
334. Anterior (= lesser) trochanter: **0**, absent; **1**, separated from femoral head by cleft; **2**, nearly confluent with femoral head. **UO**
335. Anterior trochanter of femur shape: **0**, absent; **1**, conical prominence; **2**, alariform; **3**, cylindrical in cross-section; **4**, trochanteric crest (fusion of greater and anterior trochanters). **UO**
336. Anterior trochanter of femur position: **0**, absent; **1**, proximalmost point below femoral head; **2**, proximalmost point above distal margin of femoral head; **3**, proximalmost point extends above proximal margin of femoral head. **O**
337. Fourth trochanter of femur: **0**, developed, alariform; **1**, little developed; **2**, absent. **O** (GAUTHIER, 1986)
338. Trochanteric shelf of femur: **0**, moderately developed ridge transversely directed; **1**, well developed; **2**, absent. **UO** (PÉREZ-MORENO *et al.*, 1993)
339. Muscle scar in craniodistal region of femur: **0**, absent; **1**, present, non-elliptical in shape; **2**, elliptical in shape. **UO** (PÉREZ-MORENO *et al.*, 1993)
340. Medial epicondyle (= mediodistal crest): **0**, absent or weakly developed; **1**, pronounced, extends one quarter or more the length of the femoral shaft.
341. Extensor groove in craniodistal region of femur: **0**, absent; **1**, shallow and not conspicuous; **2**, deep and conspicuous. **O** (HARRIS, 1998)
342. Groove in lateral condyle of femur: **0**, absent; **1**, present. (ROWE & GAUTHIER, 1990)
343. Adductor fossa and associated caudodistal crest of distal femur: **0**, present, prominent; **1**, reduced or absent. (CHIAPPE, NORELL & CLARK, 1996)
344. Ectocondylar tuber: **0**, proximodistally short, proximally placed; **1**, proximodistally long, pronounced, and extends almost to distal end of femur.
345. Sulcus along medial side of base of crista tibiofibularis: **0**, absent; **1**, present. (ROWE & GAUTHIER, 1990)
346. Cnemial process: **0**, projects caudally; **1**, arises out of the lateral surface of tibial shaft. (HOLTZ, 1994)
347. Incisura tibialis cranialis: **0**, occupies less than 50% of medial surface of proximal tibia; **1**, occupies more than 66% of medial surface of proximal tibia. (HARRIS, 1998)
348. Lateroproximal condyle (fibular condyle) on proximal end of tibia position: **0**, large and posteriorly situated; **1**, small and medially situated. (RUSSELL & DONG, 1993a)
349. Lateroproximal condyle of tibia development in proximal view: **0**, bulge from main surface of tibia; **1**, conspicuous waisting between body of condyle and main body of tibia.
350. Crista fibularis size: **0**, absent; **1**, not well developed; **2**, well developed. **O** (PÉREZ-MORENO *et al.*, 1993)
351. Crista fibularis position: **0**, absent; **1**, proximal; **2**, distal. **UO** (HOLTZ, 1994)
352. Tibia distal end: **0**, not backing calcaneum; **1**, expanded to back calcaneum. (SERENO *et al.*, 1996)
353. Fibula: **0**, broadly separated from tibia throughout main shaft; **1**, closely appressed to tibia throughout main shaft. (HOLTZ, 1994)
354. Fibula proximal end: **0**, less than 75% proximal width of tibia; **1**, 75% or more proximal width of tibia. (SERENO *et al.*, 1996)
355. Proximal region of fibular medial face: **0**, flat; **1**, slightly concave; **2**, well excavated. **O** (PÉREZ-MORENO *et al.*, 1993)
356. Sulcus in proximomedial region of fibula: **0**, absent; **1**, present. (SERENO *et al.*, 1994)
357. Cranial protuberance on fibula below expansion: **0**, absent; **1**, present. (HOLTZ, 1994)
358. Fibular tubercle for M. iliofibularis (= "anterolateral process"): **0**, craniolaterally projecting; **1**, laterally projecting. (NOVAS, 1996)
359. Anterior surface of distal fibula: **0**, does not overlap ascending process of astragalus cranially; **1**, overlaps ascending process of astragalus cranially. (ROWE & GAUTHIER, 1990)
360. Fibular distal end: **0**, greater than twice craniocaudal width at midshaft; **1**, less than twice craniocaudal width at midshaft, and consequently astragalar cup for fibula reduced; **2**, pinches out less than half-way down tibia length. **O**
361. Fibular fusion with distal tibia: **0**, absent; **1**, present.
362. Astragalar ascending process: **0**, not reduced in horizontal dimension, proximodistally very low ("ceratosauroid condition"); **1**, mediolaterally reduced, craniocaudally wide and proximodistally low ("allosauroid condition"); **2**, craniocaudally reduced and proximodistally tall, with dorsal margin sigmoid ("ornithomimid/albertosauroid condition"). **O** (GAUTHIER, 1986)
363. Round external fossa at base of ascending process of astragalus: **0**, absent; **1**, present. (HOLTZ, 1994)
364. Astragalar distal condyles: **0**, oriented ventrally; **1**, oriented cranioventrally. (SERENO *et al.*, 1996)
365. Pronounced horizontal groove across cranial face of astragalar condyles: **0**, absent; **1**, present. (HOLTZ, 1994)
366. Astragalocalcaneum: **0**, absent, astragalus and calcaneum separate; **1**, present, astragalus fused to calcaneum.
367. Medial tuber on calcaneum: **0**, small; **1**, enlarged. (RUSSELL & DONG, 1993a)
368. Tibiotarsus: **0**, absent, proximal tarsals unfused with tibia; **1**, present, astragalocalcaneum fused to tibia.
369. Metatarsus proportions: **0**, moderate; **1**, elongate relative to most other theropods of same femur length; **2**, shortened relative to most other theropods of same femur length. **UO** (HOLTZ, 1994)
370. Metatarsal ossification: **0**, proximally separate; **1**, co-ossified proximally; **2**, co-ossified throughout shaft. **UO**
371. Metatarsal cross-sectional proportions: **0**, subequal or wider mediolaterally than craniocaudally at midshaft; **1**, deeper craniocaudally than mediolaterally at midshaft. (HOLTZ, 1994)
372. Metatarsal V: **0**, not reduced; **1**, vestigial or absent. (GAUTHIER, 1986)
373. Metatarsals II and IV: **0**, separated at midshaft on plantar surface by metatarsal III; **1**, contact at midshaft on the plantar surface. (HOLTZ, 1994)
374. Metatarsal IV size: **0**, subequal in length to metatarsal II; **1**, longer than metatarsal II and closer to metatarsal III in length. (HOLTZ, 1994)

A NEW PHYLOGENY OF THE CARNIVOROUS DINOSAURS

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Coelurus

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Compsognathidae

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Dilophosaurus

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Dromaeosauridae

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Dryptosaurus

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Elaphrosaurus

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Eustreptospondylus

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Gasosaurus

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Giganotosaurus

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Megalosaurus bucklandi

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Microvenator

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Monolophosaurus

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Neovenator

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Ornitholestes

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Ornithomimidae

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Ornithothoraces

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Oviraptoridae

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Pelecanimimus

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Piatnitzkysaurus

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Proceratosaurus

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Rahonavis

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Scipionyx

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Sinraptor

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Spinosauridae

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Therizinosaurioidea

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