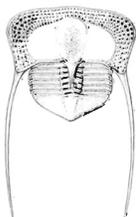
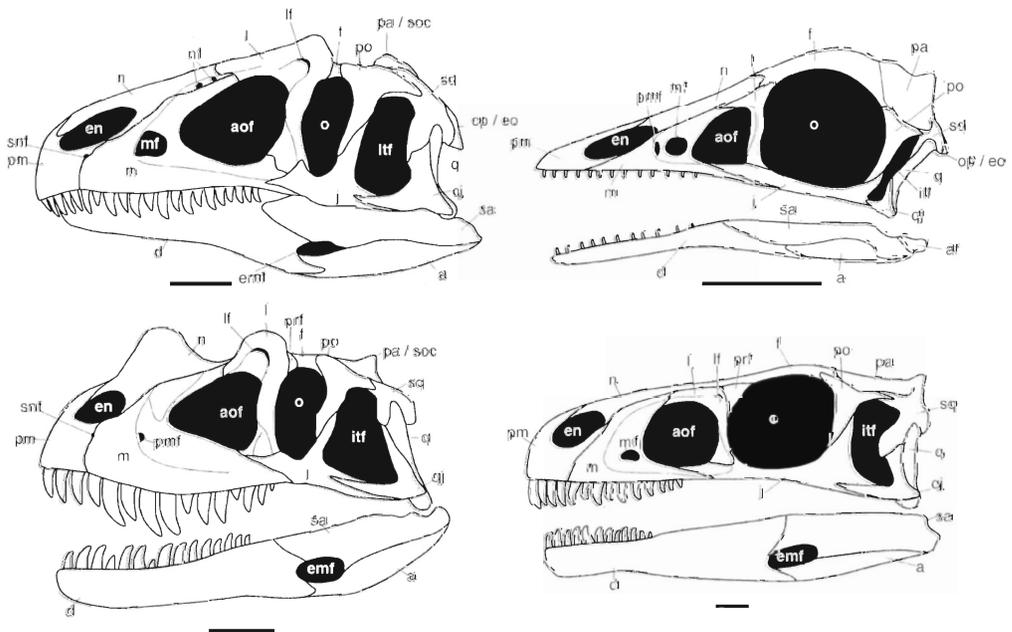


# The interrelationships and evolution of basal theropod dinosaurs

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with 61 text-figures

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ABSTRACT. Many recent studies of theropod relationships have been focused on the phylogeny of coelurosaurs and the question of the origin of birds, but the interrelationships and evolution of basal theropods are still poorly understood. Thus, this paper presents a phylogenetic analysis of all theropods, but focuses on the basal members of this clade. The result supports the inclusion of *Eoraptor* and herrerasaurids in the Theropoda, but differs from other recent studies in two main aspects: (1) The taxa usually grouped as ceratosaurs form two monophyletic clades that represent successively closer outgroups to tetanurans. The more basal of these clades, the Coelophysoidea, comprise the majority of Late Triassic and Early Jurassic theropods. The other clade of basal theropods that are usually included in the Ceratosauria comprises *Ceratosaurus*, *Elaphrosaurus*, and abelisaurids. (2) Two monophyletic groups of basal tetanurans are recognized: the Spinosauroidae and the Allosauroidae. In contrast to other recent phylogenetic hypotheses, both clades are united in a monophyletic Carnosauria. The branching pattern of the present cladogram is in general accordance with the stratigraphic occurrence of theropod taxa. Despite the differences in recent analyses, there is a significant level of consensus in theropod phylogeny. At least four different radiations of non-avian theropods can be recognized. These radiations show different patterns in Laurasia and Gondwana, and there are increasing differences between the theropod faunas of the two hemispheres from the Triassic to the Cretaceous.

KEY WORDS: Dinosauria, Theropoda, phylogeny, evolution, fossil record.

THEROPODS form a large group of dinosaurs that were predominantly carnivorous, but also included several highly specialised herbivores or omnivores. Ever since the first discoveries in the early nineteenth century, they have been of interest to experts and the general public alike. Already well before the great success of the movie 'Jurassic Park', even (or maybe better, especially) small children were familiar with names such as *Tyrannosaurus* and *Allosaurus*.

The Theropoda is also one of the most diverse groups of dinosaurs. It includes not only the smallest known non-avian dinosaurs, such as *Compsognathus*, and the largest land predators found so far, the gigantic *Tyrannosaurus*, *Giganotosaurus* and *Carcharodontosaurus*, but also the elegant ornithomimids and the bizarre therizinosaurs. Moreover, the proposed inclusion of one particular group of vertebrates in the Theropoda triggered a renewed interest in these animals: in the mid 1970s, J. H. Ostrom (1973, 1976a) argued that birds were direct descendants of small theropod dinosaurs. This theory had far-reaching implications for our view of the history of life; not only did dinosaurs survive the mysterious Cretaceous/Tertiary boundary event, but a particular lineage of theropods is now one of the most successful groups of extant tetrapods. It is therefore rather surprising that, although the first non-avian dinosaur described was a Middle Jurassic theropod (Buckland 1824), the origin and early evolution of this group is still poorly understood.

The Cretaceous theropod fauna exhibits great diversity, and recent research indicates that many Cretaceous lineages probably reach back into Jurassic times (e.g. Sereno 1997). So far, however, there have not been any detailed studies of early theropod evolution, and many influential analyses were mainly based on Cretaceous taxa.

## HISTORICAL REVIEW

In 1824, Buckland described and figured the fossil remains of a gigantic reptile from the Middle Jurassic Stonesfield Slate of Oxfordshire and named them *Megalosaurus*. This was the first non-avian theropod to be named.

The first superfamily taxon created for the animals now known as Theropoda was erected by Cope (1866), who referred *Laelaps aquilunguis* (now *Dryptosaurus*) and *Megalosaurus* to a distinct order within the Dinosauria, which he named Goniopoda.

The name Theropoda was created by Marsh (1881a) to include the family Allosauridae, represented by the genera *Allosaurus*, *Creosaurus* and *Labrosaurus*. In subsequent papers, Marsh (1882, 1884, 1896) elevated Theropoda from the status of a suborder to ordinal status and included the suborders Coeluria and Hallopora. In his 1896 monograph, the order Theropoda included the families Megalosauridae,

Drytosauridae, Labrosauridae, Plateosauridae, Anchisauridae, Coeluridae, Compsognathidae, Ceratosauridae, Ornithomimidae, and Hallopidae (Marsh 1896, pp. 239–241). Thus, Marsh's Theropoda now included animals that are currently considered to be theropods, prosauropods and the genus *Hallopus*, which is now regarded as a crocodile (Walker 1970). Since the Theropoda as defined by Marsh represented a more inclusive systematic concept than Cope's Goniopoda, many subsequent authors adopted this name.

The most important phylogenetic studies of theropod dinosaurs in the first half of the twentieth century were carried out by Huene (1914, 1926a, 1932). Huene regarded the Theropoda as an unnatural group and divided the Saurischia into two suborders: the Coelurosauria and the Pachypodosauria. The Coelurosauria included mainly, but not exclusively, small theropod dinosaurs, while the Pachypodosauria were divided into the Carnosauria and the Sauropodomorpha (Huene 1932). The proposed close relationships between prosauropods and carnosaurs were based on the erroneous association of cranial remains or teeth of carnivorous Triassic archosaurs with prosauropod postcrania (see Galton 1985a, b; Benton 1986). However, although Huene's phylogeny is not supported by recent analyses, his approach was rather modern; his system was based on the assumed relationships of the taxa, rather than on similarities.

Matthew and Brown (1922) proposed a quite different scheme. They rightly excluded the prosauropods from the Theropoda and revived Cope's Goniopoda for the inclusion of the families Megalosauridae, Spinosauridae, Coeluridae, Deinodontidae (= Tyrannosauridae), and Ornithomimidae. They rejected the phylogeny proposed by Huene for the reason that too little was known about the true relationships of saurischian taxa, and based their classification 'upon concrete facts of structural characters' (Matthew and Brown 1922, p. 381). Although Matthew and Brown's concept represented a cautious and rather sound systematic scheme, it did not find many supporters in several of its important conclusions, including the exclusion of the prosauropods from the carnivorous dinosaurs and a preference for the name Goniopoda.

The era between 1939 and the 1960s saw few new advancements in research on theropod palaeontology. Romer (1956) proposed a new classification of saurischians, in which he recognized two suborders within the order Saurischia: the Theropoda and the Sauropoda. Within the Theropoda, three infraorders were distinguished: the Coelurosauria, the Carnosauria, and the Prosauropoda. The theropodan infraorder Prosauropoda was regarded as ancestral to the Sauropoda, and thus paraphyletic.

Abundant new discoveries, new interpretations of old material and new phylogenetic techniques led to rapid progress in our understanding of theropod evolution since the 1960s. Colbert (1964) noticed significant similarities in the pelvis of carnosaurs and coelurosaurs and therefore rejected Huene's (1932) classification, arguing for a monophyletic Theropoda. Within the suborder Theropoda, he distinguished two infraorders: the Coelurosauria, to include all small theropods then known, and the Carnosauria, to include the large taxa. Although this largely size-dependant distinction seems rather arbitrary, both infraorders were believed to be monophyletic by Colbert (1964) and subsequent workers (Charig *et al.* 1965; Romer 1966; Steel 1970). The discovery of the dromaeosaurid *Deinonychus* (Ostrom 1969a, b), which did not seem to fit within either of the two infraorders, and the gigantic, but ornithomimid-like genus *Deinocheirus* (Osmólska and Roniewicz 1969) led to new considerations of theropod systematics (Ostrom 1972). Ostrom (1973, 1976a) also revived the theory of the theropod origin of birds, based on his studies of *Deinonychus*, other small theropods and *Archaeopteryx*. Barsbold (1976a, 1977a) subdivided the Theropoda into six infraorders (Coelurosauria, Deinonychosauria, Oviraptorosauria, Carnosauria, Ornithomimosauria, Deinocheirosauria), but did not specify the relationships between these infraorders in detail.

With the growing acceptance of phylogenetic systematics (Hennig 1966) in palaeontology, the first cladistic analyses of theropod interrelationships were published in the 1980s. Thulborn (1984) was the first to publish a detailed cladistic analysis of proposed theropod interrelationships, in an attempt to resolve the phylogenetic position of *Archaeopteryx*. His results differed radically from older ideas about theropod interrelationships (Text-fig. 1A): the carnivorous families Allosauridae and Tyrannosauridae were widely separated and internested within taxa that were, until then, considered as coelurosaurs. *Archaeopteryx* was not regarded as the most basal bird, but a more basal theropod sharing a considerable amount of

convergences with later birds. However, Thulborn's phylogenetic study received surprisingly little attention.

The pioneering phylogenetic work of Gauthier (1986) had a major impact on our view of theropod phylogeny (Text-fig. 1B). Gauthier recognized a basal dichotomy between a group termed Ceratosauria and a group he named Tetanurae. According to this study, the Ceratosauria included several taxa that were formerly regarded as coelurosaurs, as well as some taxa that were traditionally regarded as carnosaur. Within Tetanurae, Gauthier found another dichotomy between carnosaur and coelurosaurs. Gauthier's Carnosauria included the genera *Allosaurus* and *Acrocanthosaurus* and the family Tyrannosauridae. The ornithomimosaurs were regarded as the most basal coelurosaurs and formed a sister-group to a clade that Gauthier named Maniraptora. Maniraptora included a basal polytomy of several genera and clades, including oviraptorosaurs, the Deinonychosauria (a clade that included dromaeosaurids and troodontids), and birds. The latter two clades were regarded as sister-groups. Gauthier's phylogeny became widely accepted in the following years and it also formed the basis for the theropod phylogeny presented in the influential compendium 'The Dinosauria' (Text-fig. 1C; Weishampel *et al.* 1990).

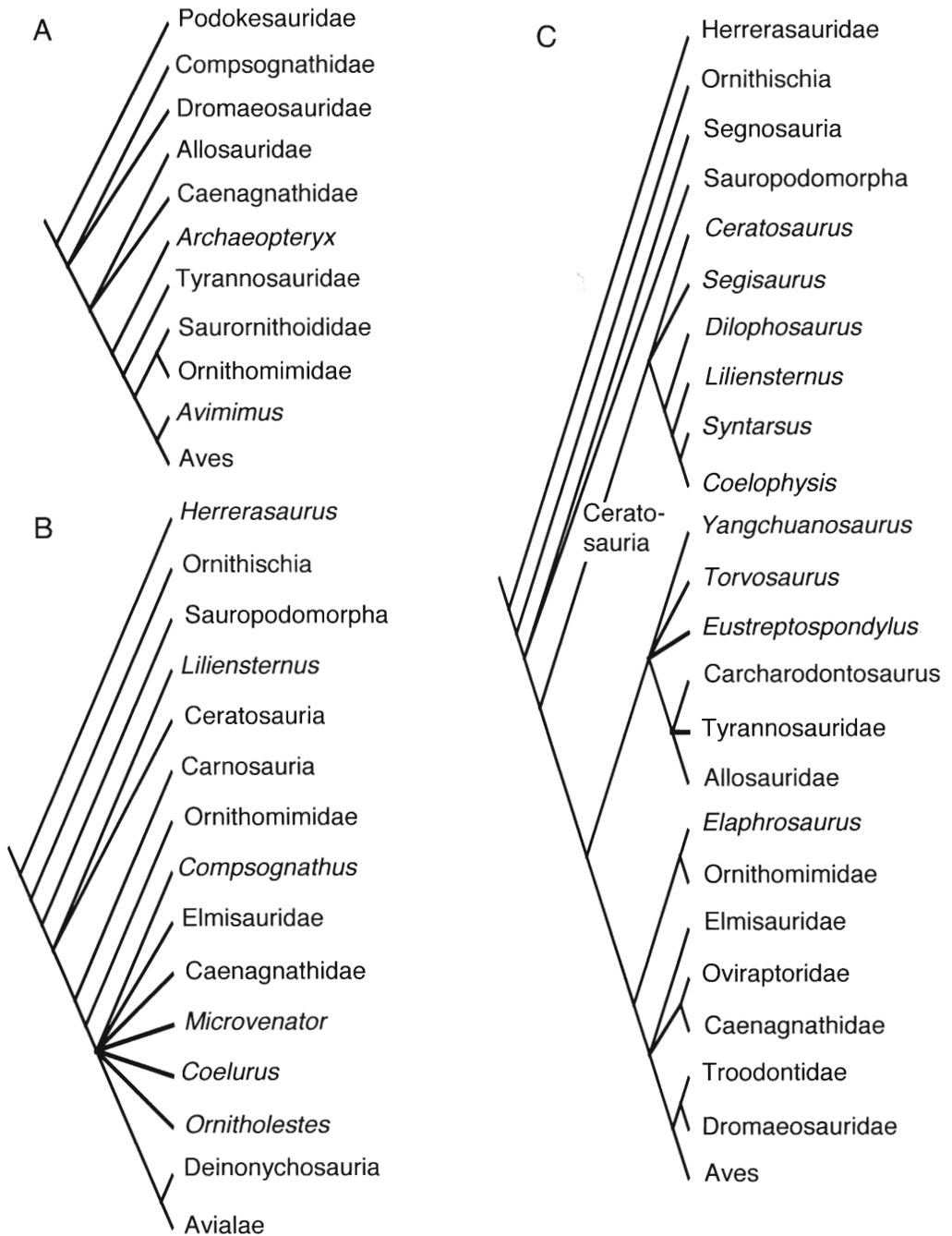
In a new cladistic analysis, Novas (1992a) argued for carnosaur polyphyly and included the tyrannosaurids in the Coelurosauria (Text-fig. 2A). Furthermore, Novas included the abelisaurids in the Ceratosauria, as a sister-group to the genus *Ceratosaurus*. This hypothesis was followed by Pérez-Moreno *et al.* (1993) who, furthermore, argued for a sister-group relationship between tyrannosaurids and ornithomimids.

Another influential analysis was published by Holtz (1994). Like Novas (1992a) and Pérez-Moreno *et al.* (1993), he concluded that tyrannosaurids were members of the Coelurosauria and closely related to ornithomimosaurs (Text-fig. 2B). According to Holtz's analysis, troodontids, ornithomimids, tyrannosaurids, elmsaurids (=caenagnathids), and *Avimimus* formed a monophyletic clade he termed Arctometatarsalia. Within this clade, troodontids formed the sister-group to ornithomimosaurs. Oviraptorids were regarded as the sister-group to Arctometatarsalia, and a bird/dromaeosaurid clade as the sister-group to all of these coelurosaurs. Within the more basal tetanurans, *Torvosaurus*, *Megalosaurus*, and allosaurids were considered as successively more closely related outgroups to coelurosaurs.

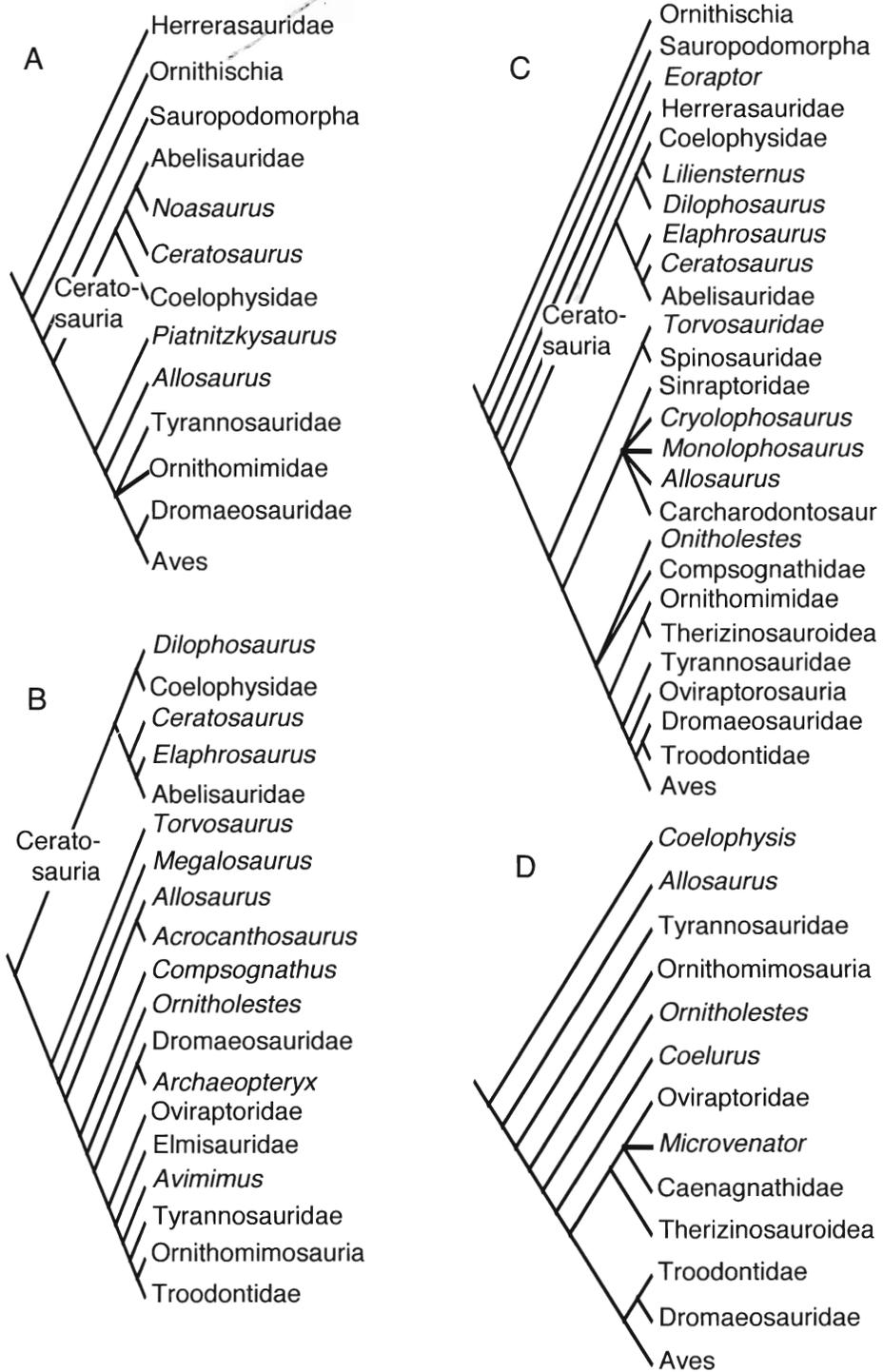
In a more detailed analysis of basal tetanurans, Sereno *et al.* (1996) found two monophyletic clades, the Spinosauroida and the Allosauroida, which formed successively closer outgroups to Coelurosauria. According to this work, Spinosauroida included the Spinosauridae and Torvosauridae, as well as the genus *Afrovenator*, while the Allosauroida included *Cryolophosaurus*, *Monolophosaurus*, *Allosaurus*, the Sinraptoridae and the Carcharodontosauridae. These findings were confirmed in new analyses by Sereno (1997, 1999), who also presented new information on the interrelationships of coelurosaurs (Text-fig. 2C). As in Gauthier's (1986) analysis, Sereno found a monophyletic Deinonychosauria, including troodontids and dromaeosaurids, as a sister-group to birds. Oviraptorosaurs and tyrannosaurids were regarded as successively closer outgroups to this clade, which was termed Paraves by Sereno (1998). An ornithomimosaur/therizinosaur clade was considered as one of the most basal groups of coelurosaurs.

Different phylogenetic hypotheses were published by Russell and Dong (1993a), Sues (1997), Forster *et al.* (1998) and Makovicky and Sues (1998). According to Russell and Dong (1993a), a major dichotomy exists in theropod evolution above ceratosaurs (only represented by *Coelophysus* in their analysis). The first clade of this dichotomy corresponded more or less to Gauthier's Carnosauria and included *Baryonyx*, as the most basal taxon, *Yangchuanosaurus*, *Allosaurus*, tyrannosaurids, and, as a novelty, dromaeosaurids, which were regarded as a sister-group to tyrannosaurids. The second clade consisted of ornithomimids, therizinosaur, troodontids, and oviraptorosaurs. The latter two taxa were regarded as sister-groups, with the other two as successively closer outgroups. Unfortunately, I could not confirm the results of Russell and Dong's analysis in a reanalysis of their data-matrix, using PAUP 3.1.1 and 4.0b.

Sues' (1997) and Makovicky and Sues' (1998) analysis of coelurosaur interrelationships differed from the hypothesis represented by Sereno (1997, 1999) mainly in the placement of therizinosaur and



TEXT-FIG. 1. Early cladistic hypotheses of the phylogeny of theropod dinosaurs. A, phylogenetic hypothesis of Thulborn (1984). B, the influential hypothesis published by Gauthier (1986). C, composite tree based on Weishampel *et al.* (1990).



TEXT-FIG. 2. Recent phylogenetic hypotheses of theropod interrelationships. Note the inclusion of most basal taxa in a monophyletic Ceratosauria in A–C. A, Novas (1992a). B, Holtz (1994). C, Sereno (1997). D, Makovicky and Sues (1998).

ornithomimosaur (Text-fig. 2D). According to these analyses, therizinosaur formed a sister-group to oviraptorosaurs, while ornithomimids were more closely related to birds than tyrannosaurids. The phylogenetic analysis of Forster *et al.* (1998) exhibited the same basic topology as these analyses, but differed from the latter in the placement of troodontids. This clade was found to be more closely related to birds than to dromaeosaurids.

Another important analysis has been published more recently by Holtz (2000). This very extensive analysis included more basal theropod taxa (especially more basal tetanurans) than the previous one (Holtz 1994) and produced some novel results. Spinosaurids, *Megalosaurus*, *Eustreptospondylus*, *Torvosaurus*, *Piatnitzkysaurus*, and *Afrovenator* were found as successively closer outgroups to an allosauroid/coelurosaur clade, the Arctometatarsalia *sensu* Holtz (1994) turned out to be polyphyletic, ornithomimosaur was placed as the sister group of tyrannosaurids, and troodontids had an uncertain phylogenetic position as either the sister group to ornithomimosaur or to a dromaeosaurid/bird clade.

#### OBJECTIVES OF THIS PAPER

As mentioned above, most Triassic and Early Jurassic taxa, plus some Late Jurassic and Cretaceous forms, are usually regarded as representatives of a monophyletic clade named Ceratosauria (Text-figs 1–2). It is rather surprising that the interrelationships of these basal theropods are essentially the same in all the analyses listed above, while the interpretations of coelurosaur interrelationships differ widely. This is reflected in the characters used in the analyses; the characters used to establish ceratosaur monophyly and the interrelationships of ceratosaurian taxa are always those originally proposed by Gauthier (1986), Rowe (1989), and Rowe and Gauthier (1990), whereas characters used for the analysis of the interrelationships of more derived taxa differ widely. However, the definition and distribution of some of the characters used to define Ceratosauria is problematic (see Cuny and Galton 1993 for a critical discussion of proposed ceratosaurian synapomorphies). A further problem for the resolution of basal theropod interrelationships is that most analyses carried out so far concentrate mainly on Cretaceous taxa and/or coelurosaurs. Sereno *et al.* (1996) and Sereno (1997, 1999), included a larger number of Jurassic taxa and basal tetanurans in their analyses. However, Sereno's cladograms only partially reflect the high amount of homoplasy that exists in basal tetanurans, since only characters that constitute synapomorphies at particular nodes were included in the analysis. It should be noted, however, that two other analyses have dealt recently with basal tetanurans in more detail: those of Currie and Carpenter (2000) and Holtz (2000). Whereas the analysis of Currie and Carpenter only concerns minor changes within the Allosauroidae, Holtz' phylogeny differs greatly from those published by Sereno (1997, 1999) in excluding *Eustreptospondylus*, *Torvosaurus* and *Afrovenator* from the Spinosauridae. These conflicting results highlight the need for further investigations into this important part of theropod phylogeny.

Thus, the aim of the present paper is to produce a new cladistic analysis of all theropods, but it is focused on the interrelationships and evolution of the basal members of this clade.

#### MATERIAL AND METHODS

A large number of theropod specimens and fossils of non-theropodan outgroups were examined for the analysis. For a complete list of specimens examined and institutional abbreviations, see the Appendix. Further information was taken from the literature (see also Appendix).

First, the Operational Taxonomic Units (OTUs) were defined, using data from actual specimens and the literature. Questions to be solved included validity of genera and species, and taxonomic contents of supergeneric OTUs. The principal reference work for this taxonomic review is the 1992 paperback edition of the compendium 'The Dinosauria' (Weishampel *et al.* 1990): taxa regarded as *nomina dubia* in the latter work are not discussed here, unless my interpretation differs from that presented there. Taxa not included in the analysis are either regarded as *nomina dubia* (e.g. *Camposaurus*, *Chindesaurus*, *Ozraptor*, *Variraptor*), were not examined personally and published reports are too poor for coding characters (e.g. *Cryolophosaurus*, *Dilophosaurus sinensis*), or overlap completely with other, better-known taxa in all codable characters (e.g. *Megalosaurus bucklandi*, *Piveteausaurus*, *Labocania*, *Dryptosaurus*). *Scipionyx*,

although known from an almost complete and well-preserved specimen (DalSasso and Signore 1998), was not included in the analysis, since the taxon is only known from a very young, presumably hatchling individual. Since almost nothing is known about the ontogeny of theropods, character codings based on such an early ontogenetic stage might be misleading. Taxa described since 1999 are only included in the analysis if they are members of some higher-category clade. A complete review of the taxa concerned is presented in Rauhut (2000). Diagnoses of Operational Taxonomic Units are based on apomorphic characters, unless the OTU is labelled as 'Metataxon'. In the latter case, diagnoses contain differences that distinguish the OTU from other taxa of the same age.

The terminology of pneumatic openings in the skull follows Witmer (1997). In the description of characters of the scapulocoracoid, orientation of the elements is assumed to be horizontal, to simplify the terminology. The real orientation of the elements in the articulated skeleton is oblique; thus, the ventral side, as used here, faces posteroventrally. It might be noted that this is in contrast to Gauthier (1986), who assumed that the scapulocoracoid was oriented vertically. Therefore, posterior in Gauthier's descriptions is the same as ventral in this work. Frequently used anatomical abbreviations are Mc for metacarpal and Mt for metatarsal. In the manus and pes, Roman numbers indicate the number of the digit, while Arabic numbers refer to the number of the phalanx within the digit.

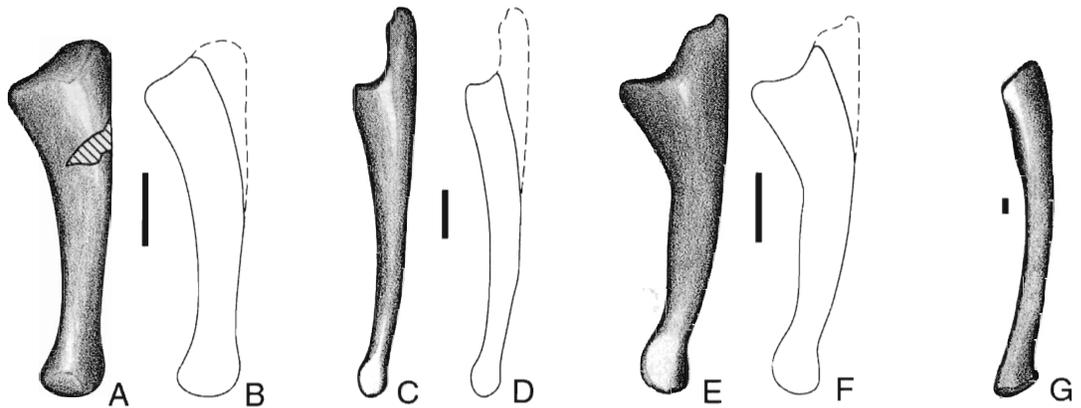
Aside from personal observations, characters were compiled from previous phylogenetic analyses. The most important sources for characters were papers by Welles and Long (1974), Gauthier (1986), Rowe and Gauthier (1990), Molnar *et al.* (1990), Novas (1992a), Russell and Dong (1993a), Holtz (1994), Sereno *et al.* (1996), Sereno (1997), Sues (1997), Harris (1998), and Makovicky and Sues (1998). Many characters have been modified from the original description. In most cases, these modifications only concern phrasing and precision of characters; a discussion of the modifications is only presented if these modifications concern character polarity or essential aspects of the character.

Not all characters used in other analyses were used in the present one. The reasons for not using certain characters are mainly the following:

1. Especially in cases where characters were not discussed, but only listed (e.g. Holtz 1994; Sereno *et al.* 1996), some characters were not understandable, or could not be confirmed in my own examinations of the taxa concerned. An example of this kind of character is the presence of a pterygoid canal (Holtz 1994, character 61). The pterygoid canal is a canal for the palatal artery and the palatal branch of the facial nerve that pierces the basisphenoid, or parasphenoid. According to Kurzanov (1976a, p. 136) this character is only found in the ornithomimosaur *Gallimimus* and the troödontid *Saurornithoides* within dinosaurs. However, Kurzanov also noted that the presence of this feature in *Saurornithoides* needs to be confirmed.

According to Osmólska *et al.* (1972), in *Gallimimus* the palatal artery branches off the internal carotid within a lateral depression of the braincase just above the basiptyergoid processes and pierces the basisphenoid anteriorly to enter the basisphenoid recess through a distinct foramen. Barsbold (1974) noted a foramen in a similar position in the anterior part of the lateral depression of the braincase of *Saurornithoides* below the opening for the internal carotid, and, consequently, interpreted this structure as a foramen for the palatal artery. However, in his description of the braincase of the closely related form *Troödon formosus*, Currie (1985; see also Currie and Zhao 1993a) interpreted this lower foramen as a pneumatic opening leading into the parasphenoid capsule and the interior of the basisphenoid. According to this description, the palatal arch of the facial nerve and the palatal artery left the lateral depression through a ventrally directed groove just behind the basiptyergoid processes (Currie 1985, fig. 5). Since the latter interpretation is in general accordance with the pattern seen in other archosaurs (see e.g. Walker 1990), and there seems to be no foramen for the exit of the palatal artery in both *Saurornithoides* and *Troödon*, Currie's view is supported here. Thus, a pterygoid canal may be present in ornithomimids, but it is probably absent in troödontids. It should be noted, though, that the similar position of the foramen in troödontids and *Gallimimus* might indicate that it also served as a pneumatopore in the latter genus. However, the matter is beyond proof; therefore, the character is not used here.

2. Other characters are difficult to assess, because they are too variable, or frequently obliterated by other anatomical features. An example of this kind of character is 'ulna bowed posteriorly' (Gauthier 1986, character 74). This character has repeatedly been used in phylogenetic analyses of theropod dinosaurs



TEXT-FIG. 3. Ulnae of saurischian dinosaurs, showing the flexure of the shaft of this bone. A, *Plateosaurus* sp. (SMNS F 65), right ulna in lateral view (reversed). B, same as A, but with the olecranon process 'removed' to highlight the flexure of the bone shaft. C, *Syntarsus rhodesiensis* (QG 1), left ulna in lateral view. D, same as C, but with the olecranon process 'removed' to highlight the flexure of the bone shaft. E, *Allosaurus fragilis* (MOR 693), left ulna in lateral view. F, same as E, but with the olecranon process 'removed' to highlight the flexure of the bone shaft. G, *Deinonychus antirrhopus* (YPM 5220), left ulna in lateral view. Scale bars represent 50 mm (A-B, E-F) and 10 mm (C-D, G).

(e.g. Holtz 1994; Sereno *et al.* 1996; Sues 1997; Makovicky and Sues 1998). However, the distribution of this character is much more complex than previously recognized (Text-fig. 3).

Apart from maniraptorans, a bowed ulna has been observed in *Plateosaurus* (e.g. SMNS F 65; Text-fig. 3A-B), *Syntarsus rhodesiensis* (QG 1; Text-fig. 3C-D), and *Allosaurus* (MOR 693; Text-fig. 3E-F), whereas this bone is straight in *Dilophosaurus*, tyrannosaurs, and ornithomimosaurs. In *Liliensternus* (MB R. 2175), one of the preserved ulnae is completely straight, while another is slightly bowed. In many of these taxa, the curvature is not directly obvious, because the posteroproximally bulging olecranon process obliterates it. Thus, the striking curvature of the bone in maniraptorans may be at least partially due to the reduction of the olecranon process (character 144 of the present analysis) in these animals. Since bone curvature in long bones is also highly influenced by function and loading in the living animal (e.g. Lanyon 1980), this character is not used here.

A character used in this analysis that might appear similar to the character discussed above is character 143 [humerus in lateral view: sigmoidal (0) or straight (1)]. However, in this case, this shape depends on the orientation of the articular facets relative to the bone shaft; thus the character is not entirely dependent on the curvature of the shaft of the bone, which might be influenced by function and loading.

3. For similar reasons, fusion characters have been omitted completely. Fusion of elements often depends on the ontogenetic stage of the individual (e.g. Brochu 1996) and might also be variable between individuals of the same age due to mechanical stresses, pathologies, or size variation. Thus, for example, the metatarsals are fused (Holtz 1994, character 7) in the holotype of *Ceratosaurus nasicornis* (USNM 4735), but not in a slightly larger, and thus presumably older, individual from the Cleveland-Lloyd Quarry (UMNH VP 5278).

Despite the objections against the use of continuous (often numerical) characters that have been brought forward by several authors (e.g. Pimentel and Riggins 1987), ratio characters were used in my analysis, since I agree with Rae (1998) that omission of numerical characters results in a considerable loss of information. Multistate characters have been considered as ordered in cases where higher character states unambiguously include lower ones.

Character polarity has not been resolved *a priori*, but is determined by rooting the tree, as outlined by Nixon and Carpenter (1993). However, in the vast majority of characters, state '0' refers to the plesiomorphic character state. Instead of a hypothetical, all-zero ancestor, real outgroups were used to root the tree (Nixon and Carpenter 1993; Bryant 1997).

*Euparkeria* was used as the basal taxon (default outgroup in PAUP), since it represents a well-known basal archosaur that is clearly outside Dinosauria. This was important since one of the questions to be resolved was whether *Herrerasaurus* and *Staurikosaurus* represent basal dinosaurs, outside of the Saurischia-Ornithischia dichotomy (e.g. Benton 1990), or basal theropods (e.g. Sereno and Novas 1992, 1993). More closely related dinosaurian outgroups are either too strongly modified (e.g. basal crurotarsans such as phytosaurs and aëtosurs), their systematic position is uncertain (e.g. pterosaurs: see Padian 1984; Sereno 1991a; Wellnhofer 1991; Bennett 1996, and Unwin 1999, for conflicting views), or their anatomy is too poorly known (e.g. *Scleromochlus* and basal dinosauriforms: Romer 1971, 1972; Bonaparte 1975; Arcucci 1986, 1987; Sereno and Arcucci 1993; Benton 1999) to be of use for outgroup comparison. Only the best represented basal dinosauriform, *Marasuchus lilloensis*, was also included in the analysis as an outgroup (Sereno and Arcucci 1994).

The data matrix was created in MacClade 3.07 (Maddison and Maddison 1992) and analyzed using PAUP 3.1.1 (Swofford 1992) and PAUP 4.0b2a (Swofford 1999). Before the analysis, several taxa were excluded from the data matrix, using the principles of safe taxonomic deletion as outlined by Wilkinson (1995). The trees resulting from the PAUP analyses were reanalyzed using Strict 2.0 (Thorley and Wilkinson 1997) to create reduced consensus trees (Wilkinson 1994).

For the interpretation of character state transformations, the 'tree description' option of PAUP and the 'character tracing' option of MacClade were used. Character transformation was evaluated under both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options of PAUP. While ACCTRAN favours reversals over convergences and assumes character transformation at the lowest possible node if character states are unknown in terminal taxa, DELTRAN favours convergences over reversals and assumes character transformations at the highest possible node.

De Queiroz and Gauthier (1990) proposed a method for phylogenetic definitions of taxon names in a cladogram based on common ancestry, and this method has been applied to theropod phylogeny by several workers (Holtz 1996; Sereno 1998; Padian *et al.* 1999). However, as forcefully argued by Dominguez and Wheeler (1997), the method advocated by De Queiroz and Gauthier (1990) does not result in taxonomic stability, but only in the stability of taxon names; phylogenetically defined taxon names might have completely different taxonomic contents if applied to different cladograms. As pointed out by Dominguez and Wheeler, taxon names should reflect changing views of phylogenetic relationships, and thus applying the same name to widely differing taxonomic units in different phylogenetic hypotheses is undesirable. Dinosauria, for example, has been defined as 'all descendants of the most recent common ancestor of birds and *Triceratops*' (Padian and May 1993, p. 379). If further research should prove that birds are in fact descended from crocodiles, as argued by Walker (1972), or from euparkeriids, as argued by Welman (1995), Dinosauria might include all crown group archosaurs, or an even more inclusive clade under this definition. Although the clade 'Dinosauria' will always be monophyletic, this example highlights that it should not be the sole aim of the systematist to achieve complete stability of a name, regardless of what this name signifies.

Sereno (1998) and Padian *et al.* (1999) gave phylogenetic definitions for all major clades of theropods; unfortunately, however, the definitions are sometimes contradictory, and, if applied to the same cladogram, result in clades with completely different taxonomic contents. Furthermore, if rigorously applied, these definitions sometimes result in taxonomic concepts that are not compatible with the concepts of taxon names as devised by the original author. The name Ceratosauria, for example, was originally proposed by Marsh (1884) to include *Ceratosaurus* and potentially its closest relatives. Sereno (1998, p. 64) defined the Ceratosauria as 'all neotheropods closer to *Coelophysis* than to Neornithes'. Thus, if *Ceratosaurus* is found to be more closely related to Neornithes than to *Coelophysis* in an analysis, the Ceratosauria as defined by Sereno does not include the taxon for which the name was originally created. In summary, the phylogenetic taxonomy as proposed by De Queiroz and Gauthier (1990) can lead to more confusion rather than to stability in classification.

In view of the lack of any consensus in regard to taxonomic systematic procedures, only a few, well-established nodes are named here. The application of names was guided by more traditional criteria ('closeness' to original taxonomic concepts, general acceptance of a group), rather than by node- or stem-based definitions of this group.

## OPERATIONAL TAXONOMIC UNITS

*Outgroups*

*Euparkeria capensis* Broom, 1913

Age. Scythian–Anisian.

Occurrence. *Cynognathus* assemblage zone of the Beaufort Group, South Africa.

Diagnosis. Premaxilla with a vertical, dorsally rounded postnasal process.

Remarks. Ever since its original description (Broom 1913), *Euparkeria* (Text-fig. 4A) has played a pivotal role in the discussion of archosaur interrelationships. Long believed to be ancestral to dinosaurs and sometimes birds (Heilmann 1926; Welman 1995), it is now generally considered to be the sister group of the clade comprising all the recent representatives of Archosauria (see Gower and Wilkinson 1996 and references therein). Because of this basal phylogenetic position, its unspecialized morphology and our relatively complete knowledge of its anatomy, *Euparkeria* is used here as the most basal outgroup to dinosaurs, and it is the taxon used to root the tree.

*Marasuchus lilloensis* (Romer, 1972)

Age. Ladinian.

Occurrence. Los Chañares Formation, La Rioja, Argentina.

Diagnosis. Posterior cervical neural spines project anterodorsally; neural spines of mid- to posterior dorsal vertebrae contact each other dorsally.

Remarks. *Marasuchus lilloensis* is a small carnivorous dinosauriform from the Middle Triassic of South America. The taxon was originally described as a new species of *Lagosuchus* by Romer (1972) and later even synonymized with the type species of the genus, *Lagosuchus talampayensis* (Bonaparte 1975). However, Sereno and Arcucci (1994) argued that the holotype of *Lagosuchus talampayensis* is undiagnostic and consequently referred *Lagosuchus lilloensis* to a new genus, *Marasuchus*.

*Marasuchus* is closely related to dinosaurs (Sereno and Arcucci 1994; Novas 1996a) and is therefore used as an outgroup here.

*Triassic OTUs*

*Coelophysis bauri* (Cope, 1887); metataxon

Age. Norian.

Occurrence. Chinle Formation, Arizona, New Mexico; ?Dockum Group, Texas, USA.

Diagnosis. *Coelophysis* differs from *Eoraptor*, *Herrerasaurus* and *Staurikosaurus* in the presence of pleurocoels in the dorsal vertebrae, the more elongated dorsal vertebrae, five fused sacral vertebrae, dolichoiliac ilium, presence of a small lateral projection on the distal end of the tibia and the functionally tridactyl foot with a Mt I that is attached to Mt II and does not reach the ankle joint. It differs from *Gojirasaurus* in the relatively lower dorsal neural spines and the significantly smaller size, from *Liliensternus* in the absence of a broad ridge that extends from the posterior end of the diapophyses to the posterior end of the vertebral centra in cervical vertebrae and the smaller size, from *Procompsognathus* in the considerably larger overall size, from *Shuvosaurus* in the lack of any of the derived cranial features of the latter taxon, and from the slightly younger, but very similar *Syntarsus* in the lack of a postnasal fenestra.

*Remarks.* In agreement with Colbert *et al.* (1992), the name *Coelophysis bauri* is used here for the common small theropod dinosaur of the Ghost Ranch locality in New Mexico. A problem with the Ghost Ranch material is the variation between individuals. Colbert (1989, 1990) noted many differences between several individuals of *Coelophysis* from this locality and explained them as either ontogenetic differences or sexual dimorphism. Other workers believe that there is more than one species of theropod represented in the material from this locality (Cuny, pers. comm. 1998). Although my own observations of specimens and close inspections of published photographs revealed several differences between different specimens from this locality, these differences seem to be too insignificant to indicate different taxa. Pending a detailed revision of the Ghost Ranch material, it is assumed here that all the material represents a single species, *Coelophysis bauri* (Text-fig. 4F).

*Eoraptor lunensis* Sereno, Forster, Rogers and Monetta, 1993

Age. Carnian.

*Occurrence.* Ischigualasto Formation, San Juan, Argentina.

*Diagnosis.* Strongly heterodont dentition, with leaf-shaped anterior maxillary tooth crowns; ventral process of the postorbital flexed sharply anteriorly in its lower part.

*Remarks.* *Eoraptor* (Text-fig. 4D) is one of the oldest and most primitive dinosaurs known to date, but preliminary cladistic analyses indicate that it is a member of the Theropoda (Sereno *et al.* 1993), although this is not yet generally accepted (Holtz 1995a; Holtz and Padian 1995; Langer 2001). The taxon is represented by two almost complete skeletons (Sereno *et al.* 1993; Sereno, pers. comm. 1997), and a detailed description of its anatomy is presently under way by P. Sereno.

*Gojirasaurus quayi* Carpenter, 1997; metataxon

Age. Norian.

*Occurrence.* Cooper Canyon Formation of the Dockum Group, New Mexico, USA.

*Diagnosis.* Differs from *Coelophysis* and *Liliensternus* in the greater relative height of the neural spines of the mid to posterior dorsals; from *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus* in the elongation of the dorsal vertebrae and the presence of a small lateral projection on the distal end of the tibia; and from *Procompsognathus* in the significantly larger overall size. There are no elements that can be compared with known remains of *Shuvosaurus* (see comments below).

*Remarks.* The holotype material of *Gojirasaurus* was first described as 'procompsognathid indet.' by Parrish and Carpenter (1986), and only later designated as the holotype of a new taxon of theropod (Carpenter 1997).

The presence of a premaxilla of the edentulous theropod *Shuvosaurus* in the same quarry as the type of *Gojirasaurus* is interesting (Parrish and Carpenter 1986, fig. 11.8; Carpenter 1997). The holotype skull of *Shuvosaurus* is approximately 17 cm long (Chatterjee 1993), but represents a juvenile individual, indicating that adult *Shuvosaurus* would have been among the largest known Triassic theropods. Since the holotype of *Gojirasaurus* represents the largest theropod postcrania known from the Triassic of North America (Carpenter 1997), it seems quite possible that *Gojirasaurus quayi* Carpenter, 1997, might be a junior synonym of *Shuvosaurus inexpectatus* Chatterjee, 1993. However, given the uncertain association of the remains, and the lack of comparable elements in the holotype specimens, both taxa are treated separately here.

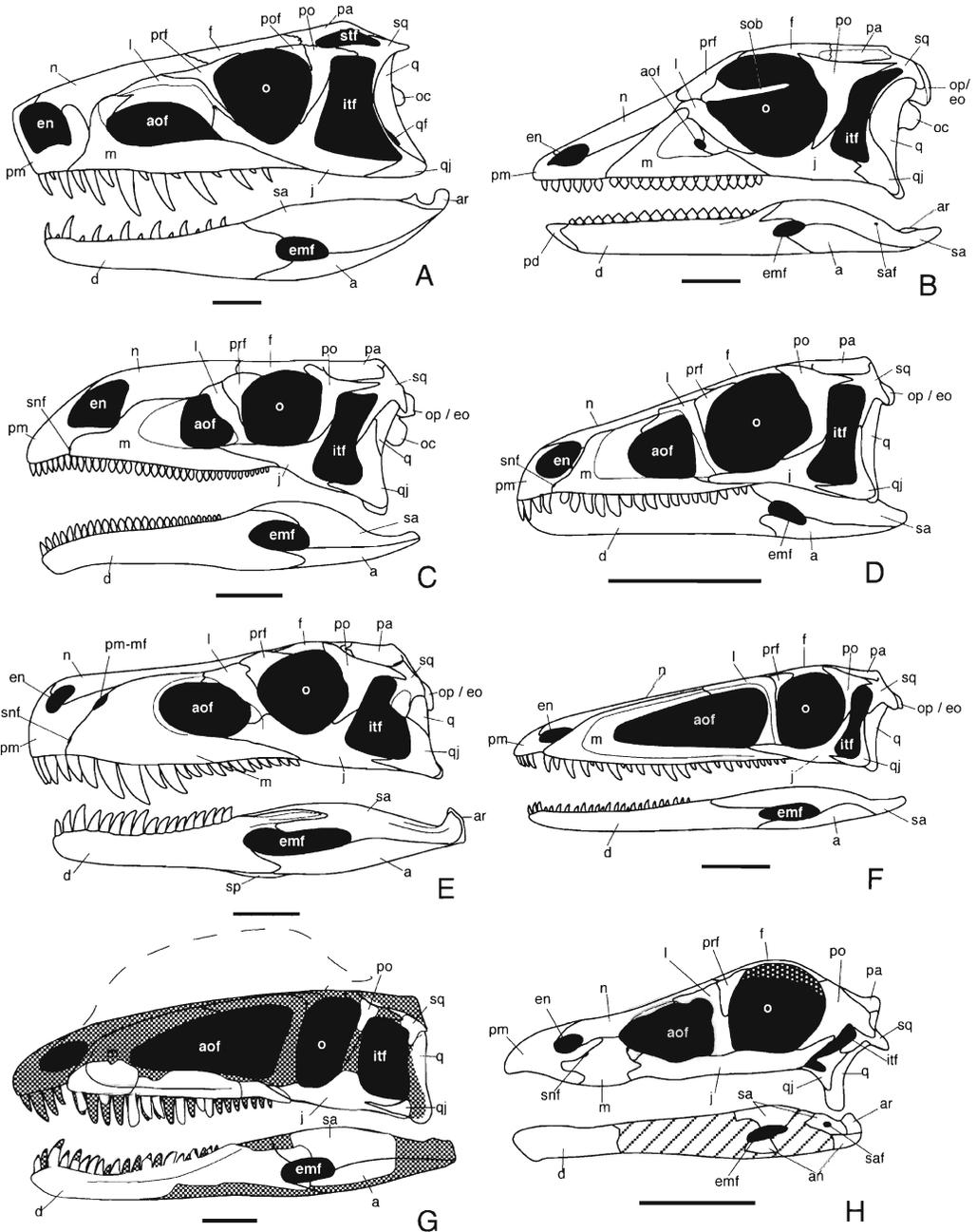
*Herrerasaurus ischigualastensis* Reig, 1963

Age. Carnian.

*Occurrence.* Ischigualasto Formation, San Juan, Argentina.

**Diagnosis.** Large premaxillary-maxillary fenestra; dorsal part of supratemporal fenestra less than half as wide as ventral part; pronounced suborbital ridge on the jugal; lateral depression on quadratojugal process of squamosal; very slender posterior dorsal process of the dentary.

**Remarks.** In 1963, Reig described three taxa of saurischian dinosaurs from the Ischigualasto Formation of Argentina as *Herrerasaurus ischigualastensis*, *Ischisaurus cattoi*, and *Triassoolestes romeri*. *Herrerasaurus*



(Text-fig. 4E) received relatively little attention until the discovery of a complete skeleton in the late 1980s (Serenó and Novas 1992). The osteology of this taxon was described in detail in a series of papers by Novas (1993), Sereno (1993) and Sereno and Novas (1993). The type specimens of *Ischisaurus* and *Triassoolestes*, and other theropod specimens from the Ischigualasto Formation described as *Freguellsaurus ischigualastensis* by Novas (1986), and cf. *Staurikosaurus* sp. by Brinkman and Sues (1987), respectively, were referred to *Herrerasaurus ischigualastensis* (Novas 1993).

*Liliensternus airelensis* Cuny and Galton, 1993

Age. Rhaetian–Hettangian.

Occurrence. Moon-Airel Formation, Normandy, France.

**Diagnosis.** Cervical vertebrae with dorsoventrally narrow, anteroposteriorly elongated posterior pleurocoel; deep infradiapophyseal fossa in anterior cervical vertebrae; horizontal ridge at the basis of the neural spine in cervical vertebrae; ilium with a triangular lateral bulge above the supraacetabular crest.

**Remarks.** Larssonneur and Lapparent (1966) described associated and partially articulated remains of a theropod dinosaur from the Moon-Airel Formation of Normandy and referred them to *Halticosaurus* sp., based on comparisons with *Halticosaurus liliiensterni* (now *Liliensternus liliiensterni*) from the Norian of Germany. The material received little attention in the following decades, until Cuny and Galton (1993) redescribed it and showed that it represents a distinct taxon. They designated the specimen as the holotype of a new species of the genus *Liliensternus*, *Liliensternus airelensis*. Although the material is very incomplete, the rather large number of apomorphic characters in the cervical vertebrae alone clearly establishes it as a valid taxon.

*Liliensternus liliiensterni* (Huene, 1934); metataxon

Age. Norian.

Occurrence. Knollenmergel, Thüringen and Württemberg, Germany; ?Frick, Switzerland.

**Diagnosis.** Differs from all other theropods, with the exception of *Liliensternus airelensis*, in the presence of a broad rounded ridge on the cervical vertebrae that extends from the posterior end of the diapophyses to the posteroventral end of the vertebral centrum (less well-developed than in *Liliensternus airelensis*).

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TEXT-FIG. 4. Skull reconstructions of representatives of Triassic OTUs in left lateral view. A, *Euparkeria capensis*, Early Triassic (Scythian–Anisian), Beaufort Group, South Africa; redrawn from Ewer (1965). B, basal ornithischian *Lesothosaurus diagnosticus*, Early Jurassic (Hettangian–Sinemurian), Elliot Formation, Lesotho; redrawn from Sereno (1991b). C, prosauropod sauropodomorph *Plateosaurus* sp., Late Triassic (Norian), Knollenmergel, Germany; based on MB R. 1937. D, *Eoraptor lunensis*, Late Triassic (Carnian), Ischigualasto Formation, Argentina; based on PVSJ 512. E, *Herrerasaurus ischigualastensis*, Late Triassic (Carnian), Ischigualasto Formation, Argentina; redrawn from Sereno and Novas (1993). F, *Coelophysis bauri*, Late Triassic (Norian), Chinle Formation, south-western USA; modified from Paul (1993). G, *Liliensternus liliiensterni*, Late Triassic (Norian), Knollenmergel, Germany; based on MB R. 2175, unpreserved elements shaded. H, *Shuvosaurus inexpectatus*, Late Triassic (Norian), Dockum Group, Texas, USA; based on TTU P 9280. Abbreviations: a, angular; aof, antorbital fenestra; d, dentary; emf, external mandibular fenestra; en, external nares; eo, exoccipital; f, frontal; itf, infratemporal fenestra; j, jugal; l, lacrimal; m, maxilla; n, nasal; o, orbit; oc, occipital condyle; op, opisthotic; pa, parietal; pd, predentary; pm, premaxilla; pm-mf, premaxillary-maxillary fenestra; po, postorbital; pof, postfrontal; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; saf, surangular foramen; snf, subnarial foramen; sob, supraorbital; soc, supraoccipital; sp, splenial; sq, squamosal; stf, supratemporal fenestra. Scale bars represent 10 mm (A–B) and 50 mm (C–H).

Differs from *Liliensternus airelensis* in the presence of only one pair of pleurocoels in the cervical vertebrae, the less-developed infradiapophyseal fossa, the absence of a horizontal ridge at the base of the cervical neural spines, and the absence of a lateral bulge on the ilium.

*Remarks.* *Liliensternus liliensterni* (Text-fig. 4G) is the best represented Triassic theropod from Europe. The taxon was originally described as *Halticosaurus liliensterni* by Huene (1934) based on the associated, but disarticulated remains of two individuals from the Knollenmergel of Thüringen (MB R. 2175). Later, Welles (1984) showed that *Halticosaurus liliensterni* cannot be referred to the genus *Halticosaurus* and assigned the species to the new genus *Liliensternus*. Welles (1984, p.166) also designated the larger individual as the lectotype. It must be noted, however, that the material may represent more than two individuals, and it seems almost impossible to separate the remains belonging to the larger and smaller individual (pers. obs. and Heinrich, pers. comm. 1996); therefore it seems, at present, best to retain the entire material as the syntypes for the species.

### Ornithischia Seeley, 1887

*Included taxa.* *Lesothosaurus*, *Technosaurus*, *Pisanosaurus*, Thyreophora, Ornithopoda, and Marginocephalia, and all dinosaurs that are more closely related to these taxa than to saurischians.

*Temporal range.* Carnian–Maastrichtian.

*Distribution.* Global.

*Diagnosis.* Ossified palpebral over the orbit; presence of an unpaired predentary; maxillary and dentary tooth crowns triangular in lateral view; ossified epaxial tendons along the neural spines; ilium with elongate, dorsoventrally low preacetabular process; opisthopubic pelvis; pubic shafts slender, rod-like.

*Remarks.* Seeley (1887, 1888) first noted the fundamental differences in the pelvic girdles of different taxa of dinosaurs, and referred all the opisthopubic members then known to a clade he named Ornithischia, in reference to the opisthopubic condition of the pelvis in birds. Whereas the monophyly of the other major group of dinosaurs, the Saurischia, has repeatedly been doubted (e.g. Charig *et al.* 1965; Bakker and Galton 1974; Bakker 1986), the Ornithischia were generally accepted as a monophyletic group, even after the discovery of nonavian theropod dinosaurs with an opisthopubic pelvis (Barsbold 1979).

The monophyly of the Ornithischia is supported by a large number of synapomorphies (Serenó 1986), many of which are in some way related to the herbivorous diet of all known members of this clade. Following Sereno (1986, 1991b, 1997), *Lesothosaurus* (Text-fig. 4B) and basal Thyreophora (*Scutellosaurus*, *Scelidosaurus*, *Emausaurus*) are regarded here as some of the most basal taxa of ornithischians, and most character codings are based on these animals.

### *Procompsognathus triassicus* Fraas, 1913; metataxon

*Age.* Norian.

*Occurrence.* Weißer Steinbruch, Pfaffenhofen, Baden-Württemberg, Germany; Middle Stubensandstein of the middle Keuper.

*Diagnosis.* Small theropod; differs from the contemporaneous *Liliensternus liliensterni* in the overall size and the greater elongation of the posterior dorsal vertebral centra. Differences from the contemporaneous taxon *Coelophysis* are difficult to establish due to the inadequate preservation of the type specimen and the probable close relationships of these two taxa. However, the distal hindlimb elements are slightly more elongated in *Procompsognathus triassicus* than in any specimen of *Coelophysis* measured by Colbert (1989), although this might be size-related (Holtz 1995b), and the scapular blade seems to be wider in the latter taxon. Furthermore, even if the holotype is a juvenile individual, adult *P. triassicus* probably were of

slightly smaller average size than *Coelophysis*. *Procompsognathus* differs from herrerasaurids in the presence of pleurocoels in the cervical vertebrae, the much more elongated posterior dorsal vertebrae, the elongated distal hindlimb elements, and attachment of Mt I to the shaft of Mt II and not reaching the ankle joint proximally. The genus differs from *Alwalkeria maleriensis* in the more elongated dorsal vertebrae and the shorter femoral neck. Differences from *Liliensternus airelensis* are again found in the more elongated posterior dorsal vertebrae of *P. triassicus* and the significantly larger size of the former taxon.

*Remarks.* *Procompsognathus triassicus* was named by Fraas (1913) on the basis of ‘. . . the major part of an extremely delicate dinosaur skeleton, including the skull, the middle part of the body with the legs and the anterior part of the tail’ (p. 1099; my translation). In 1992, Sereno and Wild reviewed the type material and argued that the skull and the postcranial skeleton represent different animals. Thus, the name *Procompsognathus* is used here only for the partial postcranial skeleton (see Rauhut and Hungerbühler 2000).

#### Sauropodomorpha Huene, 1932

*Included taxa.* *Saturnalia*, prosauropods, sauropods, and all dinosaurs that are more closely related to these taxa than to theropods.

*Temporal range.* Carnian–Maastrichtian.

*Distribution.* Global.

*Diagnosis.* Relatively small skull (about 5 per cent of body length); lanceolate teeth with coarsely serrated crowns; at least ten elongate cervical vertebrae; very large pollex with enlarged unguis; fused, deep, apron-like pubes that are twisted proximally.

*Remarks.* Huene (1932) proposed the Sauropodomorpha to include those members of the Saurischia that are more closely related to the Sauropoda than to the Carnosauria. In his phylogenetic scheme, sauropodomorphs and carnosaurs were grouped together as Pachypodosauria and seen as the sister group to coelurosaurs. The supposedly close relationships between carnosaurs and prosauropods was based on the association of remains of certainly carnivorous archosaurs (see e.g. Huene 1932). Although they accepted the association of cranial remains of carnivorous archosaurs and prosauropod-like postcrania, Colbert (1964) and Charig *et al.* (1965) argued that coelurosaurs and carnosaurs formed a monophyletic Theropoda and concluded that all prosauropods were more closely related to the Sauropoda than to the Theropoda. This view has since been accepted and was supported by more recent cladistic analyses (Gauthier 1986; Benton 1990). Galton (1985*a, b*) and Benton (1986) argued that the association of cranial remains of carnivorous archosaurs with prosauropod postcrania is either erroneous or not demonstrable, and Galton (1985*b*) made a strong argument that all prosauropods for which clearly referable cranial material is known were herbivorous.

The interrelationships of taxa within Sauropodomorpha are still problematic. While the monophyly of the Sauropoda is generally accepted (Gauthier 1986; Benton 1990; Upchurch 1995, 1998; Wilson and Sereno 1998), the relationships between basal taxa are poorly understood. Sereno (1989), Galton (1990), and Upchurch (1995) argued for a monophyletic Prosauropoda to include all known basal forms, whereas Benton (1990) regarded prosauropods as paraphyletic. A solution to this problem will have to come from a more detailed analysis of basal sauropodomorph relationships.

The character codings in this analysis are mainly based on the Late Triassic taxon *Plateosaurus* (Text-fig. 4c), with additional information taken from *Thecodontosaurus*, *Sellosaurus*, and *Massospondylus*. Sauropodomorphs form the immediate outgroup to theropods, but they are also an important terminal taxon in this analysis in the light of the problematical phylogenetic position of *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus*.

*Shuvosaurus inexpectatus* Chatterjee, 1993

Age. Norian.

*Occurrence.* Cooper Canyon Formation of the Dockum Group, Texas and New Mexico, USA.

*Diagnosis.* Maxilla block-like, strongly reduced in length and almost entirely excluded from the ventral rim of the antorbital fenestra; nasal forms the dorsal rim of the internal antorbital fenestra anteriorly; jugal elongated underneath the antorbital fenestra and forms a peg-and-socket articulation with the maxilla anteriorly; jugal without posterior quadratojugal process; quadratojugal with two anterior process, which subdivide the infratemporal fenestra in a smaller ventral and a larger dorsal part; postorbital with broad posterior process, overlapping the anterior end of the squamosal; dentary with medial platform anteriorly.

*Remarks.* *Shuvosaurus* is one of the most bizarre of supposed theropods described recently (Text-fig. 4H). The taxon is based on a fairly well-preserved skull of a juvenile individual, to which additional skull elements and a few postcranial bones were referred (Chatterjee 1993). However, only the cranial parts that show some overlap with the holotype are accepted here as belonging to this taxon, since all the material came from the Post Quarry in the Dockum Group of Texas, which has yielded hundreds of specimens of all kinds of Triassic vertebrates (e.g. Chatterjee 1985, 1991, 1993; Long and Murry 1995), and thus the association of isolated postcranial material is rather questionable.

The genus was originally referred to the Ornithomimosauria by Chatterjee (1993). Long and Murry (1995) tentatively referred the holotype skull of *Shuvosaurus* to the genus *Chatterjeea*, a taxon of a possible poposaurian archosaur they named from the same locality. The reasons for this referral were the matching size of the specimens, the comparable preservation, and the lack of other cranial material that could have been referred to the otherwise common crurotarsan (Long and Murry 1995, p. 162). However, *Shuvosaurus* is radically different from all known crurotarsans in skull morphology (see e.g. Walker 1964; Krebs 1976; Chatterjee 1985; Parrish 1993; Long and Murry 1995), including the edentulous crurotarsan archosaur *Lotosaurus* (Zhang 1975; pers. obs. of a mounted skeleton in the IVPP). Rauhut (1997) presented a new reconstruction of the skull (Text-fig. 4H) and listed the following characters in favour of dinosaurian, saurischian, and theropodan affinities for *Shuvosaurus*: lack of postfrontal (convergent in crocodiles), paroccipital processes directed ventrolaterally rather than laterally or dorsolaterally as in other archosaurs, lacrimal elongated dorsoventrally and in the shape of an inverted L, presence of a deep basisphenoid recess, and possibly the presence of a deep ventral recess in the ectopterygoid (the identification of this element is questionable). Therefore, *Shuvosaurus* is included in the analysis here, although the highly apomorphic cranial morphology of this taxon makes it difficult to establish its theropod affinities beyond doubt, unless more material becomes available. As noted above, it might be possible that *Gojirasaurus* represents a junior synonym of *Shuvosaurus*.

*Staurikosaurus pricei* Colbert, 1970

Age. Carnian.

*Occurrence.* Santa Maria Formation, Rio Grande del Sul, Brazil.

*Diagnosis.* Postacetabular process of ilium abbreviated and straight posteriorly; pubic boot confluent with pubic shafts posteriorly; distal end of tibia roughly circular in outline.

*Remarks.* *Staurikosaurus* was described by Colbert (1970) on the basis of an incomplete skeleton from the Santa Maria Formation of Brazil. The material was redescribed by Galton (1977). The taxon has variously been regarded as a close relative of *Herrerasaurus*, and included in the same family with this taxon (Benedetto 1973; Gauthier 1986; Novas 1989, 1992b), or as a more remotely related basal dinosaur (Galton 1977; Brinkman and Sues 1987; Benton 1990; Sues 1990).

*Jurassic OTUs**Dilophosaurus wetherilli* (Welles, 1954)

Age. ?Sinemurian–Pliensbachian.

Occurrence. Kayenta Formation, Arizona, USA.

Diagnosis. Lacrimal with thickened dorsoposterior rim; cervical neural spines with a distinct central ‘cap’ and an anterior and posterior ‘shoulder’; scapular blade with squared distal expansion.

Remarks. *Dilophosaurus wetherilli* (Text-fig. 5A) was originally described as a new species of *Megalosaurus* by Welles in 1954, but it was not until 1984 that a detailed description of the holotype was published (Welles 1984). The most striking feature of the skull are the two large, very thin cranial crests, best preserved in a so-far undescribed skull (UCMP V6468). However, since similar crests have been reported for *Syntarsus* (Rowe 1989) and another species from the Lower Jurassic of China [based on the presence of these crests, this species was originally referred to the genus *Dilophosaurus* as *D. sinensis* (Hu 1993), but this referral has recently been doubted (Lamanna *et al.* 1998)], this character cannot be used to define the genus or species, but *D. wetherilli* shows enough other apomorphies to establish it as a valid genus and species.

*Segisaurus halli* Camp, 1936

Age. ?Sinemurian–Pliensbachian.

Occurrence. Navajo Sandstone, Arizona, USA.

Diagnosis. Large oval foramen in the pubic process of the ischium.

Remarks. Although the holotype and only known specimen of *Segisaurus halli* is rather fragmentary, the species is certainly valid, and has been of considerable interest since it contains the first clavicle that was described in any theropod dinosaur (Camp 1936).

*Syntarsus* Raath, 1969

Included taxa. *Syntarsus kayentakatae* Rowe, 1989; *Syntarsus rhodesiensis* Raath, 1969.

Temporal range. ?Hettangian–Pliensbachian.

Occurrence. Kayenta Formation, Arizona, USA; Forest Sandstone, Matabeleland, Zimbabwe; Upper Elliot Formation, Cape Province, South Africa.

Diagnosis. Presence of a postnasal fenestra between nasal, prefrontal, and frontal.

Remarks. *Syntarsus* (Text-fig. 5B) is among the best-represented taxa of theropod dinosaur. Both species are known from more than 15 specimens (Rowe and Gauthier 1990), but, unfortunately, only the holotypes of the species have been described in detail so far (Raath 1969; Rowe 1989). Since its original description, *Syntarsus* has been regarded as a close relative of the Triassic North American theropod *Coelophysis* (e.g. Raath 1969; Colbert 1989), and has sometimes even been synonymized with the latter genus (Paul 1988a, 1993). However, according to Colbert (1989), *Coelophysis* lacks the postnasal fenestra, a character that is diagnostic for *Syntarsus*. Given this morphological disparity, the stratigraphical difference, and the fact that *Coelophysis* must be regarded as a metataxon (Padian 1986), it seems best to retain them as different genera.

*Magnosaurus* Huene, 1932

*Included taxa.* *Magnosaurus nethercombensis* (Huene, 1923); *Magnosaurus oxoniensis* (Walker, 1964).

*Temporal range.* Bajocian–Callovian.

*Occurrence.* Inferior Oolite, Dorset; Middle Oxford Clay, Oxfordshire, England.

*Diagnosis.* Lateral nutrient foramina placed in a shallow longitudinal groove with a subrectangular cross-section on posterior part of dentary; squamosal with lateral flange on the rim of the infratemporal fenestra.

*Remarks.* The taxon *Magnosaurus nethercombensis* was originally described by Huene (1923, see also Huene 1926a) as a new species of *Megalosaurus*, based on a pair of dentaries and fragmentary associated postcrania from the Bajocian of Dorset. *Magnosaurus oxoniensis* is based on a partial skull (Text-fig. 5c) and postcranial skeleton from the Callovian Oxford Clay of Oxfordshire, which was named *Eustreptospondylus oxoniensis* by Walker (1964).

Although comparisons are limited by the fragmentary nature of the remains of *Magnosaurus nethercombensis*, this taxon and *Eustreptospondylus oxoniensis* share several characters unseen in other Middle Jurassic theropods, including a slight dorsoventral and transverse expansion of the anterior part of the dentary, the presence of a significantly enlarged third dentary tooth, and the probable synapomorphy of a shallow, longitudinal groove with a rectangular cross-section on the dentary. Since all the other skeletal elements preserved in both species are, furthermore, almost indistinguishable, *Eustreptospondylus oxoniensis* Walker, 1964, can be referred to the genus *Magnosaurus* Huene, 1932. The stratigraphical separation of the two type specimens, and slight differences in the proximal extent of the pubic apron indicate that *M. nethercombensis* and *M. oxoniensis* should be tentatively regarded as different species. Since all character codings are identical in the two species, they can be treated as a single OTU.

*Monolophosaurus jiangi* Zhao and Currie, 1993

*Age.* Middle Jurassic.

*Occurrence.* Wucuiwan Formation, Xinjiang, China.

*Diagnosis.* Large midline crest on skull, formed by the premaxillae, nasals, lacrimals and anterior ends of the frontals.

*Remarks.* *Monolophosaurus* is the only theropod from the Middle Jurassic of China for which good skull material is known (Text-fig. 5d; Zhao and Currie 1993). Although its major apomorphic character is the presence of the unusual medial crest on the skull, the postcranium is sufficiently different from that of the probable contemporaneous taxa *Gasosaurus*, '*Szechuanosaurus*' *zigongensis*, and *Xuanhanosaurus* to establish it as a separate genus beyond any reasonable doubt.

*Piatnitzkysaurus floresi* Bonaparte, 1979

*Age.* Callovian.

*Occurrence.* Cañadón Asfalto Formation, Chubut, Argentina.

*Diagnosis.* Basis of the ascending process of the maxilla strongly inflated.

*Remarks.* *Piatnitzkysaurus* is based on two associated partial skeletons from the upper Middle Jurassic of Patagonia, described by Bonaparte (1979, 1986). Being the only Middle Jurassic theropod from the Southern Hemisphere known from good skeletal material, it is of great phylogenetic and biogeographic interest.

*Poekilopleuron bucklandii* Eudes-Deslongchamps, 1838

Age. Bathonian.

*Occurrence.* Calcaire de Caen, Calvados, France.

*Diagnosis.* Radius with elongated medial process on the midshaft; metacarpal I with small lateral flange behind distal articular facet.

*Remarks.* *Poekilopleuron* was the first theropod that was described on the basis of associated material, although much of the skeleton had unfortunately been destroyed by erosion prior to collection (Eudes-Deslongchamps 1838). The species is based on a partial postcranial skeleton, including caudal vertebrae, ribs, and limb elements. All of the material was destroyed in an allied air raid on Caen in 1944.

Huene (1926a, 1932) argued that both the manus and the pes of *Poekilopleuron* retained five digits (as also shown in Eudes-Deslongchamps' reconstruction of the manus; 1838, pl. 7, fig. 27). Unfortunately, the element that Huene considered to be a fifth metacarpal has never been figured nor described in detail, and is now lost, as is the rest of the material. However, the fact that no known theropod retains a fifth digit makes me doubt this interpretation. The same applies to the pes.

*Proceratosaurus bradleyi* (Woodward, 1910)

Age. Bathonian.

*Occurrence.* Great Oolite at Minchinhampton, Gloucestershire, England.

*Diagnosis.* Ascending process of premaxilla overhangs the alveolar border of this bone; external nares enlarged, subequal in length to internal antorbital fenestra, and with squared anterior end; horn-core or medial crest on the nasals, starting at approximately mid-length of the nares.

*Remarks.* This species is based on a partial skull from the Great Oolite of England, originally described as *Megalosaurus bradleyi* by Woodward (1910). Huene (1926a) removed the species from the genus *Megalosaurus* and proposed the new genus *Proceratosaurus*. As indicated by the name, Huene believed this taxon to be a close relative of the Upper Jurassic genus *Ceratosaurus*, based on the presence of a dorsal projection on the anterior end of the nasals, the only part of the skull roof preserved. However, the position of this projection is unlike that of the horn core in *Ceratosaurus*, and, because of the incompleteness of the skull roof, it cannot be determined if it represents a nasal horn, or a median cranial crest.

'*Szechuanosaurus*' *zigongensis* Gao, 1993; metataxon

Age. Bathonian–Callovian.

*Occurrence.* Xiashaxiamo Formation, Sichuan, China.

*Diagnosis.* Differs from *Gasosaurus* and *Xuanhanosaurus* in the more rectangular deltopectoral crest and the proximal part of the humerus being less expanded transversely; from *Monolophosaurus* and *Eustreptospondylus* in the gradually sloping anterior rim of the maxilla and the lack of opisthocoelous cervical vertebrae; from *Piatnitzkysaurus* in the gradually sloping anterior rim of the maxilla and the less expanded proximal humerus; from *Iliosuchus* in the lack of a vertical ridge on the ilium; from *Poekilopleuron* in the more strongly pronounced olecranon process of the ulna and the lack of a medial process on the radius; from *Metriacanthosaurus* in the less steeply sloping posterodorsal rim of the ilium; from *Proceratosaurus* in the more massive and relatively shorter posterior part of the maxilla. There are no elements preserved that overlap with *Megalosaurus* or *Piveteausaurus*.

*Remarks.* ‘*Szechuanosaurus*’ *zigongensis* is one of five theropod taxa described from the Xiashaxiamo Formation of China. However, two of these taxa, *Chuangongocoelurus primitivus* and *Kaijiangosaurus lini*, are here regarded as *nomina dubia*, and there seem to be sufficient differences between ‘*S.*’ *zigongensis* and *Gasosaurus* and *Xuanhanosaurus* to regard the former species as a tentatively valid metataxon. It should be noted, however, that the discovery of more material might prove ‘*S.*’ *zigongensis* to be a junior synonym of *Xuanhanosaurus qilixiaensis*, since these two taxa are very similar in all comparable elements with the exception of the humerus.

It is rather unclear why ‘*Szechuanosaurus*’ *zigongensis* has been referred to the considerably younger genus *Szechuanosaurus*. The type material of this genus is not diagnostic, and the material referred to the type species by Dong *et al.* (1983) differs significantly from the type skeleton of ‘*S.*’ *zigongensis*. Thus, the latter species should be removed from *Szechuanosaurus*.

*Xuanhanosaurus qilixiaensis* Dong, 1984

Age. Bathonian–Callovian.

*Occurrence.* Xiashaximiao Formation, Sichuan, China.

*Diagnosis.* Glenoid articular facet of humerus forms a raised horizontal ridge that overhangs the humeral shaft posteriorly.

*Remarks.* *Xuanhanosaurus* is based on fragmentary material from the Middle Jurassic of the Xiashaxiamo Formation of China (Dong 1984). However, the specimen is remarkable since it includes one of the best preserved forelimbs for any Middle Jurassic theropod. Despite the fragmentary nature of the holotype, it seems to be clearly different from all other Middle Jurassic theropods with the possible exception of ‘*Szechuanosaurus*’ *zigongensis*. Apart from the possible autapomorphy given in the diagnosis, the most striking character of *Xuanhanosaurus* is the very robust humerus which has strongly expanded proximal and distal ends and is reminiscent of the humeri in *Torvosaurus* (Galton and Jensen 1979) and baryonychids (MNN GDF 500, BMNH R 9951; Charig and Milner 1997). A further similarity to these taxa is the very strongly keeled anterior dorsal vertebrae.

Some comments on the anatomy of the animal might be added. The element identified as a sternum by Dong (1984, fig. 2) is a part of the right coracoid that is only preserved as an impression in the sediment. Thus the coracoid is much larger than figured by Dong and it is high oval in shape, with a moderate, rounded ventral process anteriorly.

In contrast to a statement by Molnar (1990, p. 317), carpal and phalangeal joints of the manus do not differ significantly from those of other theropods. An enlarged distal carpal overlaps the proximal ends of metacarpal I and parts of metacarpal II, and although this carpal does not show a semilunate morphology, its shape and development is comparable with other basal tetanurans like *Afrovenator*. In particular the distal articular end of metacarpal II indicates that a great degree of extension and flexion was possible at the basis of the second digit. Whereas metacarpal I is closely appressed to the basal half of metacarpal II, phalanx I-1 is directed slightly medially, indicating that the first digit was somewhat opposable, as in many other theropods (e.g. Galton 1971). Unfortunately, the phalanges and metacarpals are in articulation and the manus is still contained within a slab of matrix, so that no detailed analysis of the morphology can be carried out. The ungual of the first digit is unusual for theropod manual unguals in being rather broad and not very strongly curved. However, despite the robustness of the forelimb, it seems rather unlikely that it was used in locomotion as argued by Dong (1984), since the humerus is rather short when compared to the size of the vertebrae.

*Allosaurus* Marsh, 1877

*Included taxa.* *Allosaurus fragilis* Marsh, 1877; *Allosaurus maximus* (Chure, 1995); *Allosaurus* sp. nov. (to be described by D. Chure).

*Temporal range.* Kimmeridgian–Tithonian.

*Occurrence.* Morrison Formation, Wyoming, Utah, Colorado, New Mexico, South Dakota, Oklahoma, all USA; Lourinhã Formation, Portugal.

*Diagnosis.* Distinct ‘step’ in the ventral margin of the jugal, leading to a significant ventral displacement of the posterior part in relation to the anterior part; neomorph element present in lower jaw (antarticular in Madsen 1976); well-developed notch in the anteroventral margin of the prearticular.

*Remarks.* Although it is one of the best known and best represented of theropod dinosaurs, the taxonomy of *Allosaurus* (Text-fig. 5E) is problematic. Originally described by Marsh (1877) on the basis of rather poor material, it was later often synonymized with the genus *Antrodemus* (e.g. Gilmore 1920), but Madsen (1976) argued that the latter taxon represents a *nomen dubium*. This view is followed here. Another matter of debate is the number and taxonomy of the species included in the genus *Allosaurus*. Pending a detailed revision of the genus, I recognize three different species within the genus: *Allosaurus fragilis*, which is the most common large theropod of the Late Jurassic Morrison Formation; *Allosaurus maximus*, which is based on the remains of at least two individuals of a very large theropod from the Morrison Formation of Oklahoma that differ in some anatomical details from *A. fragilis* (Chure 1995; Smith 1998), and a new, undescribed species from Dinosaur National Monument, which exhibits all the synapomorphies of the genus, but differs from both of the other species in several morphological details (Chure, pers. comm. 1998).

Aves Linnaeus, 1758

*Definition.* Following Padian and Chiappe (1998), and in contrast to Gauthier (1986), Aves are defined here with their fossil stem-group representatives included. Thus, Aves may be defined as *Archaeopteryx* and Neornithes, and all descendants of their most recent common ancestor.

*Temporal range.* Tithonian–Recent.

*Distribution.* Global.

*Diagnosis.* Asymmetric, aerodynamic contour feathers; humerus longer than femur; radius longer than humerus.

*Remarks.* Birds are the only living group of dinosaurs. More than 9000 extant species of birds are known, and our knowledge of their fossil history is increasing rapidly. In 1960, Brodkorb estimated the total number of bird species that have existed as more than 1.5 million; of course, such estimates are rather speculative, but they might give an idea of the disparity in taxonomic diversity between this OTU and others.

Unfortunately, improved knowledge of the anatomy of advanced theropods and the discovery of connecting links has made a formal diagnosis of Aves increasingly difficult, since the acquisition of avian characters in theropod evolution was gradual. The matter is further complicated by the high diversity of birds; the characters listed in the diagnosis above are lost in many avian lineages, and the first reversals might have occurred soon after the origin of this group (see Chiappe 1995; Chiappe *et al.* 1996; Padian and Chiappe 1998). However, it is assumed here that flight arose only once in birds, and it is the main diagnostic feature of this group, as expressed by aerodynamic feathers and forelimb proportions. Following Chiappe *et al.* (1996) and Novas (1996b), alvarezsaurids are regarded here as basal birds (see Sereno 1999, for an alternative view) and are thus not treated as a separate OTU.

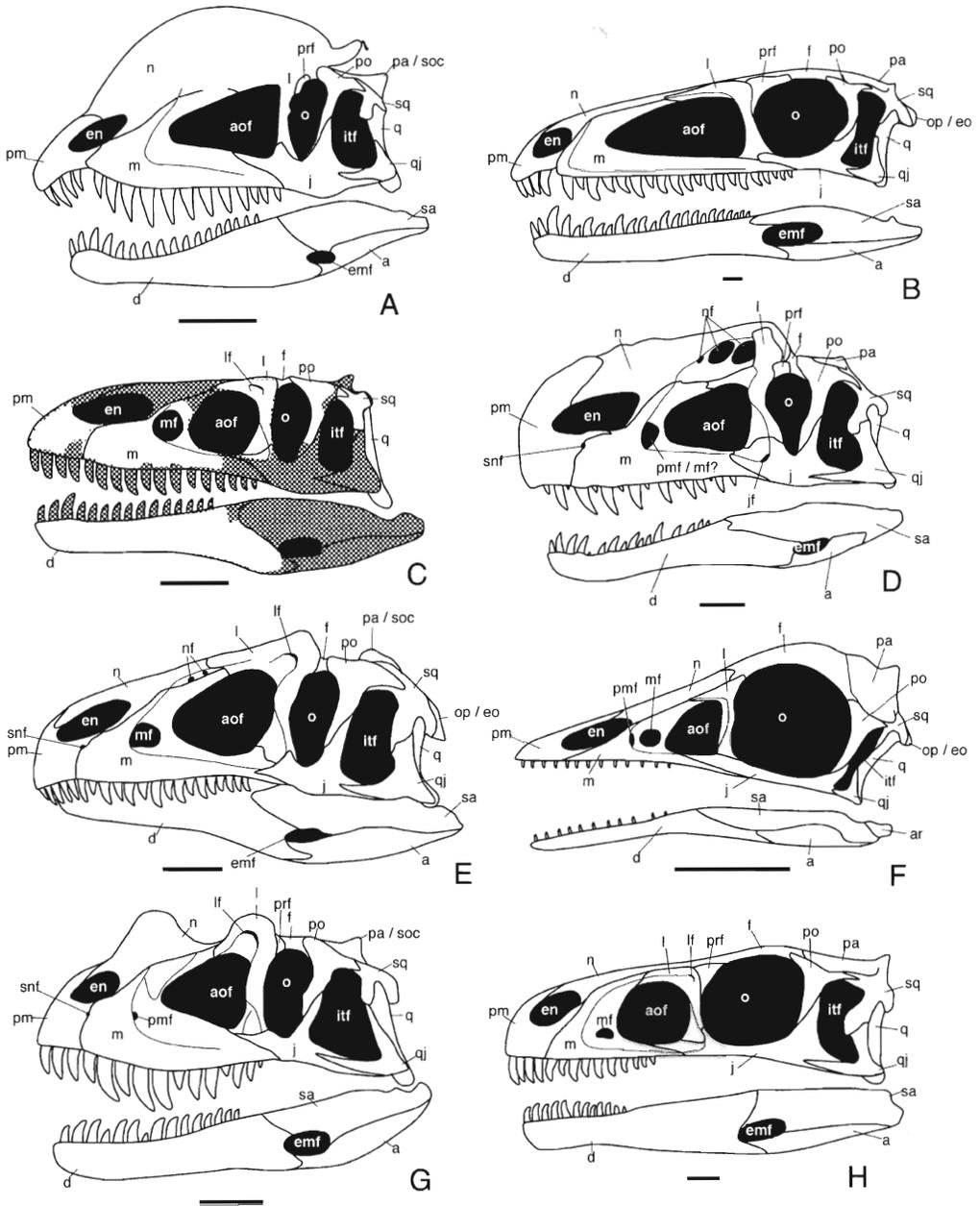
Since *Archaeopteryx* (Text-fig. 5F) is the most basal bird (Chiappe 1995), character codings are mainly based on this taxon; only if character states cannot be determined in *Archaeopteryx* is information from other basal birds used, mainly *Rahonavis* (UA 8656; Forster *et al.* 1998), *Confuciusornis* (GPIT, JM, three unnumbered specimens), *Hesperornis*, and *Ichthyornis* (Marsh 1880; Elzanowski 1991).

*Ceratosaurus nasicornis* Marsh, 1884

Age. Kimmeridgian–Tithonian.

*Occurrence.* Morrison Formation, Utah, Colorado, USA.

*Diagnosis.* Narrow rounded horn core centrally placed on the fused nasals; median oval groove on nasals behind horn core; pubis with large, rounded notch underneath the obturator foramen; small epaxial osteoderms.



*Remarks.* *Ceratosaurus* (Text-fig. 5G) certainly represents one of the more distinctive theropods of the Morrison Formation. The taxon long remained enigmatic, but the recent description of two new specimens by Madsen and Welles (2000) has greatly improved our knowledge of the anatomy of this genus, hitherto only known from the type specimen (Marsh 1884, 1892, 1896; Hay 1908; Gilmore 1920). However, the referral by Madsen and Welles (2000) of these new specimens to two new species, *C. dentisulcatus* and *C. magnicornis* is not accepted here, since the differences used to distinguish them are subjective (e.g. relative ‘massiveness’) or size-related and most probably lie within the individual variation of a single species.

*Coelurus fragilis* Marsh, 1879

Age. Kimmeridgian–Tithonian.

*Occurrence.* Morrison Formation, Wyoming, Utah, USA.

*Diagnosis.* Cervical vertebrae with one or two small, slit-like pneumatic foramina above the parapophyses; pubic boot almost half as long as pubic shafts and strongly convex ventrally.

*Remarks.* The species *Coelurus fragilis* was first described by Marsh (1879) on the basis of several vertebrae from Quarry 13 of the Como Bluff outcrop area of the Morrison Formation of Wyoming. The same author later (1884) erected a new species, *Coelurus agilis*, on the basis of mainly limb and girdle elements from the same quarry. Marsh (1881*b*, 1896) furthermore referred material from Quarries 9 and 12 to the same genus (see Ostrom 1980, pp. 255–256, for a list of the material).

Gilmore (1920, pp. 127–129) revised the original material referred to *Coelurus fragilis* and *Coelurus agilis* by Marsh. He synonymized *Ornitholestes* with *Coelurus fragilis*, which was subsequently accepted by many authors (e.g. Romer 1956, 1966; Steel 1970). The first detailed taxonomic review of *Coelurus* since Gilmore’s (1920) paper was carried out by Ostrom (1980), who made a strong case that all the material from Quarry 13 represented a single individual, and thus that *Coelurus agilis* Marsh, 1884 is a junior objective synonym of *Coelurus fragilis* Marsh, 1879*b*. He furthermore showed that *Coelurus* is quite different from *Ornitholestes* and must thus be regarded as a valid taxon. This view has been widely accepted, and it is followed here.

*Compsognathus longipes* Wagner, 1861

Age. ?Kimmeridgian–Early Tithonian.

*Occurrence.* Solnhofener Plattenkalk, Bavaria, Germany; Lithographic limestones of Canjuers, Var, France; ?Alcobaca Formation, Leiria, Portugal.

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TEXT-FIG. 5. Skull reconstructions of representatives of Jurassic OTUs in left lateral view. A, *Dilophosaurus wetherilli*, Early Jurassic (Sinemurian–Pliensbachian), Kayenta Formation, Arizona, USA; based on UCMP V 4214 and V 6468. B, *Syntarsus rhodesiensis*, Early Jurassic (Hettangian–Sinemurian), Forest Sandstone, Zimbabwe; composite reconstruction based on many isolated skull elements from the National Museum of Natural History in Harare (see Appendix). C, *Magnosaurus oxoniensis*, Middle Jurassic (Callovian), Oxford Clay, England; based on OUM J 13558, unpreserved elements shaded. D, *Monolophosaurus jiangi*, Middle Jurassic, Wucaiwan Formation, China; redrawn from Zhao and Currie (1993*b*). E, *Allosaurus fragilis*, Late Jurassic (Kimmeridgian–Tithonian), Morrison Formation, USA; based on MOR 693. F, basal bird *Archaeopteryx* sp., Late Jurassic (Tithonian), lithographic limestones of Solnhofen, Germany; based on Wellnhofer (1974), Elzanowski and Wellnhofer (1996), and the Berlin, Eichstätt, and Munich specimens. G, *Ceratosaurus* sp., Late Jurassic (Kimmeridgian–Tithonian), Morrison Formation, USA; based on USNM 4735 and UMNH VP 5278. H, *Ornitholestes hermanni*, Late Jurassic (Kimmeridgian–Tithonian), Morrison Formation, USA, based on AMNH 619. Abbreviations as in Text-figure 4, and: lf, lacrimal fenestra; mf, maxillary fenestra; nf, nasal foramen; pmf, promaxillary fenestra. Scale bars represent 10 mm (B, F, H), 50 mm (C) and 100 mm (A, D, E, G).

*Diagnosis.* Posterior half of the premaxilla edentulous, resulting in a diastema between the premaxillary and maxillary teeth; premaxillary and anterior dentary teeth with rounded, inflated base, lacking serrations and carinae, and abruptly recurved in their upper third.

*Remarks.* *Compsognathus longipes*, originally described as a new genus and species of lizard (Wagner 1861), was the first theropod dinosaur known from a reasonably well-preserved, articulated skeleton. The species is of great historical importance because of the role it played in the initial discussion about evolution (Desmond 1982). It is, therefore, not surprising that many well-known vertebrate palaeontologists have commented on the specimen (e.g. Cope 1867; Huxley 1868; Marsh 1881a, 1895, 1896; Huene 1925, 1926a, 1932; Stromer 1934a). However, it was not until 1978 that a detailed description of the specimen was published (Ostrom 1978).

In 1972, Bidar *et al.* described a new, slightly larger specimen of *Compsognathus* from the lithographic limestones of Canjuers, and made it the type of a new species, *C. corallestris*. However, Ostrom (1978) argued strongly that *C. corallestris* was only a larger, probably more mature individual of *C. longipes*. Recently, Zinke (1998) described isolated teeth from the Alcobaça Formation of Portugal which might be referable to that taxon, although they are slightly older (Kimmeridgian) than the other two specimens (Early Tithonian).

*Elaphrosaurus bambergi* Janensch, 1920

Age. Kimmeridgian.

*Occurrence.* Middle Dinosaur beds, Tendaguru, Tanzania.

*Diagnosis.* Cervical vertebrae with thin lateroventral laminae bordering the posterior pleurocoel ventrally; cervical vertebrae strongly concave ventrally, the ventral margin arching above the mid-height of the anterior articular facet at its highest point; scapular blade broader than height of vertebral column; brevis fossa of ilium extremely widened so that the brevis shelf forms an almost horizontal lateral flange.

*Remarks.* *Elaphrosaurus bambergi* is known from a partial postcranial skeleton from the famous dinosaur beds of Tendaguru, Tanzania. It was first described briefly by Janensch in 1920, followed by a detailed description in 1925 and some additional notes on its anatomy in 1929. In the latter paper, Janensch referred previously unrecognized ribs and pectoral girdle elements, as well as an isolated left radius to the same species. Since the ribs and pectoral girdle are from the type locality and probably even from the type specimen, their referral is accepted here. The radius, however, came from another locality in the Upper Dinosaur beds, while the holotype is from the slightly older Middle Dinosaur beds. Since the radius is, furthermore, not preserved in the type, the element from the Upper Dinosaur beds (MB R. 1755) cannot be shown to belong to *Elaphrosaurus* with any certainty.

Nopcsa (1928) first referred *Elaphrosaurus bambergi* to the Ornithomimidae, a view that became widely accepted in the 1970s–1980s (Russell 1972; Russell *et al.* 1980; Galton 1982; Barsbold and Osmólska 1990; Smith and Galton 1990). However, the ornithomimid status of *Elaphrosaurus* has recently been questioned by several authors (Paul 1988a; Holtz 1994; Sereno 1997; Rauhut 1998), who argued for close relationships with more basal taxa. Therefore, *E. bambergi* is treated separately here.

*Ornitholestes hermanni* Osborn, 1903

Age. Kimmeridgian–Tithonian.

*Occurrence.* Morrison Formation, Wyoming, Utah, Colorado, USA.

*Diagnosis.* Premaxillary teeth massive, larger than maxillary teeth, with distally flattened tip, and without serrations; articular facet of quadrate subrectangular in outline; retroarticular processes offset medially from lateral margin of mandible.

*Remarks.* *Ornitholestes* (Text-fig. 5H) is the only small theropod dinosaur from the Morrison Formation that is represented by a fairly complete skeleton and is, therefore, of considerable interest. The original material comprises a crushed skull and partial postcranium (Osborn 1903, 1916). A partial articulated manus from the same locality was referred to the same taxon (Osborn 1903), although this referral is questionable (Holtz 2000, pers. comm. 2001). It is rather surprising that no detailed description of the material has been published so far. Fortunately, the type skull (AMNH 619) has recently been reprepared, so that many important cranial characters are visible now for the first time.

Paul (1988*a, b*) argued for a close relationship between *Ornitholestes* and *Proceratosaurus*, and reconstructed the skull of the former taxon with a nasal horn. My observations of the type specimen of *Ornitholestes* (AMNH 619) revealed little evidence for the presence of such a structure; the apparent upward flexure of the posterior border of the external nares on the left side of the skull is caused by a break and subsequent ventral displacement of the ascending process of the maxilla and the nasals.

#### Sinraptoridae Currie and Zhao, 1993*b*

*Included taxa.* *Sinraptor dongi* Currie and Zhao, 1993*b*; *Sinraptor hepingensis* (Gao, 1992); *Yangchuanosaurus magnus* Dong, Zhou and Zhang, 1983; *Yangchuanosaurus shangyouensis* Dong, Chang, Li and Zhou, 1978.

*Temporal range.* Late Jurassic.

*Occurrence.* Shishugou Formation, Xinjiang, China; Shangshaxiamiao Formation, Sichuan, China.

*Diagnosis.* Promaxillary foramen enlarged and larger than maxillary foramen; large, deep excavatio pneumatica in the ascending process of the maxilla, enclosing one or several pneumatic openings; a further synapomorphy of sinraptorids may be the presence of a medial posterior prong in the jugal; the existence of this prong is known in *S. dongi*, but its presence cannot be confirmed in the other species because these taxa are based on articulated skulls.

*Remarks.* Although all of the taxa included in the Sinraptoridae have been described as separate species, their morphology seems to be almost identical, as far as can be judged from published accounts (Dong *et al.* 1983; Gao 1992; Currie and Zhao 1993*b*). Since both species of *Yangchuanosaurus* are also from the same formation, it seems possible that all the specimens represent only one species. The differences between *Sinraptor dongi* and *Sinraptor hepingensis* listed by Currie and Zhao (1993*b*, p. 2039) are very slight and probably lie within the limits of individual variation. However, since I have not examined this material, all described species are provisionally retained as valid taxa, pending a revision of the Sinraptoridae. Given that all character codings within sinraptorids are identical, they are treated as one operational unit.

#### *Stokesosaurus clevelandi* Madsen, 1974; metataxon

*Age.* Kimmeridgian–Tithonian.

*Occurrence.* Morrison Formation, Utah, USA.

*Diagnosis.* Differs from all other Late Jurassic theropods in the presence of a sharply defined vertical ridge on the ilium above the acetabulum.

*Remarks.* Although *Stokesosaurus clevelandi* is based only on an isolated ilium from the Cleveland Lloyd Quarry in the Morrison Formation of Utah (Madsen 1974), the specimen is distinct from all other Jurassic theropods. In the original description, Madsen (1974) also referred a premaxilla to the same species, and just recently, Chure and Madsen (1998) described a braincase from the type locality as ?*Stokesosaurus*. Although the braincase in particular may well be referable to *Stokesosaurus*, this assignment is not accepted here, since there is no information about the association of these remains, and the Cleveland

Lloyd Quarry has yielded thousands of theropod bones of at least four different species (Chure and Madsen 1998).

Despite its fragmentary nature, *Stokesosaurus clevelandi* is of considerable interest since the type ilium and referred ilia (Madsen 1974) show many similarities to tyrannosaurids, a group that is otherwise only known from the Cretaceous. Therefore, *Stokesosaurus* is included in the analysis, although only a few characters can be coded for this taxon.

*Torvosaurus tanneri* Galton and Jensen, 1979

Age. Kimmeridgian–Tithonian.

Occurrence. Morrison Formation, Colorado, ?Wyoming, ?Utah, USA.

Diagnosis. Opisthocoelous cervical vertebrae with a pronounced flat rim around the anterior ball; fenestra in neural arch of dorsal vertebrae in front of hyposphene.

Remarks. *Torvosaurus* is one of the most recent species to be recognized as a distinct taxon of theropod dinosaur from the Late Jurassic Morrison Formation. The original type material included the long bones of a left and right forelimb from the Dry Mesa Quarry of western Colorado to which a dentary and a variety of postcranial elements from the same locality were referred (Galton and Jensen 1979). More material from the same quarry was referred to *Torvosaurus* by Jensen (1985) and Britt (1991). Britt (1991, p. 10) noted that the elements of the type were not found in association and designated the left humerus as the lectotype. The species *Edmarka rex*, described on the basis of fragmentary material from the Morrison Formation of Wyoming (Bakker *et al.* 1992), probably represents a junior synonym of *Torvosaurus* (Sues, pers. comm. 1998).

*Genera and species from the Lower Cretaceous*

*Afrovenator abakensis* Sereno, Wilson, Larsson, Dutheil and Sues, 1994

Age. Pre-Aptian Early Cretaceous (?Barremian).

Occurrence. Tiouaren Formation, northern Niger.

Diagnosis. Third cervical vertebra with a low, rectangular, almost axis-like neural spine; metacarpal I with broad flange for articulation against Mc II.

Remarks. *Afrovenator abakensis* is one of the very few theropods from the Cretaceous of Africa known from an associated skeleton, including parts of the skull and all regions of the postcranial skeleton, and is, therefore, of considerable interest. Its very generalized, basal tetanuran morphology makes a formal diagnosis based on apomorphic characters difficult. However, the species is clearly different from all other theropods described, and the few possible autapomorphies listed above indicate that it is not a metataxon.

*Caudipteryx zoui* Ji, Currie, Norell and Ji, 1998

Age. Barremian.

Occurrence. Jiulongsong Member of the Chaomidianzi Formation, Liaoning, China.

Diagnosis. Elongate, hooked premaxillary teeth; teeth only present in the premaxilla.

Remarks. *Caudipteryx* is one of the most important theropod dinosaurs to be described recently (Ji *et al.* 1998). It is especially noteworthy for the preserved feathers along its arms and at the tip of the tail, since

the animal clearly represents a non-avian theropod. Together with the filaments in *Sinosauropteryx*, *Beipiaosaurus*, and *Sinornithosaurus*, and the feathers in *Protarchaeopteryx*, *Caudipteryx* provides clear evidence for the presence of feathers in non-avian coelurosaurs and thus greatly strengthens the arguments for the theropod origin of birds.

*Chilantaisaurus tashuikouensis* Hu, 1964

Age. Aptian–?Albian.

*Occurrence.* Unnamed unit, Nei Mongol Zizhiqu, China.

*Diagnosis.* Humerus with distally placed, subrectangular, pterosaur-like deltopectoral crest.

*Remarks.* *Chilantaisaurus tashuikouensis* is based on a partial postcranial skeleton, including elements of both the fore- and hindlimbs, from the Lower Cretaceous of China (Hu 1964). In the original description, Hu (1964) described two species of *Chilantaisaurus*, based on non-comparable material. However, it seems very unlikely that both species belong to the same genus (Chure 1998; see below). Since *C. tashuikouensis* is the first-described taxon in the original paper, it is designated as the type species of the genus here.

The species *Allosaurus sibiricus* Riabinin, 1914 has also been referred to the genus *Chilantaisaurus* (Molnar *et al.* 1990). However, this species is only based on an *Allosaurus*-like metatarsal that is specifically and generically indeterminate, and should, therefore, be regarded as a *nomen dubium*.

'*Chilantaisaurus*' *maortuensis* Hu, 1964

Age. Aptian/Albian.

*Occurrence.* Unnamed unit, Nei Mongol Zizhiqu, China.

*Diagnosis.* Maxilla very high underneath the antorbital fenestra; medial crest on the fused frontals; caudal vertebrae with a small, deep depression underneath the transverse process.

*Remarks.* '*Chilantaisaurus*' *maortuensis* is based on an incomplete skull, an axis and several caudal vertebrae (Hu 1964). The material comes from a different locality and slightly lower horizon than *C. tashuikouensis*. The two species were referred to the same genus because of similarities in the teeth and caudal vertebrae (Hu 1964, p. 63). However, the teeth of '*C.*' *maortuensis* do not differ significantly from teeth of other theropods, such as *Afrovator* and *Torvosaurus*, and the teeth referred to *C. tashuikouensis* cannot be shown to belong to this taxon with any certainty. Three vertebrae in the collections of the IVPP bear the same specimen number (IVPP V 2884) as the holotype of *C. tashuikouensis*. One of them shows the same depressions underneath the transverse process as found in '*C.*' *maortuensis*; however, this specimen is much too small to belong to the gigantic holotype of *C. tashuikouensis*. The two other vertebrae are the right size, but they are very unlike the vertebrae of '*C.*' *maortuensis*, and one of them seems to represent a sauropod rather than a theropod. Furthermore, the holotype of '*C.*' *maortuensis* represents a considerably smaller animal than that of *C. tashuikouensis*, although the intensive fusion of some of the skull bones (frontals, braincase) indicates that it represents an adult individual. Thus, it seems very unlikely that both species can be referred to the same genus and a new generic name for '*C.*' *maortuensis* will be proposed in a forthcoming publication by D. Chure.

Compsognathinae indet. SMNK 2349 Pal

Age. ?Albian.

*Occurrence.* Santana Formation, Pernambuco, Brazil.

*Remarks.* The specimen SMNK 2349 Pal represents a three-dimensionally preserved partial skeleton, including dorsal and sacral vertebrae, most of the pelvis and parts of the hindlimb, of a generically and specifically indeterminate small theropod dinosaur from the Lower Cretaceous of Brazil (Martill *et al.* 2000). The pelvis and dorsal vertebrae show great similarities to those of *Compsognathus*, suggesting that SMNK 2349 Pal represents a closely related taxon. Since all other closely related species are so far only known from compressed, rather two-dimensionally preserved lithographic limestone specimens (Wagner 1861; Bidar *et al.* 1972; Chen *et al.* 1998), SMNK 2349 Pal might provide important additional anatomical information for these animals, and thus it is included as a separate OTU in this analysis.

*Ligabueino andesi* Bonaparte, 1996 \

Age. Hauterivian.

*Occurrence.* La Amarga Formation, Neuquén, Argentina.

*Diagnosis.* Femur with a deep longitudinal groove on its anterior side, below the lesser trochanter.

*Remarks.* *Ligabueino*, known from only a few postcranial elements (Bonaparte 1996), is one of the smallest known theropods, with a femur length of 61 mm. The articular surfaces of the femur are well formed, and the neural arch of a caudal vertebra is fused with the centrum without any visible suture, indicating that the holotype does not represent a hatchling or very young individual. Despite the fragmentary nature of the type material, it is thus of great potential interest, being one of the few small theropods known from the Cretaceous of Gondwana. The morphology of the ilium, and especially the greater and lesser trochanters on the femur, indicate that it is a non-avian theropod.

*Microvenator celer* Ostrom, 1970

Age. Aptian–Albian.

*Occurrence.* Cloverly Formation, Montana and Wyoming, USA.

*Diagnosis.* Cervical neural arches without neural spines; cervical vertebral centra with two pairs of pleurocoels, the posterior pair being significantly smaller than the anterior pair, slightly dorsal to them and located at the midlength of the centrum.

*Remarks.* *Microvenator* is an enigmatic small theropod, so far only known from the holotype (Ostrom 1970; Makovicky and Sues 1998). The taxon was originally referred to the Coeluridae by Ostrom (1970), but recently Makovicky and Sues (1998) made a strong case for *Microvenator* to represent one of the oldest known oviraptorosaurs. Unfortunately, not much is known of the skull of this taxon, with the exception of some rather uninformative fragments (Makovicky and Sues 1998). Since the diagnosis of Oviraptorosauria, as presented here, is mainly based on cranial characters, *M. celer* is treated as a distinct taxon.

*Neovenator salerii* Hutt, Martill and Barker, 1996

Age. Barremian.

*Occurrence.* Wessex Formation, Isle of Wight, England.

*Diagnosis.* Nares trapezoidal and very large; pila interfenestralis very thin, rod-like; pedal unguals with longitudinal groove on the dorsal surface.

*Remarks.* *Neovenator* is the only theropod from the famous English Wealden deposits of the Isle of Wight that is represented by good skeletal material, but unfortunately, only a preliminary description of its anatomy has been published so far (Hutt *et al.* 1996), although some new illustrations have been published very recently (Naish *et al.* 2001).

*Siamotyrannus isanensis* Buffetaut, Suteethorn and Tong, 1996

*Age.* Neocomian.

*Occurrence.* Sao Khu Formation, Phu Wiang, Thailand.

*Diagnosis.* Two parallel vertical ridges on iliac blade above and in front of the acetabulum; ischial peduncle of pubis with ventral flange, forming the posterior and most of the ventral rim of the obturator foramen, which is open ventrally anteriorly.

*Remarks.* *Siamotyrannus* is the only large theropod known from the Lower Cretaceous of south-east Asia. In the original description it was referred to the Tyrannosauridae by Buffetaut *et al.* (1996), but the species shows several primitive characters and lacks any of the tyrannosaurid synapomorphies used to define the group here, so it is treated as a separate OTU.

*Sinosauropteryx prima* Ji and Ji, 1996

*Age.* Barremian.

*Occurrence.* Yixian Formation, Liaoning, China.

*Diagnosis.* Tail with more caudal vertebrae (64) than any other known theropod; ungual of the first manual digit subequal in length to radius.

*Remarks.* *Sinosauropteryx* is known from three articulated specimens from the Early Cretaceous Yixian Formation of China. Unfortunately, the bone preservation is rather poor, so many anatomical details cannot be seen. However, the taxon is of great interest since it preserves integumentary structures that may be proto-feathers (Chen *et al.* 1998; Unwin 1998). Thus, its systematic position is of importance, because it might indicate when an insulatory body cover evolved in theropods.

#### *Genera and species from the Upper Cretaceous*

*Avimimus portentosus* Kurzanov, 1981

*Age.* Santonian–Campanian.

*Occurrence.* Djadochtan Svita, Omnogov, Ovorkhangai, Mongolia.

*Diagnosis.* Pleurocoels in mid-cervical vertebrae on mid-length of vertebral centrum, behind the parapophyses; ectepicondyle of humerus significantly expanded anteroposteriorly.

*Remarks.* *Avimimus* is a very interesting, but unfortunately also problematical small theropod from the Upper Cretaceous of Central Asia. In his detailed description of the holotype, Kurzanov (1987) referred a partial skull, several vertebrae, an ischium, and a pair of articulated ilia to the same taxon. However, there is some uncertainty as to whether all these elements really represent a single taxon (Novacek 1996, p. 251; Unwin, pers. comm. 1998). Based on my own observations on a cast of the material (ROM 46144), the vertebrae are thought to represent a single taxon or even a single individual, because of their closely corresponding morphology and size, and the cranial remains also correspond well in size with the rest of

the material. Thus, pending a revision of the taxon, all the material is provisionally regarded as representing a single species here.

Even if the association of the material is provisionally accepted, a comment on the anatomy of the animal should be made. Kurzanov (1987) reconstructed *Avimimus* with a short, bird-like tail, although no sacral or caudal vertebrae are known. However, the well-developed fourth trochanter on the femur (the insertion of the *m. caudofemoralis longus*) and the long presacral vertebral column make this reconstruction seem rather unlikely.

*Bagaraatan ostromi* Osmólska, 1996

Age. Maastrichtian.

*Occurrence.* Nemegt Formation, Omnogov, Mongolia.

*Diagnosis.* Mandible with two surangular foramina; anterior end of dentary almost straight and obliquely inclined dorsorostrally at an angle of approximately 55 degrees (angle between ventral and anterior margins); hyposphene-hypantrum articulations present up to the mid-tail region; anterior caudal vertebrae with subrectangular, very strongly caudally-directed transverse processes; iliac blade with large lateral depressions.

*Remarks.* Although only known from fragments of the lower jaw and the posterior part of the postcranium (Osmólska 1996), *Bagaraatan* can be clearly distinguished from other small to medium-sized dinosaurs of the Nemegt Formation by the characters listed above. Furthermore, it is one of the few theropods from the Upper Cretaceous of Mongolia that cannot readily be referred to one of the suprageneric taxa defined below, and might thus be of considerable interest.

*Deltadromeus agilis* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996

Age. Cenomanian.

*Occurrence.* Kem Kem beds, eastern Morocco.

*Diagnosis.* Coracoid with slight concavity in anterior rim; femur with accessory trochanter on postero-medial side distal of the fourth trochanter; well-developed ridge medially on anterior side of distal end of femur.

*Remarks.* *Deltadromeus* is very similar to the contemporary *Bahariasaurus* from the Baharia Oasis of Egypt, and some of the elements described by Stromer (1934b) as *Bahariasaurus* might be referable to this genus (Sereno *et al.* 1996). Unfortunately, the holotype of *Bahariasaurus* no longer exists, and no diagnostic characters for this genus are apparent in Stromer's (1934b) figures. Therefore, it seems best to regard *Bahariasaurus* as a *nomen dubium*, although it may be congeneric with *Deltadromeus*.

*Unenlagia comahuensis* Novas and Puerta, 1997

Age. Turonian–Coniacian.

*Occurrence.* Río Neuquén Formation, Neuquén, Argentina.

*Diagnosis.* Deep lateral pits at the bases of the posterior dorsal and sacral neural spines; scapular blade strongly twisted against the glenoid region; postacetabular iliac blade distinctly concave dorsoposteriorly.

*Remarks.* Despite the fragmentary nature of the holotype specimen, *Unenlagia* is an important taxon supposedly close to the ancestry of birds (Novas and Puerta 1997). According to a phylogenetic analysis in Forster *et al.* (1998), it represents a member of basal birds that also includes *Rahonavis* and *Archaeopteryx*. However, the forearm proportions of *Unenlagia*, as far as can be judged from the preserved humerus, do not agree with a position within volant birds and Norell and Makovicky (1999) pointed out several characters shared with dromaeosaurids. Therefore, the species is treated as a separate OTU here.

*Velocisaurus unicus* Bonaparte, 1991a

Age. Coniacian.

*Occurrence.* Río Colorado Formation, Neuquén, Argentina.

*Diagnosis.* Shafts of Mt II and IV strongly reduced, and less than half as wide as the shaft of Mt III; Mt III straight and of subequal width throughout its length.

*Remarks.* Although *Velocisaurus* is based on an incomplete hindlimb (Bonaparte 1991a), it is a diagnosable taxon due to the peculiarities of the foot. As one of the few small theropods known from Gondwana, *V. unicus* is of potentially great phylogenetic and biogeographical importance.

#### *Cretaceous higher rank taxa*

Abelisauridae Bonaparte and Novas, 1985

*Included taxa.* *Abelisaurus comahuensis* Bonaparte and Novas, 1985; *Carnotaurus sastrei* Bonaparte, 1985; *Genusaurus sisteronis* Accarie, Beaudoin, Dejaj, Friès, Michard and Taquet, 1995; *Ilokelesia aguadagrandensis* Coria and Salgado, 2000; *Indosuchus raptorius* Huene, 1932; *Majungatholus atopus* Sues and Taquet, 1979; *Masiakasaurus knopferi* Sampson, Carrano and Forster, 2001; *Noasaurus leali* Bonaparte and Powell, 1980; *Xenotarsosaurus bonapartei* Martínez, Giménez, Rodríguez and Bochaty, 1986

*Temporal range.* Albian–Maastrichtian.

*Occurrence.* Allen Formation, Río Negro, Argentina; La Colonia Formation, Chubut, Argentina; unnamed unit (green clays and glauconitic sands of Bevens), Alpes de Haute-Provence, France; Lameta Formation, Madhya Pradesh, India; Maevarano Formation, Majunga, Madagascar; Lecho Formation, Salta, Argentina; Bajo-Barreal Formation, Chubut, Argentina.

*Diagnosis.* Maxilla in front of the antorbital opening very short and high; posterior border of lacrimal convex over its entire length; anterior process of lacrimal reduced; jugal process of postorbital expanded, strongly anteriorly directed and intrudes into the orbit (convergently present in *Tarbosaurus bataar* and *Tyrannosaurus rex*, but not in other tyrannosaurids); epiphyses in the cervical vertebrae hypertrophied and higher than the neural spines.

*Remarks.* Abelisaurids have recently been recognized as a distinct family of theropod dinosaurs (Bonaparte and Novas 1985). Their diagnosis and taxonomy is still problematic, mainly due to the fragmentary nature of the remains of all members of the family with the exception of *Carnotaurus* (Bonaparte *et al.* 1990) and recently described new specimens of *Majungatholus* (Sampson *et al.* 1998). Given the many peculiarities in the skeleton of these genera, it seems very probable that the discovery of more complete material of other taxa will provide more diagnostic characters for this family.

*Carnotaurus sastrei* (Text-fig. 6A), *Majungatholus atopus*, and *Abelisaurus comahuensis* share all of the cranial synapomorphies listed above, and so their referral to the Abelisauridae is well supported. However, many other, very incompletely known taxa have been assigned to this family (Martínez *et al.* 1986; Bonaparte *et al.* 1990; Molnar 1990; Bonaparte 1991b; Le Loeuff and Buffetaut 1991), and many of these

assignments are problematical. Therefore, a short review of poorly known taxa that are included in the Abelisauridae here is given below.

*Noasaurus leali* was originally assigned to its own family, Noasauridae (Bonaparte and Powell 1980). Later, Bonaparte (1991b) noted the close similarities between *Noasaurus* and abelisaurids and created the superfamily Abelisauoidea to include these two families (Bonaparte 1991b, p. 22). *Noasaurus* shares the first diagnostic character with *Abelisaurus*, *Carnotaurus*, and *Majungatholus*, and the fifth character with *Carnotaurus* and *Majungatholus*, and may therefore be regarded as a close relative of these taxa. Since the differences between the Noasauridae and Abelisauridae, as defined by Bonaparte (1991b), are only slight and may partly reflect size-dependant and/or ontogenetic differences, the recognition of two families is not accepted here. Although Coria and Salgado (2000) presented a cladogram of neoceratosaurs supporting the distinction of noasaurids and abelisaurids, their results must be seen as preliminary since only some taxa of the Abelisauria were included, characters were restricted to synapomorphies defining each node, and the majority of abelisaurid taxa considered in this analysis are known from less than 20 per cent of the skeleton. A more inclusive analysis might yield quite different results; therefore, all abelisaurids known are included in a single clade, Abelisauridae, here. However, apart from *Noasaurus*, the recently described *Masiakasaurus* also indicates an important diversity of small abelisaurids (Sampson *et al.* 2001).

Although based on very fragmentary material, *Ilokelesia aguadagrandensis* can be demonstrated to be an abelisaurid with some certainty, since it shares the peculiarities of the postorbital and the hypertrophied cervical epiphyses with other abelisaurid taxa (Coria and Salgado 2000).

*Indosuchus raptorius* was described by Huene (1932) and Huene and Matley (1933) on the basis of a posterior end of a skull roof from the Maastrichtian Lameta Formation of India, and more material was later referred to this taxon (Chatterjee 1978; Chatterjee and Rudra 1996). Sometimes considered to be a tyrannosaurid (Chatterjee 1978; Paul 1988a), *Indosuchus* has recently been placed in the Abelisauridae by several authors (Bonaparte and Novas 1985; Buffetaut *et al.* 1988; Bonaparte *et al.* 1990; Bonaparte 1991b). Since there seem to be several large theropods in the Lameta Formation, the material referred to *Indosuchus* by Chatterjee (1978) cannot be shown to represent this taxon with certainty (Molnar 1990). However, the type specimen shows the same arrangement of the supratemporal fenestrae as found in *Abelisaurus*, *Majungatholus*, and *Carnotaurus*; thus, this species is referred to the Abelisauridae.

*Genusaurus sisteronis* was described as a ceratosaurian theropod by Accarie *et al.* (1995) on the basis of several vertebrae and an incomplete pelvis and hindlimb. *Genusaurus* clearly represents a valid taxon, based on the peculiar morphology of the anterior end of the ilium (Accarie *et al.* 1995, fig. 4A; the anterior end of this element seems to be lacking only minor parts, and its overall morphology is real, not a result of preservation; Carrano, pers. comm. 1999). Although none of the diagnostic characters of the abelisaurids is evident from the published illustrations, *Genusaurus* is referred here to this clade, since it shares two apomorphic characters with *Carnotaurus*: the almost completely straight dorsal margin of the ilium, and the very long and vertically oriented ischial peduncle of the ilium. These characters are not present in an ilium of *Majungatholus* (UA 8678; Sampson *et al.* 1998, fig. 2F), indicating that, within abelisaurids, *Genusaurus* may be more closely related to *Carnotaurus* than to *Majungatholus*.

*Xenotarsosaurus* is based on a dorsal vertebra and hindlimb elements, including femur, tibia, fibula, and astragalocalcaneum, from the Upper Cretaceous of Argentina (Martínez *et al.* 1986). Although none of the diagnostic characters of the family as diagnosed here is found in the holotype, the taxon is tentatively referred to the Abelisauridae, based on the great overall similarity of the preserved elements to the comparable elements of *Carnotaurus*.

The recently described supposed abelisaurid *Tarascosaurus salluvicus* Le Loeuff and Buffetaut, 1991, from the Upper Cretaceous of southern France, is based on extremely fragmentary material that does not show any diagnostic characters and is, therefore, regarded as a *nomen dubium*. However, the presence of abelisaurids in the Upper Cretaceous of southern Europe is also supported by other material (Buffetaut *et al.* 1988).

#### Baryonychidae Charig and Milner, 1986

*Included taxa.* *Angaturama limai* Kellner and Campos, 1996; *Baryonyx walkeri* Charig and Milner, 1986; *Irritator challengeri* Martill, Cruickshank, Frey, Small and Clark, 1996; *Spinosaurus aegyptiacus* Stromer, 1915, *partim*;

*Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998.

*Temporal range.* Barremian–Cenomanian.

*Occurrence.* Romualdo Member of the Santana Formation, Ceará, Brazil; Upper Weald Clay, Surrey, England; Baharia Formation, Marsa Matruh, Egypt; Elrhaz Formation, Agadez, Niger; Kem Kem beds, Morocco.

*Diagnosis.* Dentary with strongly developed anterior expansion; anterior dentary teeth much larger than the relatively small and closely spaced posterior teeth; medial alveolar border is as high as the lateral border and formed by a sheet of bone of the dentary rather than by separately ossified interdental plates; teeth almost round in basal cross section and only slightly recurved; very long premaxillae, forming a rostral rosette; seven premaxillary teeth; ventral margin of premaxilla strongly concave; anterior ramus of maxilla strongly elongated; angle between anterior and ventral ramus of the lacrimal less than 45 degrees; dorsal vertebrae with several small vertical laminae connecting the transverse process with the neural spine dorsally; humerus extremely robust, with strongly expanded internal tuberosity and distal condyles; ulna with a broad and very strongly developed olecranon process; ischium with a long and low obturator flange.

*Remarks.* The family Baryonychidae (Text-fig. 6B) was proposed by Charig and Milner (1986) to include a single species, *Baryonyx walkeri*. Buffetaut (1989, 1992) noted similarities between the jaws of *Baryonyx* and the slightly younger *Spinosaurus* from the Cenomanian of Egypt, and concluded that both animals probably belong to the family Spinosauridae. This view has since been accepted by several authors (e.g. Sereno *et al.* 1994, 1996, 1998). Although Charig and Milner (1997) retained *Baryonyx* in its own family, they acknowledged the similarities between this genus and *Spinosaurus* and united the Baryonychidae and the Spinosauridae in the superfamily Spinosaurioidea.

The matter is complicated by the problematic status of *Spinosaurus aegyptiacus*. The holotype of this genus was found in the Baharia Oasis of Egypt at the beginning of the twentieth century and was subsequently described by Stromer (1915). The material consisted of two dentaries, a maxillary fragment, and several vertebrae. The only other accounts of the original specimen were by Stromer (1934b, 1936), before all the material was destroyed during a bombing raid in 1944.

In the introduction to his original description Stromer (1915, p. 3) commented on the association and preservation of the specimen:

‘Many of the bones had already been broken and deformed in the sediment; furthermore, the remains were completely jumbled. The skull seems to have originally been present, but due to its exposed position had been almost completely eroded away. Especially the maxillary fragment shows signs of erosion of an exposed bone; cracks in the posterior ends of the lower jaws and the especially anteriorly eroded cervical vertebrae also indicate a superficial position of the fossils.

No parts of the appendicular skeleton were found, indicating that the skeleton was already incomplete when it was covered by sediment. The soft parts had surely decayed before burial, thus allowing the dislocation of the bones. Several teeth, some of them already loosened by erupting replacement teeth, fell out of the jaws, complete with their roots, and all the bones were jumbled, perhaps due to scavengers or water flow. However, given the preservation of fine details and the lack of abrasion, prolonged transport of the bones can be excluded. In the sediment, the fossils suffered from pressure, probably caused by gypsum- and salt-flow rather than by tectonic events.

Given their positions in the sediment and their preservation, the remains represent one individual. Only the size of the sacral and caudal vertebrae are problematic in this respect, which will be discussed in the respective descriptions.’ (my translation).

Stromer later (1934b, p. 21) stated that: ‘It remains questionable, if . . . especially the oversized anterior caudal vertebra . . . belongs to *Spinosaurus* at all.’ (my translation). Judging from Stromer’s illustration (1915, pl. 1, fig. 1A–B) the vertebra in question looks more like an ornithischian caudal than a theropodan element. Given this probable mix of taxa in the original type material, it cannot be excluded that the rest of the material also represents more than one taxon. The following points may indicate that the holotype of *S. aegyptiacus* actually represents a mixture of remains of different theropods:

1. The dentary figured by Stromer (1915, pl. 1, figs 6, 12) agrees with dentaries of *Baryonyx* and material referred to *Suchomimus* in almost every detail and shows all the baryonychid synapomorphies listed above.
2. The dorsal vertebrae of the type of *Spinosaurus aegyptiacus* lack the strong pneumatisation and additional laminae seen in both *Baryonyx* and *Suchomimus*. Their principal characters are comparable to those seen in allosauroids, with the exception of the strongly elongated neural spines. Elongated neural spines are present in the carcharodontosaur *Acrocanthosaurus*, though to a lesser degree than in *S. aegyptiacus* (Stovall and Langston 1950). Since large carcharodontosaurs are present in Baharia, the vertebrae might represent these animals.
3. The cervical vertebrae figured by Stromer (1915, pl. 2, figs 1–2) differ significantly from the dorsal vertebrae in respect of the height of their neural spines. This difference is so marked that it might be questionable that they belong to the same taxon, although an abrupt change in spine height is present in other high-spined dinosaurs (e.g. *Ouranosaurus*; Taquet 1976).

Given this uncertainty of the association of the holotype material of *Spinosaurus aegyptiacus*, it seems at present better to use the family name Baryonychidae than the name Spinosauridae until new material becomes available to clarify the status of *Spinosaurus*. However, the dentary of the type of *Spinosaurus* can at least be referred to the Baryonychidae.

*Suchomimus tenerensis* from the Aptian of Niger is based on a partial postcranial skeleton (MNN GDF 500) and several referred specimens, including a partial skull (MNN GDF 501; see Sereno *et al.* 1998). All the material is very similar to *Baryonyx*, and can thus be referred to the Baryonychidae with certainty.

Two baryonychids from South America were described in 1996: *Irritator challengeri*, based on a skull lacking the anterior part of the snout (SMNS 58022), by Martill *et al.*, and *Angaturama limai*, based on the tip of a snout, by Kellner and Campos. *Irritator* (SMNS 58022) shows the diagnostic angle in the lacrimal, as well as a braincase that is very similar to that of *Baryonyx* and can, therefore, be referred to the Baryonychidae. *Angaturama* can also be referred to this clade, based on the presence of a rostral rosette and a premaxilla with seven tooth positions (Kellner 1996; Kellner and Campos 1996). Since both specimens come from the same horizon, they might represent the same taxon (in which case the name *Irritator challengeri* would be the senior synonym), but more material is needed to confirm this (see Kellner 1996).

The recently described species *Spinosaurus marocannus* Russell, 1996, and *Cristatusaurus lapparenti* Taquet and Russell, 1998, are regarded as *nomina dubia*.

#### Carcharodontosauridae Stromer, 1931

*Included taxa.* *Acrocanthosaurus atokensis* Stovall and Langston, 1950; *Carcharodontosaurus saharicus* (Depéret and Savornin, 1927); *Giganotosaurus carolinii* Coria and Salgado, 1995.

*Temporal range.* Aptian–Cenomanian.

*Occurrence.* Antlers Formation, Oklahoma; Twin Mountains Formation, Texas, USA; 'Continental intercalaire', Wilaya Adrar, Algeria; Baharia Formation, Marsa Matruh, Egypt; Kem Kem beds, Kasr-es-Souk, Morocco; Río Limay Formation, Neuquén, Argentina.

*Diagnosis.* Dentary with squared anterior end (unknown in *Carcharodontosaurus saharicus*); femoral head strongly elevated.

*Remarks.* The species *Megalosaurus saharicus* was first described by Depéret and Savornin (1927) on the basis of isolated teeth from the Albian of Algeria. Later, Stromer (1931) referred a partial skeleton from the Cenomanian of Egypt to the same species and changed the generic name to *Carcharodontosaurus*. Recently, Sereno *et al.* (1996) described an almost complete skull from the Cenomanian of Morocco, which is referable to *C. saharicus* (Text-fig. 6C). Together with the data published by Stromer (1931, 1934, 1936) this new material allowed the identification of *Acrocanthosaurus atokensis* Stovall and Langston, 1950, and *Giganotosaurus carolinii* Coria and Salgado, 1995, as members of the same family, Carcharodontosauridae.

## Dromaeosauridae Matthew and Brown, 1922

*Included taxa.* *Adasaurus mongoliensis* Barsbold, 1983; *Bambiraptor feinbergi* Burnham, Derstler, Currie, Bakker, Zhou, and Ostrom, 2000; *Deinonychus antirrhopus* Ostrom, 1969a; *Dromaeosaurus albertensis* Matthew and Brown, 1922; *Hulsanpes perlei* Osmólska, 1982; *Megaraptor namunhaiquii* Novas, 1998; *Microraptor zhaoianus* Xu, Zhou and Wang, 2000; *Saurornitholestes langstoni* Sues, 1978; *Sinornithosaurus millenii* Xu, Wang and Wu, 1999; *Utahraptor ostrommaysi* Kirkland, Burge and Gaston, 1993; *Velociraptor mongoliensis* Osborn, 1924.

*Temporal range.* Barremian–Maastrichtian.

*Occurrence.* Nemegt Svita, Bayankhongor, Mongolia; Cloverly Formation, Montana and Wyoming, USA; Judith River Formation, Alberta, Canada, and Montana, USA; Barun Goyot Formation, Omnogov, Mongolia; Río Neuquén Formation, Neuquén, Argentina; Judith River Formation, Alberta, Canada, and Montana, USA; Two Medicine Formation, Montana, USA; Yixian Formation, Liaoning, China; Cedar Mountain Formation, Utah, USA; Djadokhta Formation, Beds of Toogreg, Omnogov, Mongolia; Minhe Formation, Bayan Mandahu redbeds, Nei Mongol Zizhiqu, China.

*Diagnosis.* Quadratojugal is in the form of an inverted T-shape; paroccipital processes very long, extending laterally to the head of the quadrate; enlarged, triangular internal mandibular fenestra; fusion of interdental plates to each other and the margin of the jaws without clearly visible suture in adults; Mt. II with strongly ginglymoid distal articular facet. The following characters are not preserved in *Dromaeosaurus*, the type genus of the family, but probably represent synapomorphies of the family: mid-cervical vertebrae with hypertrophied epiphyses, pointing laterally; distal caudal vertebrae with extremely elongate prezygapophyses (equivalent to the length of more than two centra); distal chevrons inverted T-shaped and extremely anteroposteriorly elongated; second digit of the pes bearing a strongly enlarged ungual, with an asymmetric arrangement of the claw grooves and a sharp ventral margin.

*Remarks.* The first dromaeosaurid, *Dromaeosaurus albertensis*, was described in 1922 by Matthew and Brown, followed by the description of *Velociraptor mongoliensis* (Text-fig. 6D) in 1924 by Osborn. However, it was not until the discovery of *Deinonychus antirrhopus* that the peculiar anatomy of these animals became known and their significance for theropod phylogeny was recognized (Colbert and Russell 1969; Ostrom 1969a, b, 1972, 1973). Since then, our knowledge of the anatomy of these animals has rapidly increased following the discovery of more species and further studies of known taxa (Ostrom 1974a, 1976b, 1990; Sues 1977, 1978; Osmólska 1982; Barsbold 1983; Kirkland *et al.* 1993; Currie 1995; Norell and Makovicky 1997, 1999; Norell *et al.* 1997; Xu *et al.* 1999; Xu and Wang 2000).

Unfortunately, *Dromaeosaurus*, the type genus of the family, is based mainly on an imperfect skull and very fragmentary associated pedal remains. Originally, the recognition of *Dromaeosaurus* as a close relative of the much better known *Deinonychus* was based largely on the enlarged claw on the second pedal digit (Colbert and Russell 1969). Subsequent work showed that troödontids, which also have an enlarged second pedal ungual and were, therefore, thought to be very closely related to *Dromaeosaurus*, are sufficiently different from taxa such as *Deinonychus* and *Velociraptor* to merit their own family (Barsbold 1974, 1983; Currie 1985, 1987), so that the simple presence of this character cannot be used to define dromaeosaurids. Furthermore, Currie (1995) pointed out that the claw figured and described by Colbert and Russell (1969, fig. 15D) may actually belong to the contemporaneous dromaeosaurid *Saurornitholestes*. However, similarities in skull morphology between *Dromaeosaurus* and the better known velociraptorines seem to be sufficient to justify their treatment as a single clade (see Currie 1995).

*Megaraptor* was described as a coelurosaurian theropod of uncertain systematic position on the basis of extremely fragmentary material from the Upper Cretaceous of Argentina (Novas 1998). However, the presence of asymmetric claw grooves and a sharp ventral margin of the second pedal ungual indicates a dromaeosaurid relationship for this taxon (Rauhut and Werner 1995). Novas (1998) hesitated to refer the taxon to the Dromaeosauridae because of the presence of a straight shaft and an enlarged olecranon in the ulna, both regarded as primitive characters. However, a bowed ulnar shaft is present not only in maniraptorans but also in most theropods and even prosauropods, although in these groups the bend is usually less striking in lateral view due to the expansion formed by the olecranon process (see also

discussion of this character in the materials and methods section), and this also seems to be the case in *Megaraptor* (Novas 1998, fig. 1B). An enlarged olecranon is found in some coelurosaurs, including the basal bird *Mononykus* (Perle *et al.* 1994), and its presence in *Megaraptor* might be an autapomorphy of this taxon within dromaeosaurids.

#### Ornithomimosauria Barsbold, 1976a

*Included taxa.* *Deinocheirus mirificus* Osmólska and Roniewicz, 1969; *Garudimimus brevipes* Barsbold, 1981; *Harpymimus okladnikovi* Barsbold and Perle, 1984; *Pelecanimimus polyodon* Pérez-Moreno, Sanz, Buscalioni, Moratalla, Ortega and Rasskin-Gutman, 1994. Ornithomimidae Marsh, 1890: *Anserimimus planinychus* Barsbold, 1988; *Archaeornithomimus asiaticus* (Gilmore, 1933); *Dromiceiomimus brevitertius* (Parks, 1926); *Dromiceiomimus samueli* (Parks, 1928); *Gallimimus bullatus* Osmólska, Roniewicz and Barsbold, 1972; *Ornithomimus edmontonicus* Sternberg, 1933; *Ornithomimus velox* Marsh, 1890; *Struthiomimus altus* (Lambe, 1902).

*Temporal range.* ?Hauterivian–Maastrichtian.

*Occurrence.* Nemegt Formation, Omnogov, Mongolia; Baynshiren Svita, Omnogov, Mongolia; Shinekhuduk Svita, Dundgov, Mongolia; Calizas de La Huérguina Formation, Cuenca, Spain; Nemegt Svita, Bayankhongor, Mongolia; Iren Dabasu Formation, Nei Mongol Zizhiq, China; Horseshoe Canyon Formation, Alberta, Canada; Judith River Formation, Alberta, Canada; Denver Formation, Colorado, USA; Kaiparowits Formation, Utah, USA.

*Diagnosis.* Maxilla excluded from external nares by broad posterior ascending process of the premaxilla (this is a reversal to the ancestral dinosaurian condition, convergently present in *Herrerasaurus ischigualastensis*; condition unknown in *Harpymimus okladnikovi*); humerus long, slender and straight; manual unguals only slightly curved or straight, with reduced, distally placed flexor tubercles; obturator process on ischium is small, triangular and placed entirely on the uppermost fifth of the ischial shaft (unknown in *H. okladnikovi* and *P. polyodon*); pedal unguals ventrally flattened, with a semicircular depression instead of a flexor tubercle.

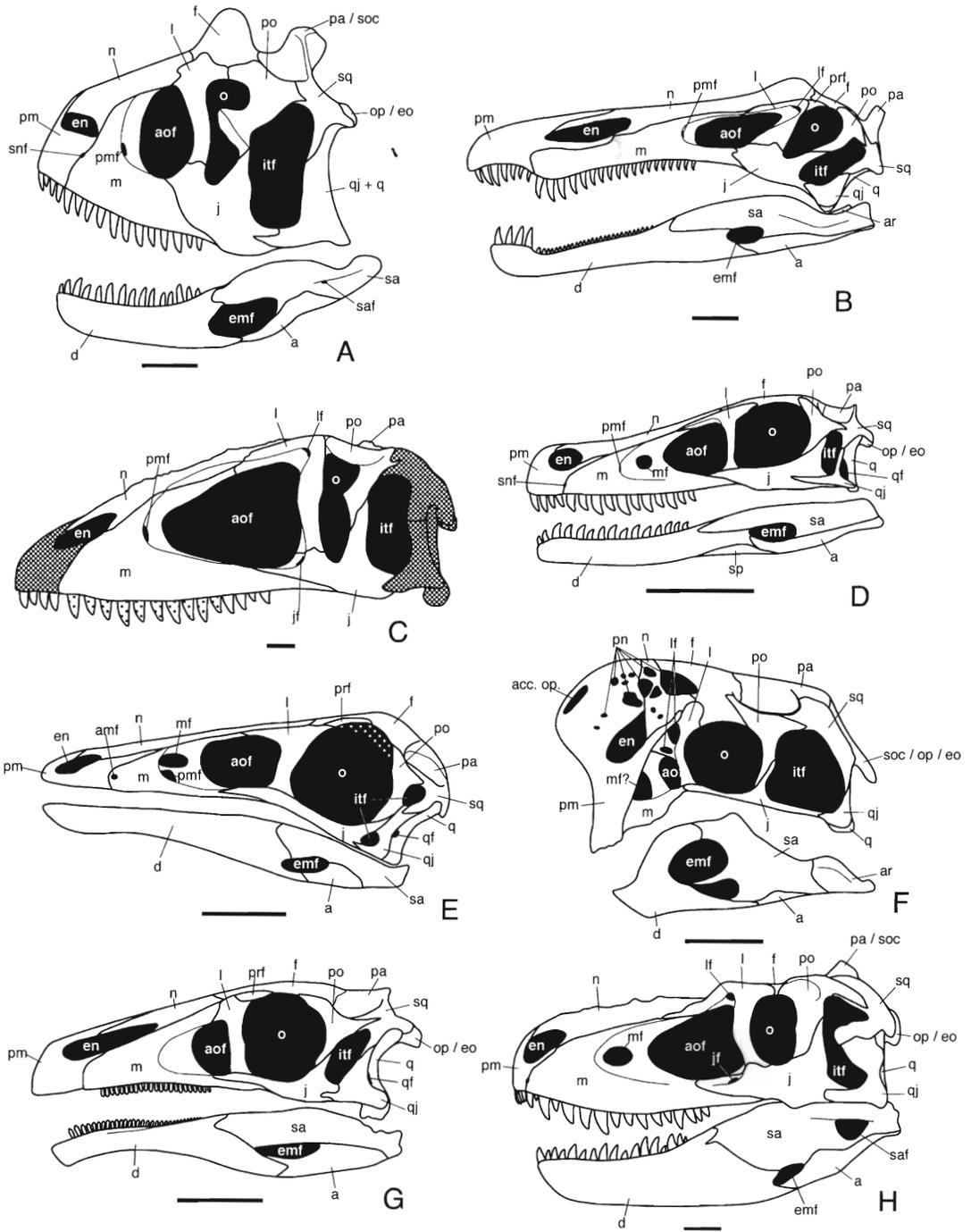
*Remarks.* Ornithomimids (Text-fig. 6E) have long been recognized as a monophyletic clade of theropods (e.g. Marsh 1890; Osborn 1916; Russell 1972; Barsbold 1976a; Barsbold and Osmólska 1990). However, the discovery of primitive forms intermediate between ornithomimids and other theropods during the last 25 years (Barsbold 1981; Barsbold and Perle 1984; Pérez-Moreno *et al.* 1994) makes a formal diagnosis of this group more problematic, since several characters that were usually used to define ornithomimids (e.g. Russell 1972) are absent from these more primitive forms or convergently present in other theropods.

*Deinocheirus mirificus* has repeatedly been compared with, or even referred to, the Ornithomimosauria (Ostrom 1972; Gauthier 1986; Paul 1988a), but it was listed as a theropod of uncertain taxonomic position

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TEXT-FIG. 6. Skull reconstructions of representatives of Cretaceous OTUs in left lateral view. A, abelisaurid *Carnotaurus sastrei*, Late Cretaceous (Campanian), Gorro Frigio Formation, Argentina; based on Bonaparte *et al.* (1990) and MACN CH 894. B, composite skull of a generalized baryonychid; mainly based on *Suchomimus tenerensis* (MNN GDF 501, 503–506) and *Irritator challengerii* (SMNS 58022), with some elements reconstructed after *Baryonyx walkeri* (BMNH R 9951). C, carcharodontosaurid *Carcharodontosaurus saharicus*, Late Cretaceous (Cenomanian), Kem Kem beds, Morocco; based on Sereno *et al.* (1996) and SGM-Din 1, unpreserved elements shaded. D, dromaeosaurid *Velociraptor mongoliensis*, Late Cretaceous (Campanian), Djadokhta Formation, Mongolia; based on Barsbold (1983), Barsbold and Osmólska (1999), and AMNH 6515. E, ornithomimosaur *Dromiceiomimus brevitertius*, Late Cretaceous (Maastrichtian), Horseshoe Canyon Formation, Alberta, Canada; redrawn from Russell (1972). F, oviraptorosaur *Oviraptor philoceratops*, Late Cretaceous (Campanian), Djadokhta Formation, Mongolia; redrawn from Barsbold *et al.* (1990). G, therizinosauroid *Erlikosaurus andrewsi*, Late Cretaceous (Cenomanian–Turonian), Baynshiren Svita, Mongolia; based on Clark *et al.* (1994). H, tyrannosaurid *Gorgosaurus libratus*, Late Cretaceous (Campanian), Judith River Formation, Alberta, Canada, redrawn from Molnar *et al.* (1990). Abbreviations as in Text-figures 4 and 5, and: acc. op., accessory opening of unknown function in the premaxilla of *Oviraptor* (Barsbold *et al.* 1990); amf, anterior maxillary foramen; pn, pneumatic openings. Scale bars represent 50 mm (D–G) and 100 mm (A–C, H).

by Norman (1990a). However, the differences between ornithomimids and *Deinocheirus* listed by Nicholls and Russell (1985) all represent plesiomorphies in the latter taxon, and might, therefore, only indicate that *Deinocheirus* is not a member of the most advanced ornithomimosaur, the ornithomimids. *D. mirificus* shares with all ornithomimosaur the apomorphic presence of an especially long, slender and



straight humerus, and with all members of this clade which are more derived than *Harpymimus* the apomorphic characters of the first metacarpal being subequal in length to metacarpal II, and the presence of a reduced, proximally placed, triangular deltopectoral crest on the humerus. Therefore, the taxon is referred to the Ornithomimosauria here.

Even after the inclusion of the more primitive members, the monophyly of the ornithomimosauria is still well supported by apomorphic characters (see above); therefore, they are treated as a single OTU. The phylogenetic relationships within ornithomimosauria are probably (*Harpymimus* (*Pelecanimimus*, *?Deinocheirus* (*Garudimimus*, Ornithomimidae))) (modified from Barsbold and Osmólska 1990).

#### Oviraptorosauria Barsbold, 1976a

*Included taxa.* Caenagnathidae Sternberg, 1940: *Caenagnathasia martinsoni* Currie, Godfrey and Nessov, 1993; *Chiostenotes elegans* (Parks, 1933); *Chiostenotes pergracilis* Gilmore, 1924a; *Elmisaurus rarus* Osmólska, 1981. Oviraptoridae Barsbold, 1976b: *Citipati osmolskae* Clark, Norell and Barsbold, 2001; *Conchoraptor gracilis* Barsbold, 1986; *Ingenia yanshini* Barsbold, 1981; *Khaan mckennai* Clark, Norell and Barsbold, 2001; *Nomingia gobiensis* Barsbold, Osmólska, Watabe, Currie and Tsogtbataar, 2000; *Oviraptor mongoliensis* Barsbold, 1986; *Oviraptor philoceratops* Osborn, 1924.

*Temporal range.* Turonian–Maastrichtian.

*Occurrence.* Bissekty Formation, Uzbekistan; Judith River Formation, Alberta, Canada, and Montana, USA; Horseshoe Canyon Formation, Alberta, Canada; Nemegt Formation, Omnogov, Mongolia; Red beds of Khermeen Tsav, Omnogov, Mongolia; Beds of Bugeen Tsav, Bayankhongor, Mongolia; Djadokhta Formation, Omnogov, Mongolia; Bayan Mandahu Red beds, Nei Mongol Zizhiqu, China.

*Diagnosis.* Maxilla with broad palatal shelf bearing two longitudinal ridges and with posteromedial tooth-like process; dentary with medial ridge; dorsal margin of dentary deeply concave; dentary with two long posterior processes separated by the external mandibular fenestra; coronoid process of dentary inflected dorsomedially; articular surface of lower jaw convex in lateral view, distinctly expanded laterally and medially, and raised above the dorsal margin of the mandibular ramus; proximal caudal vertebrae strongly pneumatised. The following characters might be synapomorphies of the Oviraptorosauria, but are currently unknown in caenagnathids: postorbital part of the skull subequal in length to the preorbital part (i.e. snout very short and high); suborbital fenestra closed, ectopterygoid contacts the palatine in a broad suture anteriorly (the condition in therizinosaurs might be similar, but is uncertain); premaxillary body as high as, or higher than the height of orbit.

*Remarks.* The first representatives of this peculiar group of dinosaurs (Text-fig. 6F) were described by Osborn (1924) and Gilmore (1924a), although it was not then recognized that *Chiostenotes* Gilmore is a close relative of *Oviraptor* Osborn. In 1940, Sternberg described two edentulous lower jaws from the Campanian Judith River Formation of Canada as a new genus of Cretaceous birds, *Caenagnathus*, and referred it to its own family, Caenagnathidae. All of these taxa received surprisingly little attention until new and better preserved material of oviraptorosaurs discovered in the Upper Cretaceous of Mongolia in the 1970s revealed the bizarre skull anatomy of these animals. Osmólska (1976) recognized the close similarities of the lower jaws of *Caenagnathus* and *Oviraptor* and Barsbold (1976a, b) created the family Oviraptoridae and the suborder Oviraptorosauria. In 1981, Osmólska described some new theropod remains from the Late Cretaceous of Mongolia as *Elmisaurus rarus* and created the family Elmisauridae to include *Elmisaurus*, *Chiostenotes* and *Macrophalangia* Sternberg, 1932. Currie and Russell (1988) confirmed the close relationships of *Elmisaurus* and *Chiostenotes*, and synonymized *Macrophalangia* with the latter genus. In the 1990 compendium ‘The Dinosauria’ (Weishampel *et al.*), Currie listed *Elmisaurus* and *Chiostenotes* as elmisaurids, and referred the species *Ornithomimus elegans* Parks, 1933 to the latter genus. In the same compendium, Barsbold *et al.* listed the Oviraptoridae and the Caenagnathidae as members of the Oviraptorosauria.

In 1997, Sues described a new specimen of *Chiostenotes* from the Horseshoe Canyon Formation of

western Canada. He presented a good case for arguing that *Caenagnathus* represents the same genus as *Chirostenotes* and consequently used the older family name Caenagnathidae Sternberg, 1940, instead of Elmisauridae Osmólska, 1981. He further concluded that caenagnathids and oviraptorids can be united as Oviraptorosauria, based on several cranial and postcranial synapomorphies. This view is followed here.

#### Therizinosauroidea (Maleev, 1954)

*Included taxa.* *Alxasaurus elesitaiensis* Russell and Dong, 1993a; *Beipiaosaurus inexpectus* Xu, Tang and Wang, 1999. Therizinosauridae Maleev, 1954; *Enigmosaurus mongoliensis* Barsbold and Perle, 1983; *Erlikosaurus andrewsi* Perle, 1980 (in Barsbold and Perle 1980); '*Nanshiungosaurus*' *bohlini* Dong and Yu, 1997; *Nanshiungosaurus brevispinus* Dong, 1979; *Nothronychus mckinleyi* Kirkland and Wolfe, 2001; *Segnosaurus galbinensis* Perle, 1979; *Therizinosaurus cheloniformis* Maleev, 1954.

*Temporal range.* Barremian–Maastrichtian.

*Occurrence.* Bayin Gobi Formation, Nei Mongol Zizhiqu, China; Yixian Formation, Liaoning, China; Baynshiren Svita, Omnogov and Dornogov, Mongolia; Xinminbao Group, Gansu, China; Nanxiong Formation, Guangdong, China; Nemeget Formation, Omnogov, Mongolia; White beds of Khermeen Tsav, Bayankhongor, Mongolia.

*Diagnosis.* Mandibular teeth set off from the lateral margin of the jaw posteriorly (convergently present in ornithischians and some prosauropods); teeth leaf-shaped with large, blunt marginal denticles (convergently present in prosauropods); anterior dorsal vertebrae with elevated neural arches such that the zygapophyseal articulation is more than three-quarters the height of the centrum above the neurocentral suture; manual unguals flat-sided and deep proximally; anterior end of iliac blade strongly expanded dorsoventrally; prominent lateral tuberosity on the postacetabular iliac blade dorsally; medial surface of Mt I hollowed to articulate with the convex lateral surface of the shaft of Mt II.

*Remarks.* The genus *Therizinosaurus*, based on isolated claws from the Upper Cretaceous of Mongolia, was described in 1954 by Maleev as a new genus of giant turtle. It was not until 1970 that the theropod nature of these remains was recognized (Rozhdestvensky 1970). However, despite the description of some new material referable to this genus (Barsbold 1976c), its affinities and most of its anatomy remained unknown until recently.

In 1979, Perle proposed a new family of enigmatic Late Cretaceous theropods from Mongolia, Segnosauridae, to include a new genus, *Segnosaurus*. Subsequently, *Enigmosaurus*, *Erlikosaurus*, and *Nanshiungosaurus* from the Upper Cretaceous of central Asia were referred to this family (Barsbold and Perle 1980, 1983; Perle 1981; Barsbold and Maryanska 1990). Paul (1984) questioned the theropod affinities of segnosaurids and regarded them as 'relics of the prosauropod-ornithischian transition' (Paul 1984, p. 507). Other subsequent workers pointed out similarities between segnosaurids and prosauropods (Gauthier 1986; Sereno 1989), and Barsbold and Maryanska (1990) listed them as *Saurischia sedis mutabilis*.

In 1993, Russell and Dong (1993a) described a new species from the upper Lower Cretaceous of China, *Alxasaurus elesitaiensis*, and demonstrated that *Therizinosaurus* is closely related to segnosaurids and consequently changed the family name to the senior synonym Therizinosauridae. *Alxasaurus*, in its own family Alxosauridae, and therizinosaurids were united in the superfamily Therizinosauroidea. Russell and Dong also made a strong case for assigning therizinosauroids to the Theropoda, the similarities between them and prosauropods being interpreted as adaptations to similar ecological conditions. This view was supported by Clark *et al.* (1994) in their detailed analysis of the skull of *Erlikosaurus* (Text-fig. 6G), and is followed here. A new therizinosauroid from the Lower Cretaceous of Liaoning, China, with integumentary filaments preserved, was recently described by Xu *et al.* (1999). This specimen shows a more conservative theropodan pes morphology and a very maniraptoran-like manus, thus furthermore strengthening the theropod affinities of therizinosauroids.

Recently, Xu *et al.* (2001) described a new supposed therizinosaur, *Eshanosaurus deguchiianus*, from the Lower Jurassic Lufeng Formation of China. However, the only material known for this taxon, an incomplete lower jaw, shows many similarities with the mandibles of prosauropods, which are the most common dinosaur fossils in this formation. Of the 11 characters listed by Xu *et al.* in support for therizinosaur affinities, six are clearly also present in prosauropods (characters 3, 6 and 8–11 of Xu *et al.*), one represents a plesiomorphy for dinosaurs ancestrally (character 4), and the rest are debatable in either their distribution or significance. For example, character 1 of Xu *et al.* (anterior teeth larger than middle or posterior teeth) might also be present in juvenile prosauropods, as noted by Upchurch (1998, p. 56). Likewise, the shape of the tooth crowns in mesial view (character 5) and the relative size of the root (character 7) might vary within one dentition depending on the position of the tooth. Indeed, some ornithischian teeth have roots that are wider than the crown (Rauhut, unpublished data). The number of teeth (character 2) is highly variable in reptiles in general and might vary significantly within one species or even on the left and right side of a single individual (e.g. Colbert 1990; Galton 1990), so a slightly higher number of teeth than in any known prosauropod might not be too significant. Furthermore, the type of *Eshanosaurus* shows one character that is not present in therizinosaur, or in any other theropod, but occurs in prosauropods: the presence of a medial ridge on the tooth crowns (Lamanna, pers. comm. in Kirkland and Wolfe 2001). In conclusion, *Eshanosaurus* is based on an intriguing specimen from the Lower Jurassic Lufeng Formation with a remarkable combination of characters, but more material is needed to confirm its therizinosaur affinities. Therefore, it has not been taken into consideration here.

#### Troodontidae Gilmore, 1924b

*Included taxa.* *Borogovia gracilicrus* Osmólska, 1987; *Byronosaurus jaffei* Norell, Makovicky and Clark, 2000; *Saurornithoides junior* Barsbold, 1974; *Saurornithoides mongoliensis* Osborn, 1924; *Sinornithoides youngi* Russell and Dong, 1993b; *Tochisaurus nemegtensis* Kurzanov and Osmólska, 1991; *Troödon formosus* Leidy, 1856.

*Temporal range.* ?Aptian–Maastrichtian.

*Occurrence.* Nemegt Formation, Omnogov, Mongolia; Nemegt Svita, Bayankhongor, Mongolia; Djadokhta Formation, Omnogov, Mongolia; Bayan Mandahu Red beds, Nei Mongol Zizhiqu, China; Ejinhorogi Formation, Nei Mongol Zizhiqu, China; Xinminbao Group, Gansu, China; Judith River Formation and Horseshoe Canyon Formation, Alberta, Canada; Judith River Formation, Two Medicine Formation, and Hell Creek Formation, Montana; Lance Formation, Wyoming, USA.

*Diagnosis.* Large maxillary fenestra that is more than half the size of the internal antorbital fenestra; bulbous parasphenoid capsule connected with internal chambers in the basisphenoid and basiptyergoid processes; nutrient foramina in lower jaw placed in a longitudinal groove; interdental plates absent and teeth held in place by interdental bone; teeth with enlarged, apically hooked denticles with distinct ‘blood-pits’ at their base; Mt IV very robust, and more than twice as wide (in anterior view) as the Mt II at midshaft.

*Remarks.* Although *Troödon formosus* was one of the first dinosaurs to be described from North America (Leidy 1856), the affinities and anatomy of this animal remained enigmatic until very recently, mainly due to the fact that the type material of *T. formosus* consists of a single tooth. The family name was proposed by Gilmore (1924b), who at that time believed *Troödon* to be a pachycephalosaur. In the same year, Osborn (1924) described a new small theropod dinosaur from the Upper Cretaceous of Mongolia, *Saurornithoides mongoliensis*. Sternberg (1932) described some new remains of a small theropod dinosaur from the Upper Cretaceous of Canada as *Stenonychosaurus inequalis*, and later (1945) noticed the theropod affinities of *Troödon*. The latter was subsequently confirmed by a find of a dentary referable to this taxon (Russell 1948). Strangely enough, these interesting taxa received little attention until Russell (1969) noticed the similarities between *Saurornithoides* and *Stenonychosaurus*, placing them in the family Troodontidae *sensu* Russell, 1948 (Russell 1969, p. 595), and considered *Troödon* to be probably a closely

related, or even synonymous taxon. In contrast to this view, Barsbold (1974) considered *Troödon* to be distinct from the closely related *Saurornithoides* and *Stenonychosaurus*, and proposed a new family, Saurornithoididae, for the latter two taxa. This assignment was accepted by many authors, and the name Saurornithoididae became widely used (e.g. Barsbold 1983; Carpenter 1982; Currie 1985; Wilson and Currie 1985) until Currie (1987) showed that *Troödon* Leidy, 1856, is a senior synonym for *Stenonychosaurus* Sternberg, 1932, *Polyodontosaurus* Gilmore, 1932, and *Pectinodon* Carpenter, 1982, and proposed to use the family name Troödontidae again, to include *Troödon* and *Saurornithoides*. Since then, the name Troödontidae has become widely accepted, and several new taxa have been referred to this family (Barsbold *et al.* 1987; Osmólska 1987; Osmólska and Barsbold 1990; Kurzanov and Osmólska 1991; Russell and Dong 1993*b*; Norell *et al.* 2000). Unfortunately, despite the discovery of an almost complete skeleton of a troödontid in the Lower Cretaceous of China (Russell and Dong 1993*b*), many aspects of the anatomy of these enigmatic theropods are still poorly known.

An additional comment on the anatomy of troödontids might be added: Russell and Dong (1993*b*, p. 2169) claimed that a pubis boot is absent in the small Early Cretaceous troödontid *Sinornithoides*. However, based on my own observations of the type specimen, I believe the distal ends of the pubes to be missing; thus the absence of a pubic boot cannot be proven. A pubis referred to *Troödon formosus* (MOR 553S 8.3.9.387) shows a well-developed pubic boot, but this element was not found in articulation with other *Troödon* material, and several characters that are more typical for oviraptorosaurs (more anteriorly than posteriorly expanded pubic boot, anteriorly concave shaft) cast doubt on its referral to this taxon.

#### Tyrannosauridae Osborn, 1906

*Included taxa.* *Albertosaurus sarcophagus* Osborn, 1905; *Alectrosaurus olseni* Gilmore, 1933; *Alioramus remotus* Kurzanov, 1976*b*; *Aublysodon mirandus* Leidy, 1868 (including *A. molnari* Paul, 1988*a*); *Daspletosaurus torosus* Russell, 1970; *Gorgosaurus libratus* Lambe, 1914; *Maleevosaurus novojilovi* (Maleev, 1955*a*); *Shanshanosaurus huoyanshanensis* Dong, 1977; *Tarbosaurus bataar* Maleev, 1955*b*; *Tyrannosaurus rex* Osborn, 1905.

*Temporal range.* Senonian–Maastrichtian.

*Occurrence.* Judith River Formation, Montana, USA; Lance Formation, Wyoming, USA; Horseshoe Canyon Formation, Alberta, Canada; Iren Dabasu Formation, Nei Mongol Zizhiqu, China; Baynshiren Svita, Omnogov, Mongolia; Beds of Nogon Tsav, Bayankhongor, Mongolia; Two Medicine and Hell Creek formations, Montana; Denver Formation, Colorado; Kirtland Shale, New Mexico, USA; Judith River Formation, Alberta, Canada; Fruitland Formation, New Mexico, USA; Nemegt Formation, Omnogov, Mongolia; Subashi Formation, Xinjiang, China; Nemegt Svita, White beds of Khermeen Tsav, Bayankhongor, Mongolia; ?unnamed unit, Heilongjiang, China; Scollard and Willow Creek formations, Alberta, Canada; Frenchman Formation, Saskatchewan, Canada; Hell Creek Formation, South Dakota, USA; Livingston Formation, Montana, USA; Lance Formation, Wyoming, USA; Laramie Formation, Colorado, USA; McRae Formation, New Mexico, USA.

*Diagnosis.* Squamosal with a broadly expanded, rostrally directed quadratojugal process, meeting the expanded dorsal process of the quadratojugal in a broad suture and strongly intruding into the lower temporal fenestra; vomer with broad rhomboid anterior expansion; surangular foramen strongly enlarged, being almost as large as the mandibular fenestra in most forms; premaxillary teeth D-shaped in cross section and significantly smaller than the maxillary teeth; cervical vertebrae considerably shorter than high; hand didactyl with splint-like Mc III [claimed to be present in *Compsognathus longipes* (Ostrom 1978) but, owing to the poor preservation of the hand in this taxon, the matter is highly debatable].

*Remarks.* The Tyrannosauridae (Text-fig. 6H) have long been recognized as a distinct family of theropod dinosaurs (Osborn 1906). However, there has been some debate as to which genera and species belong to this family and the taxonomy of some of these species.

Originally erected for the genus *Tyrannosaurus* (Osborn 1906), the family was later often confused or synonymized with the family Deinodontidae Cope, 1866 (e.g. Matthew and Brown 1922). However, as Gilmore (1946) and Russell (1970) pointed out, the type genus of the family Deinodontidae, *Deinodon* Leidy, 1856, is based on undiagnostic teeth and thus the name Tyrannosauridae should be used.

The species *Albertosaurus sarcophagus*, *Alioramus remotus*, *Daspletosaurus torosus*, *Gorgosaurus libratus*, *Maleevosaurus novojilovi*, *Tarbosaurus bataar*, and *Tyrannosaurus rex* are known from complete skeletons, or at least good skulls and partial postcrania, and these taxa can thus be referred to the Tyrannosauridae with certainty. Since the nomenclature of these animals, as listed here, differs from some of the other accounts of this clade (e.g. Russell 1970; Maleev 1974; Paul 1988a; Molnar *et al.* 1990; Carpenter 1992), some nomenclatorial comments on these well-established tyrannosaurids might be added.

Russell (1970) synonymized *Gorgosaurus libratus* with the genus *Albertosaurus*, and this was accepted by most subsequent workers (Paul 1988a; Molnar *et al.* 1990; Carpenter 1992). However, new studies of the material of *Gorgosaurus* indicate that it cannot be referred to *Albertosaurus* with any certainty (Holtz 1997, 2001a; Currie, pers. comm. 1998); therefore, it is retained as a separate genus here.

*Maleevosaurus novojilovi* was originally described as a new species of *Gorgosaurus* (Maleev 1955a), but Carpenter (1992) removed it from this genus and proposed a new generic name, *Maleevosaurus*. Rozhdestvensky (1965) and Carr (1999) suggested that *Maleevosaurus novojilovi* is a juvenile *Tarbosaurus bataar*. However, Rozhdestvensky's arguments were disputed by Carpenter (1992, pp. 256–257); thus, *Maleevosaurus novojilovi* is provisionally retained as a separate genus and species.

Gilmore (1946) described an almost complete skull of a small tyrannosaur as *Albertosaurus lancensis*. Bakker *et al.* (1988) recognized the differences of this skull to other material of *Albertosaurus*, and proposed the new generic name *Nanotyrannus*. However, Carr (1999) argued that the type of *Nanotyrannus* represents a juvenile individual of *Tyrannosaurus rex*. This view is followed here.

Several authors (e.g. Paul 1988a; Carpenter 1992) have synonymized the genus *Tarbosaurus* with *Tyrannosaurus*, but no detailed comparison of these two taxa has been carried out so far. Pending the revisions of tyrannosaurid interrelationships, currently being worked on independently by P. Currie, C. Brochu, and T. Holtz, *Tarbosaurus* is provisionally regarded as a separate genus here.

*Alectrosaurus olseni* was described as a tyrannosaur on the basis of two specimens from the Iren Dabasu Formation of Inner Mongolia, China, by Gilmore (1933). Mader and Bradley (1989) reviewed the syntype material and pointed out that one of the specimens described by Gilmore, an incomplete forelimb, represents a therizinosaur (= segnosaur in their paper), while the other one, an almost complete hindlimb (AMNH 6554), was designated as the lectotype of *Alectrosaurus*. Mader and Bradley (1989, p. 48) noted close similarities in hindlimb morphology with both tyrannosaurids and ornithomimids, but referred *Alectrosaurus* to the former clade, based on the detailed morphology of the tubercle for the insertion of the m. iliofibularis on the fibula, the presence of a hallux, and the conservative morphology of the pedal unguals. It must be noted, however, that the latter two characters represent plesiomorphies that might have been present in more basal, non-ornithomimid ornithomimosaur, such as *Deinocheirus*, so that the only evidence for a tyrannosaurid relationship in the lectotype of *Alectrosaurus* is the morphology of the muscle attachment on the fibula. However, recently discovered additional material of *Alectrosaurus* seems to confirm its tyrannosaurid affinities (Perle, pers. comm. in Currie and Eberth 1993, p. 138; see also Holtz 2001a); therefore, it is included in this clade here.

*Shanshanosaurus huoyanshanensis* is known only from a partial skeleton from the uppermost Cretaceous of Xinjiang, China (Dong 1977). The skeleton represents a small, juvenile individual. Unfortunately, the original description is rather short, and nothing has subsequently been published on this interesting specimen. However, *Shanshanosaurus* shows similarities to tyrannosaurids (Molnar 1990; Dong 1992), and probably represents a juvenile of a member of this clade (Currie, pers. comm. 1998; Holtz 2001a); thus the taxon is included in the family here.

## DEFINITION AND DESCRIPTION OF THE CHARACTERS

### *Cranial characters*

1. Shape of premaxillary body: wider than high, or approximately as wide as high (0); significantly higher than wide (1) (modified from Bonaparte 1991b; Holtz 1994)

In most dinosaurs the premaxillary body, i.e. the main part of the premaxilla beneath and in front of the external nares, but excluding the posterior process, is approximately as wide anteroposteriorly as it is high

dorsoventrally, or slightly wider. In *Ceratosaurus*, abelisaurids, and oviraptorosaurs the premaxillary body is very short and high, being significantly higher than wide (Text-fig. 7C). The situation is similar in tyrannosaurids (FMNH PR 308, ROM 1247, Text-fig. 7E), although the abbreviated appearance of the premaxilla in lateral view in articulated skulls (e.g. FMNH PR 308) is partially due to the more rounded snout in these theropods, in which a part of the premaxillary body faces anteriorly rather than laterally.

2. Premaxillary body in front of external nares: shorter than body below the nares and angle between anterior margin and alveolar margin more than 75 degrees (0); longer than body below the nares and angle less than 70 degrees (1)

In many dinosaurs, the part of the premaxillary body underneath the external nares is longer than the part in front of them, but in a variety of theropod taxa, it is only as long as, or even shorter than the part in front of the external nares. The extreme in the latter respect are the baryonychids (BMNH R 9951, MNN GAD 501), where almost the complete premaxillary body is positioned in front of the external nares.

The angle between the alveolar margin and the anterior rim of the premaxilla (as measured at the tangent along the anterior rim at the level of the ventral margin of the external nares) is usually correlated with this character: the anterior rim is usually steeply sloping in taxa with a short premaxillary body, and more posteriorly inclined in those taxa with long premaxillary bodies (Text-fig. 7B). The angle between these two margins is a useful indicator of the character state in those taxa where the two parts of the premaxillary body are of approximately subequal length and is thus also used in the character definition.

Apart from baryonychids, the derived character state is also present in many other theropods, including *Coelophysis* (AMNH 7224), *Syntarsus* (QG 202, 245), *Dilophosaurus* (UCMP V 6468), *Magnosaurus* (OUM J 13558), *Torvosaurus* (Britt 1991), *Neovenator* (Hutt *et al.* 1996), *Compsognathus* (BSP A.S.I. 563), therizinosauroids (Clark *et al.* 1994), oviraptorosaurs (Barsbold 1977a; Barsbold *et al.* 1990), the basal bird *Archaeopteryx* (Berlin and Eichstätt specimens), and several others.

3. Broad palatal shelf on medial side of premaxilla: absent (0); present (1) (Sues 1997)

In most theropods the articulated premaxillae are narrow, and a suture between the two elements is present in the anterior half or two-thirds of the premaxillary body and the ascending process. The suture usually extends furthest posteriorly directly below the external nares.

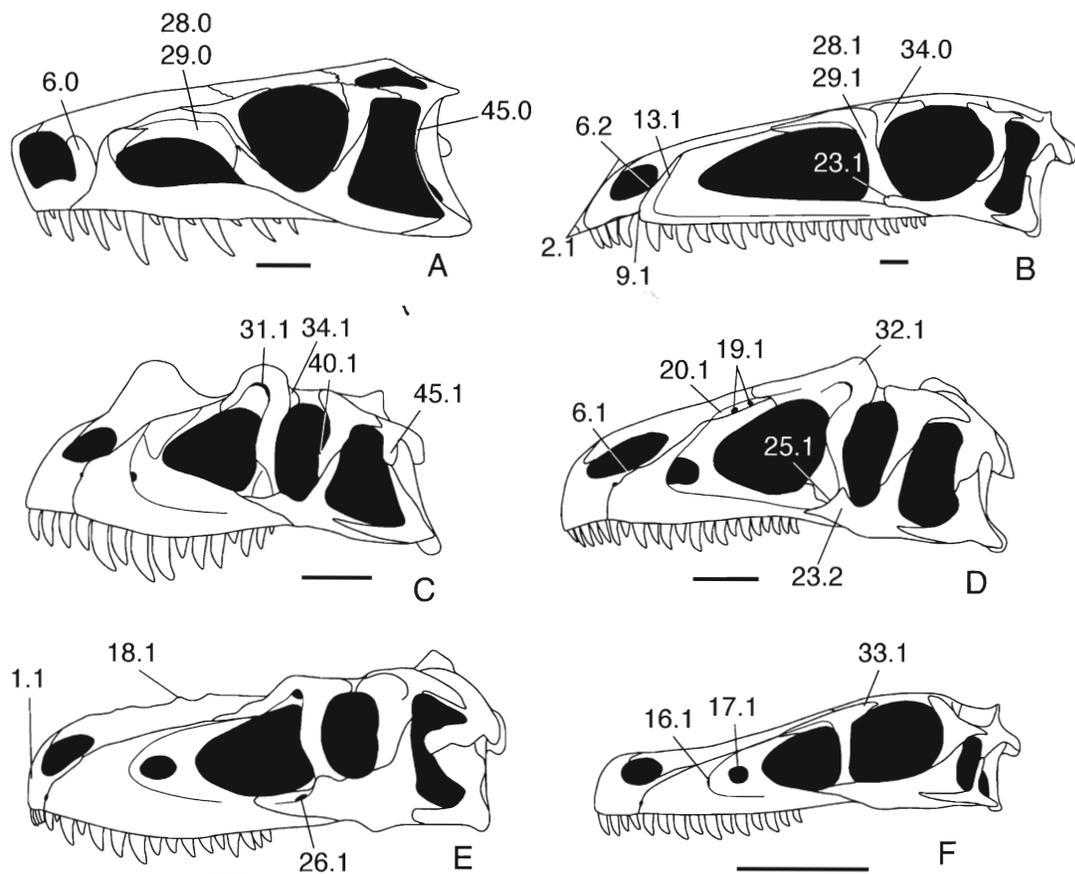
In oviraptorosaurs (e.g. Osmólska 1976; Barsbold *et al.* 1990), therizinosauroids (Clark *et al.* 1994), and ornithomimosaur (TMP 90.26.1) the articulated premaxillae are broadly rounded. In this case, the premaxillary suture is more limited to the anterior rim of the premaxillary body and the ascending process, but a broad palatal shelf is present below the external nares. The shelves of the adjacent premaxillae meet in the midline of the skull (see Text-fig. 18D).

4. Ventral process at the posterior end of premaxillary body: absent (0); present (1)

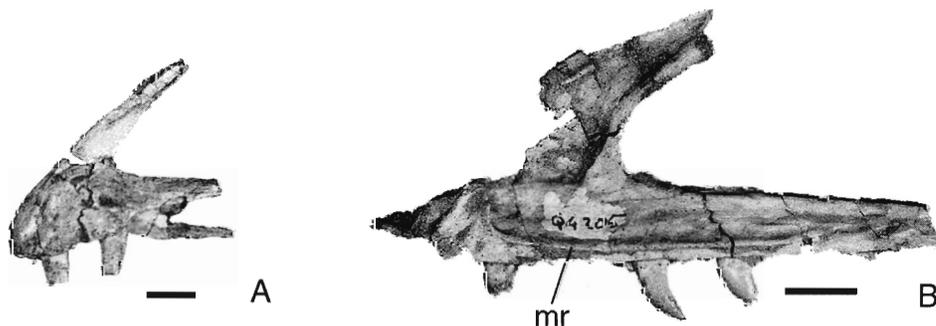
The posterior end of the premaxillary body usually has a posterior subnarial process, which extends posterodorsally and forms a part of the ventral margin of the external nares. In a few theropods, including *Syntarsus* (QG 193), *Coelophysis* (Colbert 1989), *Shuvosaurus* (TTU 9280), and *Compsognathus* (BSP A.S.I. 563), a second, more ventrally positioned posterior process is present (Text-fig. 8A). This ventral process borders an anterior process of the maxilla ventrally in *Syntarsus*, *Shuvosaurus*, and probably *Coelophysis*; the exact configuration of these bones in *Compsognathus* is uncertain.

5. Number of premaxillary teeth: three (0); four (1); five (2); more than five (3) (unordered)

The number of premaxillary teeth is variable in archosaurs. However, since some primitive archosaurs, including *Euparkeria* (Ewer 1965), most prosauropods, and the majority of theropods have four premaxillary teeth, this count is usually regarded as the primitive state in theropods (e.g. Currie and Zhao 1993b). However, *Ceratosaurus* (USNM 4735, UMNH VP 5278), *Compsognathus* (BSP A.S.I. 563), and *Torvosaurus* (Britt 1991) have three premaxillary teeth, *Allosaurus* (DNM 2560, MOR 693, USNM



TEXT-FIG. 7. Outgroup (A) and theropod (B-G) skull reconstructions in lateral view showing different character states of several cranial characters. For sources of reconstructions and identifications of the bones see Text-figures 4-6. A, *Euparkeria capensis*. B, *Syntarsus rhodesiensis*. C, *Ceratosaurus* sp. D, *Allosaurus fragilis*. E, *Gorgosaurus libratus*. F, *Velociraptor mongoliensis*. Character state indications in this and all following illustrations are as follows: numbers refer to characters discussed in the text; the first number indicates the number of the character, the second the character state. Scale bars represent 10 mm (A-B), 50 mm (F-G) and 100 mm (C-E).



TEXT-FIG. 8. *Syntarsus rhodesiensis*. A, left premaxilla in lateral view (QG unnumbered) showing the forked posterior end of the premaxillary body in this taxon (character state 1 of character 4). B, left maxilla in lateral view (QG 205) showing the horizontal ridge (mr) on the ventral border of the maxillary body (character state 1 of character 15). Scale bars represent 10 mm.

4734) and *Neovenator* (Hutt *et al.* 1996) have five, and baryonychids (BMNH R 9951, MNN GAD 501) and the basal ornithomimosaur *Pelecanimimus* seven (Pérez-Moreno *et al.* 1994).

6. Subnarial posterior process of the premaxilla: wide, plate-like, broadly contacting the nasals and excluding the maxilla from the external nares (0); strongly reduced in width, but still contacting the nasals (1); strongly reduced process does not contact the nasals, and the maxilla forms part of the posteroventral border of the external nares (2) (modified from Gauthier 1986; ordered)

In theropod outgroups and a few theropod taxa, including *Herrerasaurus* and ornithomimosaur, the maxilla is separated from the external nares by a broad, posterodorsally ascending process of the premaxilla that contacts the nasal (Text-fig. 7A). In these taxa the process is plate-like, i.e. much broader anteroposteriorly (or dorsoventrally) than wide transversely. In the vast majority of theropods, and probably in saurischians ancestrally (Gauthier 1986), this process is markedly reduced to a narrow, rod-like structure. In this case, the process might still contact the nasal (character state 1; Text-fig. 7D), as for example in *Allosaurus*, *Sinraptor*, and *Ornitholestes*, or it might be completely separated from the nasal (character state 2; Text-fig. 7B), as for example in *Syntarsus*, *Ceratosaurus*, abelisaurids, *Monolophosaurus*, and several other taxa. Since the process has to be reduced to lose contact with the nasal, this feature is treated as an ordered character.

7. External nares: facing laterally (0); facing strongly anterolaterally (1)

In most dinosaurs the external nares face more or less strictly laterally, since their posterior rim is not significantly offset laterally from their anterior border. In *Ceratosaurus* (USNM 4735) and abelisaurids (MACN CH 894, FMNH 96202-44C) the posterior rim of the nares is strongly flared laterally so that the opening faces partially anteriorly (Text-fig. 9B).

8. Constriction between articulated premaxillae and maxillae: absent (0); present (1)

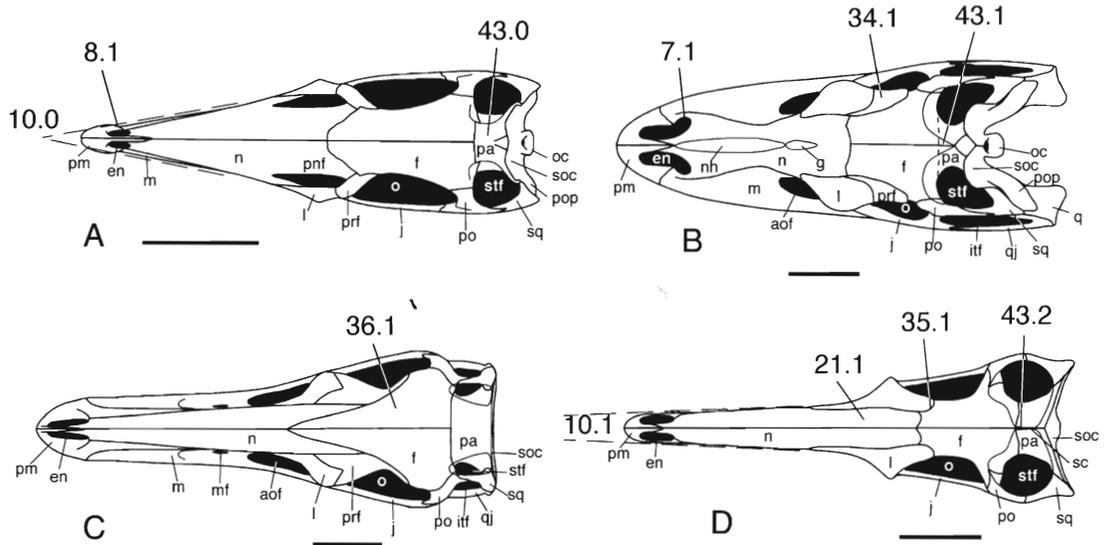
In the vast majority of theropods the lateral margin of the jaws is continuous along the premaxillary-maxillary suture in ventral or dorsal view. In a variety of taxa, including coelophysids (*Syntarsus*: QG 245, QG 202; *Coelophysis*: Colbert 1989), *Dilophosaurus* (UCMP V 6468), baryonychids (MNN GDF 501, BMNH R 9951; Charig and Milner 1997), and oviraptorosaurs (Barsbold 1977b; Barsbold *et al.* 1990), a pronounced constriction between the premaxilla and the maxilla is visible in dorsal (Text-fig. 9A) or ventral view so that the articulated premaxillae form a rosette in front of the maxillae.

9. Subnarial gap: absent (0); present (1) (Gauthier 1986)

In most crurotarsans, ornithischians, sauropodomorphs, and theropods the alveolar margin of the upper jaws is continuous. In some theropods, including *Coelophysis* (Colbert 1989), *Syntarsus* (QG 202), *Dilophosaurus* (UCMP V 6468, Welles 1984), baryonychids (MNN GDF 501, BMNH R 9951), and possibly *Compsognathus* (BSP A.S. I 563), the alveolar margin is bent upwards at the premaxillary-maxillary suture, creating a gap in the tooth row (Text-fig. 7B). This gap was termed the subnarial gap by Welles (1984). As discussed by Gauthier (1986), the presence of a subnarial gap seems to be plesiomorphic for archosaurs, but it was probably lost early in archosaur, or ornithodiran, evolution and the subnarial gap of some theropods is interpreted as a novelty.

10. Orientation of the maxillae towards each other as seen in dorsal view: acutely angled (0); subparallel (1) (Harris 1998)

In the majority of archosaurs, many non-theropodan dinosaurs, and a variety of theropods tangent lines along the lateral margins of the maxillae would converge to an acute angle in front of the premaxillae (Text-fig. 9A). In many theropods, including *Herrerasaurus* (Serenó and Novas 1993), *Allosaurus* (e.g. MOR 693, DNM 2560; Madsen 1976), baryonychids (MNN GDF 501; Sereno *et al.* 1998), and coelurosaurs (e.g. *Gorgosaurus*: FMNH PR 308; *Sinornithoides*: IVPP V 9612; ornithomimosaur: TMP 90.26.1; *Erlikosaurus*: Clark *et al.* 1994), the tangents are almost parallel (Text-fig. 9D).



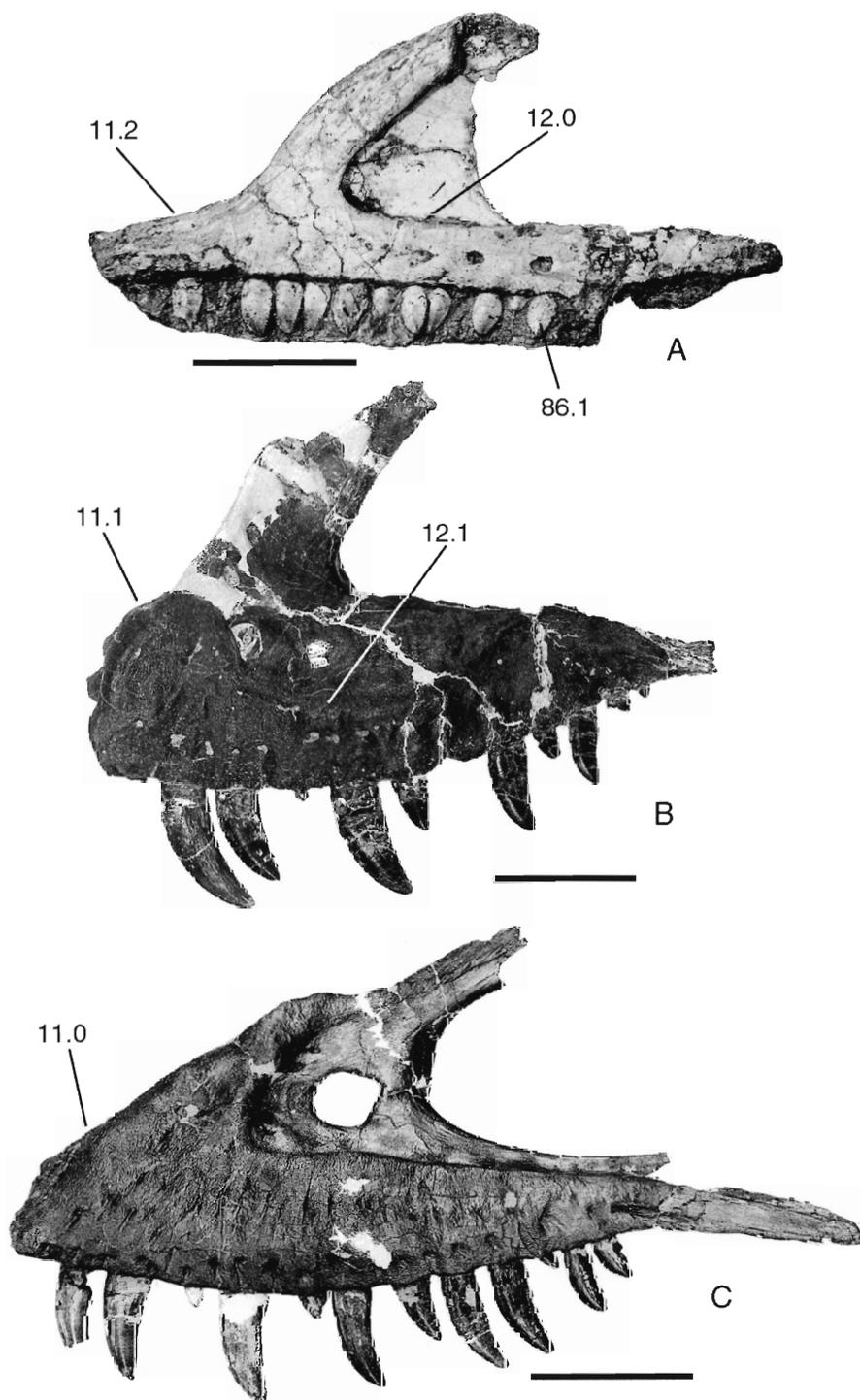
TEXT-FIG. 9. Theropod skulls in dorsal view showing different character states of several cranial characters. Character state indication as in Text-figure 7. A, *Syntarsus rhodesiensis*; modified from Raath (1977, figured in Colbert 1989). B, *Ceratosaurus nasicornis*; based on Marsh (1896), Gilmore (1920) and USNM 4735. C, generalized ornithomimosaur; based mainly on *Gallimimus bullatus*, figured in Osmólska *et al.* (1972), with some modifications based on *Ornithomimus* sp. (TMP 90.26.1). D, *Velociraptor mongoliensis*; redrawn from Barsbold and Osmólska (1999). Abbreviations as in Text-figures 4–6, and: g, groove; nh, nasal horn; pnf, postnasal fenestra; pop, paroccipital process; sc, sagittal crest. Scale bars represent 50 mm (A, C–D) and 100 mm (B).

11. Ascending process of the maxilla: confluent with anterior rim of maxillary body and gently sloping posterodorsally (0); offset from anterior rim of maxillary body, with anterior projection of maxillary body shorter than high (1); offset from anterior rim of maxillary body, with anterior projection of maxillary body as long as high or longer (2) (modified from Sereno *et al.* 1996; ordered)

In connection with the presence of the antorbital fenestra in archosaurs, members of this clade show an anteriorly placed ascending process of the maxilla. This process typically borders the antorbital fenestra anteriorly, and contacts the nasal and usually the posterior ascending process of the premaxilla.

In many basal archosaurs, crurotarsans, ornithischians, and a variety of the theropods, including *Herrerasaurus* (Sereno and Novas 1993), coelophysids (*Coelophysis*: Colbert 1989; *Syntarsus*: e.g. QG 202, QG 205, QG 206), *Dilophosaurus* (UCMP V 6468; Welles 1984), ‘*Szechuanosaurus*’ *zigongensis* (Gao 1993), Sinraptoridae (Currie and Zhao 1993b), ‘*Chilantaisaurus*’ *maortuensis* (IVPP V 2885), and the majority of coelurosaurs (e.g. *Compsognathus*: BSP A.S. I 563; *Sinosauropteryx*: NGMC 65; tyrannosaurids: AMNH 5346, FMNH PR 308; ornithomimosaurs: ROM 840, TMP 90.26.1; oviraptorosaurs: Barsbold *et al.* 1990; dromaeosaurids: AMNH 6515, TMP 94.12.844; troodontids: IVPP V 9612, MOR 553S; Aves: *Archaeopteryx*, Eichstätt specimen), the ascending process of the maxilla is confluent with the anterior rim of the maxillary body and the sutural contact with the premaxilla (Text-fig. 10c).

In a variety of other theropods, and sauropodomorphs, the ascending process is clearly offset from the anterior rim of the maxillary body, so that there is a distinct anterior projection of the body in front of the ascending process. This projection can be rather short and high (Text-fig. 10b; *Eoraptor*: PVSJ 512; *Piatnitzkysaurus*: MACN CH 895; *Proceratosaurus*: BMNH R 4860; *Ceratosaurus*: UMNH VP 5278; *Ornitholestes*: AMNH 619; abelisaurids: FMNH 96202-44C; carcharodontosaurids: SGM-Din 1), or as long or longer than high (Text-fig. 10a; sauropodomorphs: MB R. 1937; *Magnosaurus*: OUM J 13558;



TEXT-FIG. 10. Maxillae of a sauropodomorph (A) and two theropods (B–C) in left lateral view to illustrate the character states of characters 11, 12 and 86. A, *Plateosaurus* sp., left maxilla (GPIT Skelett 1). B, *Ceratosaurus* sp., left maxilla (UUVP VP 5278). C, *Gorgosaurus libratus*, right maxilla (reversed; ROM 1247). Scale bars represent 50 mm (A) and 100 mm (B–C).

*Monolophosaurus*: Zhao and Currie 1993; *Allosaurus*: DNM 2560, MOR 693; *Torvosaurus*: Britt 1991; *Afrovenator*: UC OBA 1; *Neovenator*: Hutt *et al.* 1996; baryonychids: BMNH R 9951, MNN GDF 501). Since character state 1 is included in character state 2, this character is treated as ordered.

12. Maxillary antorbital fossa: deep, and with sharp margins (0); shallow, margins formed by low ridges, a sharp rim may be present only in front of the promaxillary foramen (1) (modified from Sues 1997)

In most archosaurs a distinct antorbital fossa is present on the bones that surround the antorbital fenestra (i.e. the maxilla, the lacrimal and usually the jugal; Witmer 1997). The portion of the maxilla that participates in the antorbital fossa is usually referred to as the maxillary antorbital fossa. The maxillary antorbital fossa is depressed deeply below the lateral level of the surrounding bone, and bordered by sharp, often lamina-like margins in many non-theropodan taxa (Text-fig. 10A). In almost all theropods with the exception of *Eoraptor* (PVSJ 512), *Herrerasaurus* (Serenó and Novas 1993), abelisaurids (MACN CH 894, FMNH 96202-44C), baryonychids (MNN GDF 501), ornithomimosaurs (ROM 840, ROM 1790, TMP 90.26.1), oviraptorosaurs (ROM 43250), and therizinosauroids (Clark *et al.* 1994), the maxillary antorbital fossa is only slightly, or not at all depressed below the lateral level of the surrounding bone. Its margins are formed by low ridges, or indicated only by a change in texture of the bone (Text-fig. 10B). The maxillary antorbital fossa usually deepens towards its anterior rim, where it is pierced by the promaxillary foramen; a sharp margin is often present here.

13. Anterior margin of maxillary antorbital fossa: rounded or pointed (0); squared (1)

In the vast majority of archosaurs the maxillary antorbital fossa is rounded or tapers anteriorly. In a few theropods, including *Eoraptor* (PVSJ 512), *Coelophysis* (Colbert 1989; Witmer 1997, fig. 14), and *Syntarsus* (QG 194, 202, 205, 206), the anterior rim of the fossa is almost straight, and forms an acute angle with the ventral margin and a wide angle with the dorsal margin (Text-fig. 7B).

14. Maxillary antorbital fossa in front of the internal antorbital fenestra: 25 per cent or less of the length of the external antorbital fenestra (0); more than 40 per cent of the length of the external antorbital fenestra (1) (modified from Sereno *et al.* 1996)

In most archosaurs, including a variety of theropods, the maxillary antorbital fossa is rather small in relation to the size of the external antorbital fenestra and usually accounts for less than 25 per cent of the total length of this opening. In ornithischians and several theropods, including *Proceratosaurus* (BMNH R 4860) and all coelurosaurs (e.g. *Compsognathus*: BSP A.S. I 563; *Ornitholestes*: AMNH 619; tyrannosaurids: FMNH PR 308; ornithomimosaurs: ROM 840, TMP 90.26.1; therizinosauroids: Clark *et al.* 1994; dromaeosaurids: AMNH 6515; troodontids: IVPP V 9612, MOR 553S; Aves: *Archaeopteryx*, Eichstätt specimen), the size of the internal antorbital fenestra is reduced anteriorly, and the maxillary antorbital fossa is greatly enlarged so that it accounts for 40 per cent or more of the length of the external antorbital fenestra (e.g. Text-fig. 7E, F).

15. Horizontal ridge on the maxilla: absent (0); present (1) (Rowe and Gauthier 1990)

Whereas the ventral rim of the antorbital fossa is formed only by a low eminence in most theropods (see character 12), a strongly pronounced, rounded longitudinal ridge runs parallel to the tooth row along the ventral rim of the antorbital fossa (Text-fig. 8B) in a few taxa, including *Eoraptor* (PVSJ 512), *Coelophysis* (AMNH 7224), *Syntarsus* (QG 194, 202, 205, 206), *Liliensternus liliensterni* (MB R. 2175), and *Ornitholestes* (AMNH 619).

16. Promaxillary foramen: absent (0); present (1) (Carpenter 1992) and

17. Maxillary fenestra: absent (0); present (1) (Gauthier 1986)

The maxillary antorbital fossa is not pierced by any larger foramina in crurotarsan archosaurs, ornithischians, or sauropodomorphs. In many theropods, however, one or two, and in a few cases more,

large openings are found within this fossa, anterior to the internal antorbital fenestra. In theropods with two more or less horizontally arranged openings in the maxillary antorbital fossa, the more anterior one is usually termed the promaxillary foramen, while the posterior one, which is usually larger, is the maxillary fenestra (Witmer 1997).

The promaxillary foramen is usually small, often slit-like, and situated in the base of the ascending ramus of the maxilla (Text-fig. 7F), opening caudally to caudolaterally. Since the maxillary antorbital fossa continues somewhat into the ascending ramus in many theropods, being bordered laterally by a lamella of bone of the ramus, it is often concealed in lateral view. Internally, the promaxillary foramen leads into one or more internal chambers in the ascending ramus; these cavities are often, but not always closed medially (Witmer 1997). The promaxillary foramen is present in all theropods, with the exception of *Eoraptor* (PVSJ 512), *Herrerasaurus* (Serenó and Novas 1993), *Coelophysis* (Witmer 1997), *Syntarsus* (QG 194, 202, 205, 206), *Torvosaurus* (Britt 1991), and possibly therizinosaurs (Clark *et al.* 1994; Witmer 1997).

The maxillary fenestra is usually larger, opens laterally, and is clearly visible in lateral view (Text-fig. 7F). It is separated from the promaxillary foramen by a promaxillary strut. Internally, it opens into a large cavity, which may be open medially. A maxillary fenestra is found in *Magnosaurus oxoniensis* (OUM J 13558), *Piatnitzkysaurus* (MACN CH 895), *Allosaurus* (DNM 2560, MOR 693, USNM 4734), *Compsognathus* (BSP A.S. I 563), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b; the identification of the openings in the maxillary antorbital fossa follows Witmer 1997), *Afrovenator* (UC OBA 1), *Caudipteryx* (Ji *et al.* 1998), *Neovenator* (Hutt *et al.* 1996), *Sinosauropteryx* (NGMC 65), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 6515, TMP 94.12.844), ornithomimosaurids (ROM 840, TMP 90.26.1), troodontids (IVPP V 9612, MOR 553S), and tyrannosaurids (AMNH 5346, FMNH PR 308, ROM 1247).

*Monolophosaurus* has only one large opening in the maxillary antorbital fossa (Zhao and Currie 1993). This opening is in the right position for a promaxillary foramen (Witmer 1997), but it is larger than is usually the case for this foramen. Witmer (1997) suggested that this opening might be a joint promaxillary foramen and maxillary fenestra; however, the matter is uncertain, and character 17 has been coded as '?' for *Monolophosaurus*.

Baryonychids, '*Chilantaisaurus*' *maortuensis*, and carcharodontosaurids (SGM-Din 1) seem to lack a maxillary foramen. In the baryonychid *Suchomimus* (MNN GDF 501) and in '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), parts of the medial wall of the antorbital fossa may be missing, but enough is preserved to show that most probably no opening was present. Therefore, character 17 is coded as '0' in these taxa.

Witmer (1997) claimed that a maxillary foramen is present in *Proceratosaurus*. However, the medial wall of the antorbital fossa is damaged in the type and only known specimen (BMNH R 4860), so that the presence of this opening cannot be determined with certainty. There are matrix-filled openings in the wall at the approximate position where the maxillary fenestra would be expected, but these openings show broken edges and are not in the same position on the left and right side of the skull. Given these uncertainties, character 17 has been coded as '?' for *Proceratosaurus*.

Finally, the situation in oviraptorosaurs also seems to be somewhat uncertain. In the caenagnathid *Chirostenotes pergracilis* (ROM 43250), no maxillary fenestra seems to be present, unless it is positioned further posteriorly than in any known theropod. However, Barsbold (1977b) illustrated the skull of an oviraptorid with a maxillary fenestra (also in Barsbold *et al.* 1990, fig. 10.1.B), whereas Smith (1992) did not figure or mention an opening in the maxillary antorbital fossa of type specimen of *Oviraptor philoceratops*. Therefore, the character is coded as uncertain for oviraptorosaurs.

#### 18. Dorsal surface of the nasals: smooth (0); rugose (1)

The dorsal surface of the nasals is smooth in most crurotarsans, and in all ornithischians and sauropodomorphs. In some theropods, including *Monolophosaurus* (Zhao and Currie 1993), abelisaurids (MACN CH 894, FMNH 96202-44C), carcharodontosaurids (SGM-Din 1), and tyrannosaurids (FMNH PR 308, ROM 1247, 4591), it bears bony bumps and knobs (Text-fig. 7E), probably indicating the original presence of some type of keratinous epidermal structure covering this bone.

In *Ceratosaurus* (USNM 4735, MOR 005) the situation is equivocal: whereas the nasal horn core in this taxon shows a structured, rugose surface, the rest of the nasal is smooth.

19. Pneumatic foramen in the nasals: absent (0); present (1)

Accessory pneumatic openings in the bones surrounding the internal antorbital fenestra are found in several groups of archosaurs, but they are rarely present in the nasals (Witmer 1997). Although a nasal recess may be found in at least some prosauropods (Witmer 1997), one or more true foramina, leading into pneumatic chambers within each nasal, are only found in some theropods, including *Ceratosaurus* (USNM 4735), abelisaurids (FMNH 96202-44C), *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (DNM 2560, MOR 693), sinraptorids (Currie and Zhao 1993b), carcharodontosaurids (SGM-Din 1), and oviraptorosaurs (Witmer 1997). These pneumatic foramina are usually placed in the ventrolateral surface of the nasals, at about the mid-length of the bone or further posteriorly (Text-fig. 7D), and communicate with the paranasal air sinus of the maxillary antorbital fossa. The mode of pneumatization in oviraptorosaurs might be slightly different (Witmer 1997), probably indicating convergence in this group.

20. Dorsal extent of antorbital fossa: dorsal rim of antorbital fossa below nasal suture, or formed by this suture (0); antorbital fossa extending onto the lateroventral side of the nasals (1) (Serenó *et al.* 1994)

As noted above, a well-developed antorbital fossa surrounding the internal antorbital fenestra usually expands on the maxilla, lacrimal and jugal (Witmer 1997), but not onto the nasal. In some theropods, including *Monolophosaurus* (Zhao and Currie 1993), sinraptorids (Currie and Zhao 1993b), *Allosaurus* (DNM 2560, MOR 693), carcharodontosaurids (SGM-Din 1), and *Neovenator* (Hutt *et al.* 1996), the antorbital fossa also expands onto the nasal. This expansion is usually developed as a crescent-shaped fossa on the ventrolateral side of the posterior part of the nasal, and is confluent with the maxillary antorbital fossa at the ascending process of the maxilla (Text-fig. 7D).

A small crescent-shaped facet is found on the ventrolateral side of the nasal of at least some tyrannosaurids (e.g. ROM 1247, 4591). However, since this facet is far less developed than the fossa in the taxa mentioned above, this character is coded as uncertain for tyrannosaurs.

21. Shape of nasals: expanding posteriorly (0); of subequal width throughout their length (1) (modified from Bakker *et al.* 1988)

In most archosaurs, including many crurotarsans, ornithischians, sauropodomorphs, and several theropods, the shape of the nasals reflects the posterior widening of the skull. In *Ceratosaurus* (USNM 4735, MOR 005, 009) and abelisaurids (MACN CH 894, FMNH 96202-44C), the fused nasals are of subequal width throughout their length. However, the fused nasals are overall rather short and broad in these taxa (Text-fig. 9B).

In a variety of other theropods, including carcharodontosaurids (SGM-Din 1), tyrannosaurids (ROM 1247, 4591), ornithomimosaurs (ROM 851, TMP 90.26.1), troodontids (Barsbold 1974), dromaeosaurids (AMNH 6515), and birds (*Archaeopteryx*: Eichstätt specimen), the nasals are also of subequal width throughout their length, but they are also very long and slender (Text-fig. 9C–D).

The situation in oviraptorosaurs and therizinosaurids is equivocal. The only known skull of a therizinosaur, that of *Erlikosaurus*, only has the right nasal preserved; furthermore, the skull roof seems to be distorted in the lacrimal/prefrontal region, so the preservation does not allow a final decision about the character state (Clark *et al.* 1994).

In oviraptorosaurs the nasals are very short due to the marked shortening of the preorbital part of the skull in these animals. Whereas the nasal seems to be very slender and subequal in width throughout its length in *Oviraptor* (Barsbold *et al.* 1990, fig. 10.1C), it is very broad and widens posteriorly in *Conchoraptor* (Barsbold *et al.* 1990, fig. 10.2B). Thus, the character is coded as uncertain in oviraptorosaurs.

22. Pronounced lateral rims of the nasals, sometimes bearing lateral cranial crests: absent (0); present (1)

In most archosaurs, including most crurotarsans, ornithischians, sauropodomorphs, and the majority of theropods, the skull profile is transversely rounded above the nasals. In *Coelophysis* (AMNH 7223, 7224), *Syntarsus rhodesiensis* (QG 194, 202), *Allosaurus* (DNM 2560, MOR 693, USNM 4734), and sinraptorids (Currie and Zhao 1993b) the lateral rims of the nasals are raised and form low, longitudinal, laterodorsal ridges on the skull roof. In *Syntarsus kayentakatae* (Rowe 1989) and *Dilophosaurus* (UCMP V 6468) these ridges are expanded into high lateral cranial crests.

23. Sublacral part of jugal: tapering (0); bluntly squared anteriorly (1); expanded (2) (unordered)

The anterior end of the jugal tapers in lateral view in many crurotarsans, ornithischians, and all prosauropods. Sauropods sometimes have expanded anterior parts of the jugal, but this bone is highly modified in that group. Furthermore, the presence of an anteriorly tapering jugal in primitive ornithischians and sauropodomorphs indicates that this is the plesiomorphic character state for dinosaurs.

In *Syntarsus* (QG 278), *Shuvosaurus* (TTU P 9280), and *Liliensternus liliensterni* (MB R. 2175) the anterior end of the jugal does not taper, but is bluntly squared (Text-fig. 7B).

In many other theropods, including *Herrerasaurus* (Sereno and Novas 1993), *Dilophosaurus* (UCMP V 4214, 6468), *Monolophosaurus* (Zhao and Currie 1993), *Proceratosaurus* (BMNH R 4860), *Allosaurus* (DNM 2560), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), abelisaurids (FMNH 96202-44C), carcharodontosaurids (SGM-Din 1), and tyrannosaurids (FMNH PR 308), the jugal is strongly dorsoventrally expanded underneath the contact with the lacrimal, so that the bone is higher here than in its suborbital part (Text-fig. 7D).

The character states for this character in *Eoraptor* and *Compsognathus* are uncertain, although the bone is preserved in these taxa. However, character state '2' can be ruled out, so character 24 is coded as a '0/1' uncertainty for these taxa.

24. Anterior end of jugal: posterior to internal antorbital fenestra, but reaching its posterior rim (0); excluded from the internal antorbital fenestra (1); expressed at the rim of the internal antorbital fenestra and with a distinct process that extends anteriorly underneath it (2) (modified from Holtz 1994; unordered)

In many crurotarsans, all basal ornithischians, most sauropodomorphs, and many theropods the jugal contributes to the rim of the internal antorbital fenestra, just reaching it in its posteroventral corner.

In *Eoraptor* (PVSJ 512), *Allosaurus* (DNM 2560), *Ceratosaurus* (USNM 4735), and oviraptorosaurs (Barsbold 1977b; Barsbold *et al.* 1990) the jugal is completely excluded from the internal antorbital fenestra (Text-fig. 7C–D). The situation in *Syntarsus* is uncertain; in the partially articulated skull of the holotype of *Syntarsus kayentakatae* the jugal seems to be excluded from the internal antorbital fenestra (Rowe 1989).

Holtz (1994) obviously considered character state 1 to be the plesiomorphic state in theropods, stating 'jugal expressed on the rim of the antorbital fenestra' as the derived character state found in coelurosaurs. However, the fact that the jugal forms part of the rim of the internal antorbital fenestra in the primitive ornithischians *Lesothosaurus* (Sereno 1991b), *Scelidosaurus* (Coombs *et al.* 1990), and *Heterodontosaurus* (Weishampel and Witmer 1990a), as well as in articulated skulls of prosauropods (SMNS 13200, MB R. 1937), and what appear to be the most primitive theropods (Sereno and Novas 1993), indicates that this is the primitive character state.

In a large number of theropods the jugal has a pointed anterior process that expands anteriorly underneath the internal antorbital fenestra (e.g. Text-fig. 7E). This is the case in *Herrerasaurus* (Sereno and Novas 1993), *Dilophosaurus* (UCMP V 4214, 6468), *Monolophosaurus* (Zhao and Currie 1993), sinraptorids (Dong *et al.* 1983; Currie and Zhao 1993b), abelisaurids (FMNH 96202-44C), birds (*Archaeopteryx*: Munich specimen), baryonychids (SMNS 58022), carcharodontosaurids (SGM-Din 1), dromaeosaurids (AMNH 6515), ornithomimosaurids (ROM 840, 851, TMP 90.26.1), therizinosaurs (Clark *et al.* 1994), troodontids (IVPP V 9612), and tyrannosaurids (FMNH PR 308). In '*Chilantaisaurus*'

*maortuensis* (IVPP V 2885) the jugal is not preserved, but the articular facet for this bone on the maxilla shows that it had an anterior process.

25. Jugal antorbital fossa: absent or developed as a slight depression (0); large, crescentic depression on the anterior end of the jugal (1)

In the majority of dinosaurs, including many theropods, a jugal antorbital fossa is absent or developed only as a slight depression on the anterior part of the jugal. In a variety of theropods, including *Monolophosaurus* (Zhao and Currie 1993), *Proceratosaurus* (BMNH R 4860), *Allosaurus* (DNM 2560, MOR 693), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), carcharodontosaurids (SGM-Din 1), and tyrannosaurids (FMNH PR 308, ROM 1247), the jugal antorbital fossa is developed as a large depression that is bound posteroventrally by a pronounced, crescentic rim (Text-fig. 7D).

26. Pneumatisation of the jugal: absent (0); jugal pneumatised by a foramen in the posterior rim of the jugal antorbital fossa (1) (Serenó *et al.* 1996)

As noted above, accessory pneumatic chambers in the bones surrounding the internal antorbital fenestra are found in several archosaur groups, but a pneumatic foramen leading into the body of the jugal has not been described in any crurotarsan (although internal chambers might be present in some crocodylomorphs; Wu and Sues 1996), ornithischian, or sauropodomorph (Witmer 1997). Such a foramen is present in several theropods, including *Monolophosaurus* (Zhao and Currie 1993), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), carcharodontosaurids (SGM-Din 1), and tyrannosaurids (FMNH PR 308, ROM 1247). The foramen is situated in the posteroventral corner of the jugal antorbital fossa (Text-fig. 7E) and usually leads into more or less extensive internal chambers within the jugal.

The presence of such a foramen in *Allosaurus* is uncertain: whereas Currie and Zhao (1993b) noted that it was present in this taxon, I was unable to identify it in the articulated skulls DNM 2560 and MOR 693. If a foramen is present in *Allosaurus*, it seems to be rather small.

27. Jugal: broad, plate-like (0); very slender, rod-like (1)

In the vast majority of dinosaurs and theropods the jugal is a rather broad, plate-like element. In *Avimimus* (ROM 46144), oviraptorosaurs (Barsbold 1977b; Barsbold *et al.* 1990) and birds (*Archaeopteryx*: Munich specimen) it is strongly reduced in height and thus rather rod-like.

28. Lacrimal: block-shaped or roughly triangular in lateral view (0); dorsoventrally elongated, inverted L-shaped, and broadly exposed on skull roof (1) (modified from Gauthier 1986) and
29. Height of the lacrimal: significantly less than the height of orbit, and usually fails to reach the ventral margin of orbit (0); as high as the orbit, and contacts jugal at the level of the ventral margin of orbit (1)

Gauthier (1986, p.18) defined this character as 'lacrimal broadly exposed on the skull roof' in his definition of the Theropoda, and discussed its distribution among archosaurs. However, the lacrimal is more or less broadly exposed on the skull roof in several crurotarsans (e.g. Chatterjee 1985) and some sauropodomorphs (e.g. MB R. 1937; see Galton 1990), making a more precise definition of this character necessary.

In crurotarsans such as *Postosuchus* (Chatterjee 1985) and *Sphenosuchus* (Walker 1990), where the lacrimal is often said to be 'theropod-like' this bone is usually relatively short dorsoventrally, and the anterior process is dorsoventrally deep, being occupied largely by the lacrimal antorbital fossa (also in the basal archosaur *Euparkeria*; Text-fig. 7A). Thus, the outline of the lacrimal is roughly block-like in these animals.

In ornithischians, the lacrimal is restricted to the ventral part of the anterior rim of the orbit (e.g. Haubold 1991; Sereno 1991b). The shape of the bone is subrectangular to roughly triangular in these taxa.

In most saurischians, with the exception of *Herrerasaurus* (Sereno and Novas 1993), the lacrimal has a dorsoventrally elongated, rod-like preorbital part, thus forming more or less the entire anterior rim of the orbit and contacting the jugal at the level of the ventral rim of this opening (e.g. Text-fig. 7B). However, in articulated skulls the lacrimal of sauropodomorphs is more or less strut-like and only slightly exposed on the skull roof, if at all (e.g. Gilmore 1925; Janensch 1935–36; Galton 1990). In all theropods, with the exception of *Herrerasaurus* (Sereno and Novas 1993), the lacrimal has an inverted L-shape (e.g. Text-fig. 7B); the main body of the bone is dorsoventrally long and slender, and a slender anterior process of subequal length is present, usually set at an angle of slightly less than 90 degrees towards the main body. In addition, the anterior process is broadly exposed on the skull roof anterior to the orbit.

30. Passage of nasolacrimal duct: leading through the body of the ventral process of the lacrimal (0); ventral process of lacrimal not pierced, lateral side depressed below the level of the surrounding bones, and nasolacrimal duct passes lateral to the process (1) (Witmer, pers. comm. 1998)

The nasolacrimal duct pierces the main body of the lacrimal in almost all tetrapods (see e.g. Witmer 1997, for archosaurs). However, in ornithomimosaur (ROM 840, TMP 90.26.1), troodontids (MOR 553S), and birds (*Archaeopteryx*: Eichstätt specimen) the lateral surface of the ventral process of the lacrimal is depressed below the level of the surrounding bones, and the process is not pierced; the nasolacrimal duct passes laterally to the bone. In dromaeosaurids the lateral surface of the ventral process of the lacrimal is also slightly depressed below the level of the surrounding bones (e.g. AMNH 6515), but it exhibits a foramen for the passage of the nasolacrimal duct.

31. Lacrimal fenestra: absent (0); present (1) (Molnar *et al.* 1990)

Extensions of the paranasal air sinus system from the lacrimal antorbital fossa into the body of the lacrimal are unknown in crurotarsans, ornithischians, and sauropodomorphs (Witmer 1997). In many theropods, including *Magnosaurus* (OUM J 13558), *Allosaurus* (DNM 2560, MOR 693), *Ceratosaurus* (USNM 4735), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), baryonychids (SMNS 58022), carcharodontosaurids (SGM-Din 1), and tyrannosaurids (FMNH PR 308, ROM 1247), a large opening, situated in the rim of the lacrimal antorbital fossa in the posterodorsal angle of the bone, leads into a large chamber in this part of the bone (Text-fig. 7c). In some taxa, this chamber is further subdivided. In abelisaurids (FMNH 96202-44C) the lacrimal antorbital fossa is strongly reduced, and no fenestra is present in its dorso-posterior rim laterally. However, there is a large opening into the lacrimal body from the medial side that corresponds in position and morphology with the lacrimal fenestra of other theropods and is thus regarded as probably a homologous structure.

Witmer (1997) reported a lacrimal fenestra in a new, so far undescribed specimen of the dromaeosaurid *Deinonychus*. However, no such structure was observed in the type specimen of *Velociraptor mongoliensis* (AMNH 6515; see also Barsbold and Osmólska 1999); therefore, the character is coded as an uncertainty in dromaeosaurids.

In oviraptorosaurs the nasal and lacrimal are highly pneumatized (Barsbold *et al.* 1990; Witmer 1997). Although the pattern of pneumatization of the lacrimal in this group seems to be different from that seen in other theropods (Witmer 1997), possibly indicating convergence, the derived character state has been coded as present for this clade.

32. Lacrimal ‘horn’: absent (0); present (1) (Russell and Dong 1993a)

In crurotarsans, ornithischians, sauropodomorphs, and many theropods the posterodorsal edge of the lacrimal is usually angular, not expanded and shows a smooth external surface. In many theropods, the posterodorsal border of this bone is rounded, swollen, and often elevated, forming a horn-like structure (Text-fig. 7D). This ‘horn’ might be low, as in *Magnosaurus* (OUM J 13558), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), some baryonychids (*Irritator*: SMNS 58022), carcharodontosaurids (SGM-Din 1), and the majority of tyrannosaurs (FMNH PR 308, ROM 1247), or it can be strongly dorsally expanded, as in *Allosaurus* (DNM 2560, USNM 4734), *Ceratosaurus*

(USNM 4735), and the baryonychid *Baryonyx* (BMNH R 9951). In several of these taxa (*Allosaurus*, *Ceratosaurus*, tyrannosaurids), the bone surface of this 'horn' is roughened, probably indicating that a keratinous covering was present in life.

Owing to the strong modification of the frontal and its surrounding bones, the situation in abelisaurids is unclear. Both *Carnotaurus* (MACN CH 894) and *Majungatholus* (FMNH 96202-44C) have a thickened posterodorsal part of the lacrimal, and *Carnotaurus* also has a dorsal projection of this bone that keys into a ventral notch of the frontal horns of this taxon. However, the lacrimal of these taxa is unlike that of other theropods in showing a probably apomorphic, broad posterior process (see character 33). Although it seems probable that abelisaurids derived this condition from an ancestor that had a lacrimal horn, some uncertainty remains.

In ornithomimosaurids the derived members of this clade do not show any signs of a lacrimal horn (ROM 840, 851, TMP 90.26.1), whereas a dorsal projection on the posterodorsal corner of this bone is present in the basal ornithomimosaur *Pelecánimimus* (Pérez-Moreno *et al.* 1994). Therefore, the character is coded as an uncertainty in these animals.

33. Posterior dorsal process of lacrimal: absent (0); present (1) (Currie 1995)

As noted above, the lacrimal of theropods usually shows the shape of an inverted L. In several taxa, including abelisaurids (MACN CH 894, FMNH 96202-44C), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 6515), ornithomimosaurids (ROM 840, TMP 90.26.1), oviraptorosaurs (Barsbold *et al.* 1990; Smith 1992), and troodontids (MOR 553S), the lacrimal has a posterior supraorbital process, and is thus T-shaped (Text-fig. 7F). In abelisaurids the posterior process might be the prefrontal, fused without any visible suture to the lacrimal. In other taxa the process seems to be a true outgrowth of the lacrimal, since the prefrontal is still present as an individual element in most of these clades.

34. Prefrontal: exposed dorsally on the anterior rim of the orbit in lateral view and with a slender ventral process along the medioposterior rim of the lacrimal (0); excluded from the anterior rim of the orbit in lateral view, being displaced posteriorly and/or medially; ventral process absent (1)

In ornithischians (e.g. Sereno 1991b), prosauropods (GPIT Skelett 1, MB R. 1937), and some theropods, including *Herrerasaurus* (Sereno and Novas 1993), *Coelophysis* (Colbert 1989; Witmer 1997, fig. 14), *Syntarsus* (QG 193), *Shuvosaurus* (TTU P 9280), and *Ornitholestes* (AMNH 619), the prefrontal is a roughly triangular element that is exposed posterodorsally to the lacrimal on the anterior margin of the orbit. In prosauropods and at least *Syntarsus*, the prefrontal has a very slender ventral process that runs along the posteromedial border of the lacrimal (Text-fig. 7B).

In all other theropods the prefrontal is displaced posteriorly and often medially from the anterodorsal corner of the orbit (Text-figs 7C, 9B). Furthermore, no trace of the ventral process could be found in any of the specimens examined. In some theropods (abelisaurids, birds, dromaeosaurids) the prefrontal is absent or fused to the lacrimal without any visible suture (Text-fig. 9D).

35. Configuration of lacrimal and frontal: lacrimal separated from frontal by prefrontal (0); lacrimal contacts frontal (1)

In ornithischians, prosauropods, and many theropods the lacrimal is separated from the frontal by the prefrontal. In a variety of theropods, including *Shuvosaurus* (TTU P 9280), abelisaurids (MACN CH 894, FMNH 96202-44C), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 6515), oviraptorosaurs (Barsbold *et al.* 1990), troodontids (Currie 1985), and tyrannosaurids (FMNH PR 308), the prefrontal is strongly reduced or absent, and the lacrimal contacts the frontal (Text-fig. 9D). Thus, this character is used here instead of Gauthier's (1986, p. 30) 'prefrontal strongly reduced or absent'.

36. Frontal: rectangular (0); elongated triangular (1) (Holtz 1994)

In most crurotarsans, ornithischians, sauropodomorphs, and theropods the frontals are rectangular or polygonal in shape, often with an abrupt lateral expansion behind the orbits. The suture with the nasals is either a more or less straight transverse line or consists of interlocking alternating processes of the nasals

and frontals. In a few theropods, including *Shuvosaurus* (TTU P 9280), *Syntarsus* (QG 194), birds (*Archaeopteryx*: Eichstätt specimen), ornithomimosaurs (ROM 851, TMP 90.26.1), and troödontids (Currie 1985), the articulated frontals are roughly triangular, anteroposteriorly elongated, and form a tapering medial process between the posterior processes of the nasals (Text-fig. 9c). In therizinosaurs the frontals are similar in shape to these elements in ornithomimosaurs, but there seems to be a small lateral anterior process (Clark *et al.* 1994). Thus, the character is coded as an uncertainty in this clade.

37. Medial delimitation of the orbit on the ventral side of the frontals: not expanded ventrally (0); expanded ventrally, forming a pronounced rim for the eyeballs (1) (modified from Holtz 1994)

A facet for the eyeballs is usually found on the lateral ventral parts of the frontals in theropods. However, usually this facet is rather flat, and its medial rim is not significantly expanded ventrally (Text-fig. 11A). In *Avimimus* (ROM 46144), birds (based on modern taxa), dromaeosaurids (TMP 74.10.5), ornithomimosaurs (Currie, pers. comm. 1998), therizinosaurs (Currie 1992), and troödontids (AMNH 6174, TMP 86.36.4, 88.50.88) the facet for the eyeball is strongly concave transversely, and the medial rim of this facet is expanded ventrally (Text-fig. 11c).

38. Infratemporal fenestra: smaller than or subequal in size to orbit (0); strongly enlarged, more than 1.5 times the size of the orbit (1) (modified from Bonaparte 1991b)

In most crurotarsans, all ornithischians, and the vast majority of saurischians the infratemporal fenestra is smaller or subequal in size to the orbit. In *Ceratosaurus* (USNM 4735), sinraptorids (Currie and Zhao 1993b), and abelisaurids (MACN CH 894) this opening is greatly enlarged, being 1.5 times the size of the orbit, or larger.

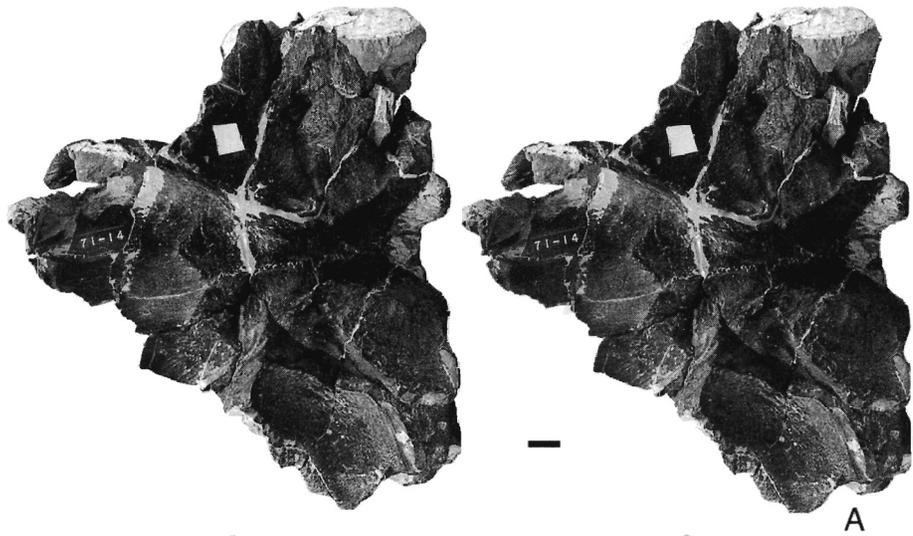
39. Contact between lacrimal and postorbital: absent (0); present (1) (Sampson *et al.* 1998)

In the vast majority of theropods the frontal forms part of the dorsal rim of the orbit, and the lacrimal and postorbital are clearly separated. In abelisaurids (MACN CH 894), carcharodontosaurids (SGM-Din 1), and in some, but not all, specimens of the tyrannosaurid *Tyrannosaurus* (Osborn 1912a), the lacrimal has a broad contact with the postorbital (Text-fig. 6A, C); thus, the frontal is excluded from the orbit. Since this is not the case in other tyrannosaurids, the character is coded as uncertain for this clade.

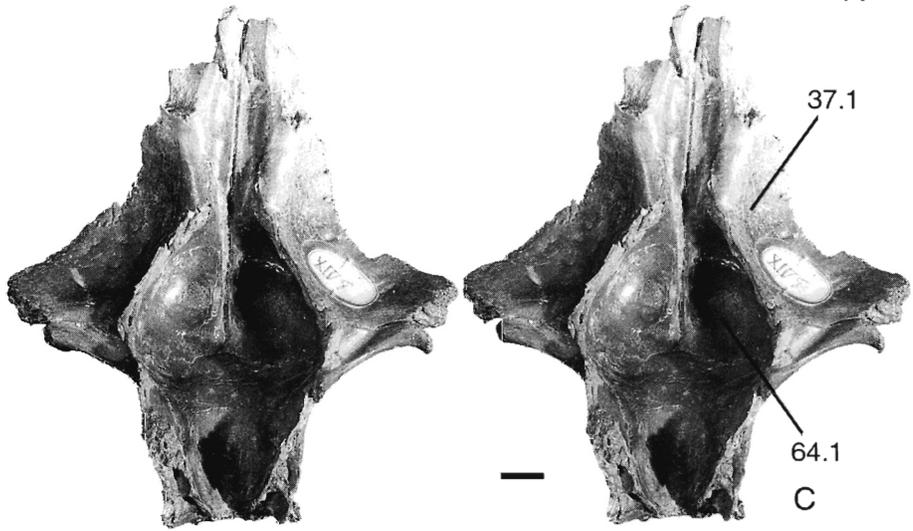
40. Jugal process of the postorbital: ventrally directed and tapering (0); with a small anterior spur indicating the lower delimitation of the eyeball (1)

In most dinosaurs the ventral process of the postorbital is a simple rod of bone that tapers ventrally where it overlaps the dorsal process of the jugal. In a few medium-sized to large theropods, including *Ceratosaurus* (USNM 4735), sinraptorids (Currie and Zhao 1993b), abelisaurids (MACN CH 894, FMNH 96202-44C), and carcharodontosaurids (SGM-Din 1), the ventral process of the postorbital has a small, triangular anterior process that projects into the orbit, and probably marks the lower limit of the eyeball (Text-fig. 7c). Although this character is probably size-related and limited in its distribution to medium-sized or large taxa, it is used here since it is not present in all large theropods and might, therefore, be useful to determine relationships between some of the larger taxa.

In *Tyrannosaurus* (Osborn 1912a; Molnar 1991) and, to a lesser extent in *Tarbosaurus* (Holtz, pers. comm. 2001), the ventral process of the postorbital also intrudes into the orbit. However, in this animal the whole ventral process is plate-like and anteriorly directed; thus, the structure seems to be significantly different from that described above. Since no other tyrannosaur taxa show this feature, it is regarded as an autapomorphy of the *Tyrannosaurus*–*Tarbosaurus* clade (Holtz 2001), and character 40 is coded as ‘0’ for tyrannosaurids.



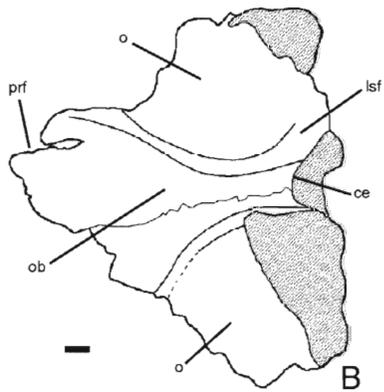
A



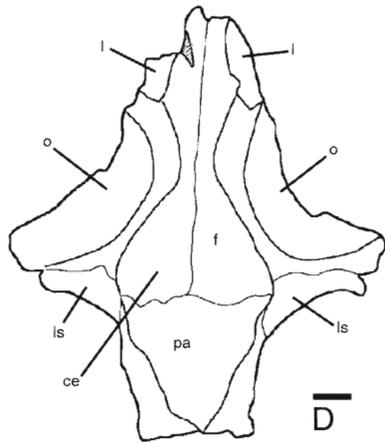
37.1

64.1

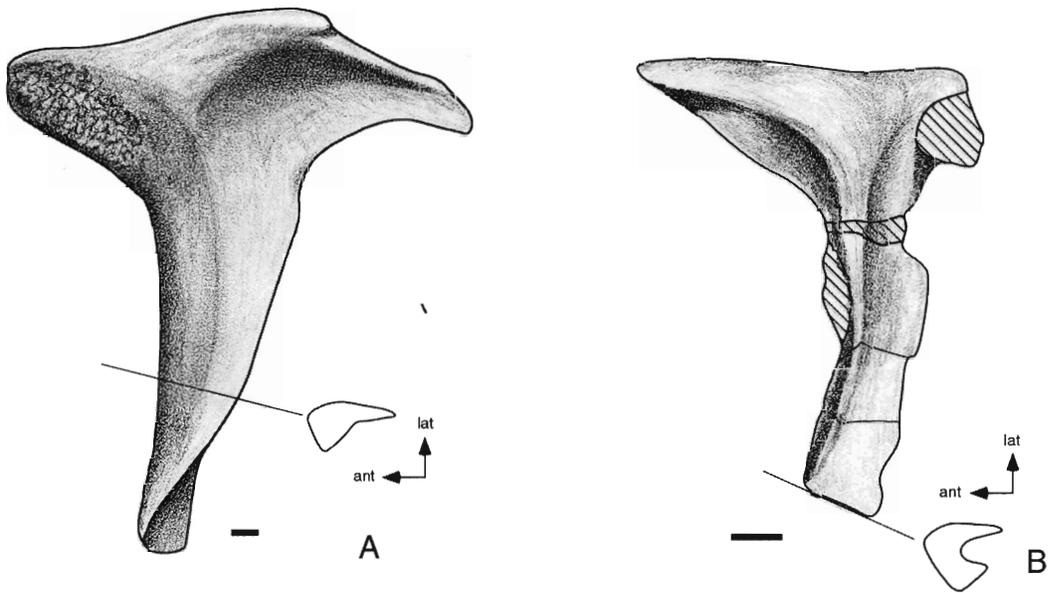
C



B



D



TEXT-FIG. 12. Left postorbital of two theropods in lateral view and cross-section through the jugal process, illustrating the differences in the outline of the cross-sections (character 41). A, *Allosaurus fragilis*, based on Madsen (1976). B, *Magnosaurus oxoniensis*, based on OUM J 13558. Abbreviations: ant, anterior; lat, lateral. Scale bars represent 10 mm.

41. Cross-section of the ventral process of the postorbital: triangular (0); U-shaped (1) (Serenó *et al.* 1994, 1996)

The jugal process of the postorbital has its greatest transverse width at the orbital border, and in the vast majority of theropods it tapers towards the infratemporal fenestra; it thus shows a triangular cross-section (Text-fig. 12A). In *Magnosaurus* (OUM J 13558), *Torvosaurus* (Britt 1991), and *Afrovenator* (UC OBA 1) the process has a medial posterior lamella, so that its cross-section is U-shaped, opening posteriorly (Text-fig. 12B).

42. Posteriorly placed, knob-like dorsal projection of the parietals: absent (0); present (1) (Bonaparte 1991b; Holtz 1994)

The posterior part of the parietals lies at the same level as the more anterior parts of the skull roof, or is slightly raised towards the supraoccipital crest in ornithischians, sauropodomorphs, and most theropods. In some theropods, including *Ceratosaurus* (MOR 005, 009), sinraptorids (Currie and Zhao 1993b), abelisaurids (MACN CH 894, FMNH 96202-44C), baryonychids (BMNH R 9951), and carcharodontosaurids (SGM-Din 1), the posterior part of the parietals develops into a median dorsal projection that is as long anteroposteriorly as it is wide transversely, or even longer (Text-fig. 14c). In abelisaurids this projection is roughly diamond-shaped in dorsal view, whereas it is oval in sinraptorids and carcharodontosaurids.

TEXT-FIG. 11. Theropod frontals in ventral view, illustrating character states for characters 37 and 64. A, stereophotographs of articulated frontals of *Allosaurus fragilis* (UMNH VP 5470); anterior is to the left. B, same as A; outline drawing. C, stereophotographs of articulated posterior skull roof (frontals, parietals, laterosphenoids) of *Troödon formosus* (AMNH 6174); anterior is to the top. D, same as C; outline drawing. Abbreviations: ce, facet for the cerebral hemispheres on the frontals; f, frontal; l, facets for the lacrimals; ls, laterosphenoid; lsf, facets for the laterosphenoids; o, orbital facet; ob, facets for the olfactory bulbs on the frontals; pa, parietal; prf, contact with the prefrontal. Scale bars represent 10 mm.

43. Supratemporal fenestrae: separated by a horizontal plate formed by the parietals (0); contact each other posteriorly, but separated anteriorly by an anteriorly widening triangular plate formed by the parietals (1); confluent over the parietals; parietals form a sagittal crest (2) (modified from Molnar *et al.* 1990; unordered)

In ornithischians, sauropodomorphs and many theropods the supratemporal fenestrae are separated from each other dorsally by a broad, horizontal plate of the parietals (Text-fig. 9A). In *Ceratosaurus* (MOR 005, 009) and abelisaurids (MACN CH 894, FMNH 96202-44C) this plate narrows rapidly posteriorly, and the supratemporal fenestrae meet at the midline posteriorly, just in front of the dorsal projection of the parietals (see character 42); thus, the parietals form a triangular plate between the openings anteriorly (Text-fig. 9B).

In several other theropod taxa, including *Ornitholestes* (AMNH 619), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), *Avimimus* (ROM 46144), dromaeosaurids (AMNH 6515), oviraptorosaurs (Barsbold 1977b; Barsbold *et al.* 1990), troodontids (AMNH 6174), and tyrannosaurids (AMNH 973, FMNH PR 308), the supratemporal fenestrae are very close together along the midline of the skull, and the parietals form only a narrow, lamella-like parasagittal crest between them (Text-fig. 9D).

44. Postorbital part of the skull roof: as high as the orbital region (0); deflected ventrally in adult individuals (1) (Holtz 1994)

In most dinosaurs the parietals (anterior to the supraoccipital crest) and the medial parts of the squamosals are approximately level with the frontals above the orbits, and their surfaces face dorsally. In several theropods, including *Avimimus* (ROM 46144), birds (*Archaeopteryx*: Berlin, Eichstätt, Munich specimens), baryonychids (SMNS 58022), ornithomimosaurids (ROM 840, TMP 90.26.1), and troodontids (AMNH 6174; Barsbold 1974; Currie 1985), the parietals slope downwards behind the orbit, and their surfaces are directed posterodorsally (Text-fig. 14c). The situation in dromaeosaurids is uncertain: according to Barsbold (1983) and Barsbold and Osmólska (1999), the dorsal roof of the braincase slopes slightly downwards, but this feature seems to be less marked than in the other taxa listed above.

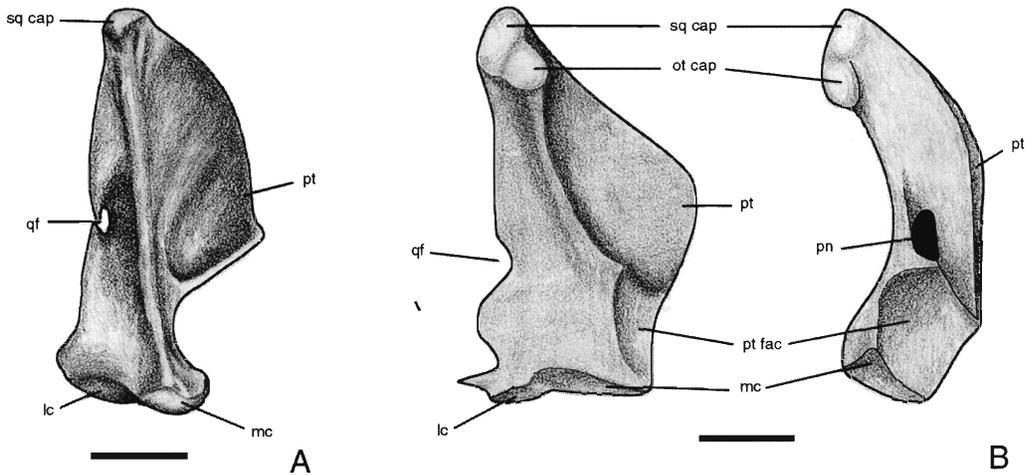
According to Carpenter (1994), the posterior part of the skull roof is deflected ventrally in very young individuals of the ornithomimid *Dryosaurus altus*, but expands dorsally during ontogeny in this taxon, so that it is level with the orbital part in adult individuals. Since there is the possibility that a similar ontogenetic change might also happen in theropods, the derived character state has only been coded as present for taxa known from subadult or adult individuals.

45. Quadratojugal process of the squamosal: tapering (0); broad, and usually somewhat expanded (1)

The quadratojugal process of the squamosal gradually tapers towards its contact with the quadratojugal in ornithischians, sauropodomorphs, and several theropods. In *Herrerasaurus* (Sereno and Novas 1993), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214, 6468), *Magnosaurus* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Proceratosaurus* (BMNH R 4680), *Allosaurus* (DNM 2560, MOR 693), *Ceratosaurus* (USNM 4735), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), abelisaurids (MACN CH 894, FMNH 96202-44C), carcharodontosaurids (Stovall and Langston 1950; Coria and Salgado 1995), and tyrannosaurids (FMNH PR 308, ROM 1247) the breadth remains the same over most of the length of the process, or the ventral two-thirds of the process is expanded (Text-fig. 7c). Only the ventralmost part is tapered, and in well-preserved skulls (e.g. MOR 693) a thin process, which overlaps the ascending process of the quadratojugal at the posterior rim of the infratemporal fenestra, is present anteriorly.

46. Squamosal-quadratojugal contact: present (0); absent (1)

As in most archosaurs, the ventral process of the squamosal contacts an ascending process of the quadratojugal behind the infratemporal fenestra in the vast majority of theropods. In some members of this clade, including *Dilophosaurus* (UCMP V 4214, 6468), *Syntarsus* (Rowe 1989), abelisaurids (MACN CH 894, FMNH 96202-44C), birds (*Archaeopteryx*: Eichstätt specimen), and oviraptorosaurs (Barsbold *et al.* 1990), the quadratojugal and squamosal do not contact each other (Text-fig. 7B).



TEXT-FIG. 13. Theropod quadrates, illustrating different character states for characters 48–50. A, *Allosaurus fragilis*; left quadrate; posterior view; based on Madsen (1976) and MOR 693. B, unspecified oviraptorid; left quadrate; posterior (left) and medial view (right); redrawn from Maryanska and Osmólska (1997). Abbreviations: lc, lateral condyle; mc, medial condyle; ot cap, otic capitulum; pn, pneumatic cavity; pt, pterygoid wing; pt fac, pterygoid facet; qf, quadrate foramen; sq cap, squamosal capitulum. Scale bars represent 50 mm (A) and 10 mm (B).

47. Quadratojugal: hook-shaped, without posterior process (0); with broad, short posterior process that wraps around the lateroventral edge of the quadrate (1)

In ornithischians, sauropodomorphs, and many theropods the quadratojugal has a simple hook shape, with an anterior and a dorsal process. In several theropod taxa, including *Caudipteryx* (Ji *et al.* 1998), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 5356, TMP 88.121.39), ornithomimosaurs (TMP 90.26.1), oviraptorosaurs (Smith 1992), therizinosaurs (Clark *et al.* 1994), and tyrannosaurids (ROM 1247), the quadratojugal has a distinct, usually broad posterior process that wraps around the lateroventral edge of the quadrate. This process is best developed in dromaeosaurids, where the quadratojugal has an inverted T shape (Text-fig. 7F).

48. Pneumatisation of the quadrate: absent (0); present (1)

In the majority of dinosaurs, including many theropods, the quadrate is a solid bone and it is not invaded by a diverticulum of the tympanic pneumatic system. In birds, ornithomimosaurs (Witmer 1997), oviraptorosaurs (Maryanska and Osmólska 1997), troodontids (MOR 553S), and tyrannosaurids (Molnar 1991) the quadrate is pneumatised by a diverticulum of the tympanic system (Text-fig. 13B; Witmer 1990). This pneumatisation may be developed as a deep recess in the body of the quadrate as, for example, in *Troödon* (MOR 553S), or as a system of internal pneumatic chambers that open externally through a small foramen as, for example, in tyrannosaurs (Molnar 1991).

The situation in dromaeosaurids is somewhat uncertain, but the quadrate seems to lack pneumatisation in this group (AMNH 5356; Barsbold and Osmólska 1999).

49. Quadrate foramen: developed as a distinct opening between the quadrate and quadratojugal (0); almost entirely enclosed in the quadrate (1); absent (2) (modified from Holtz 1994; unordered)

In most crurotarsans, ornithischians, and in a number of theropods the quadrate foramen is developed as a simple, often large opening between the ascending process of the quadratojugal and the main body of the quadrate (Text-fig. 13B). In several saurischians, including sauropodomorphs (*Plateosaurus*: GPIT Skelett 1, MB R. 1937), *Herrerasaurus* (Sereno and Novas 1993), *Liliensternus liliensterni* (MB R. 2175),

*Dilophosaurus* (UCMP V 4214), *Allosaurus* (MOR 693), *Ornitholestes* (AMNH 619), and sinraptorids (Currie and Zhao 1993b), the quadrate foramen is small and almost entirely enclosed in a lateral lamella of the quadrate (Text-figs 13A, 15B). A shallow sulcus usually extends laterally from the foramen towards the quadratojugal.

In *Ceratosaurus* (USNM 4735, MOR 005, 009) and abelisaurids (MACN CH 894, FMNH 96202-44C) the lateral lamella of the quadrate contacts the quadratojugal over its entire length so that a quadrate foramen is absent.

50. Dorsal end of the quadrate: with a single head that fits into a slot on the ventral side of the squamosal (0); double headed, medial head contacts the braincase (1) (modified from Chiappe *et al.* 1996)

The quadrate in crurotarsans, ornithischians, sauropodomorphs, and most theropods is single headed, with an oval head that fits into a slot on the ventral side of the squamosal (Text-fig. 13A). In the majority of birds and oviraptorosaurs (Maryanska and Osmólska 1997) the dorsal end of the quadrate is divided into a lateral head that contacts the squamosal, and a medial head that contacts the braincase (Text-fig. 13B). The presence of this second quadrate head is still uncertain in *Archaeopteryx*, although Walker (1985) and Elzanowski and Wellnhofer (1996) believed it to be rather unlikely. However, the character obviously appeared early in bird evolution, as indicated by its presence in the Early Cretaceous genus *Enaliornis* (Witmer 1990).

51. Mandibular joint: approximately straight below the quadrate head (0); significantly posterior to quadrate head (1); significantly anterior to quadrate head (2)

In ornithischians, the majority of basal sauropodomorphs, and many theropods the mandibular joint is situated approximately directly below the quadrate head so that the orientation of the quadrate is almost vertical (Text-fig. 14A). In *Herrerasaurus* (Serenó and Novas 1993), *Magnosaurus* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (DNM 2560, MOR 693), *Ceratosaurus* (USNM 4735), sinraptorids (Dong *et al.* 1983; Currie and Zhao 1993b), and abelisaurids (MACN CH 894) the quadrate is inclined posteriorly so that the mandibular joint is situated significantly posterior to the quadrate head (Text-fig. 14B). In several other theropod taxa, including birds (*Archaeopteryx*: Berlin and Eichstätt specimen), baryonychids (SMNS 58022), and ornithomimosaur (ROM 840, TMP 90.26.1), the quadrate is strongly inclined anteriorly, thus displacing the mandibular joint anterior to the quadrate head (Text-fig. 14C).

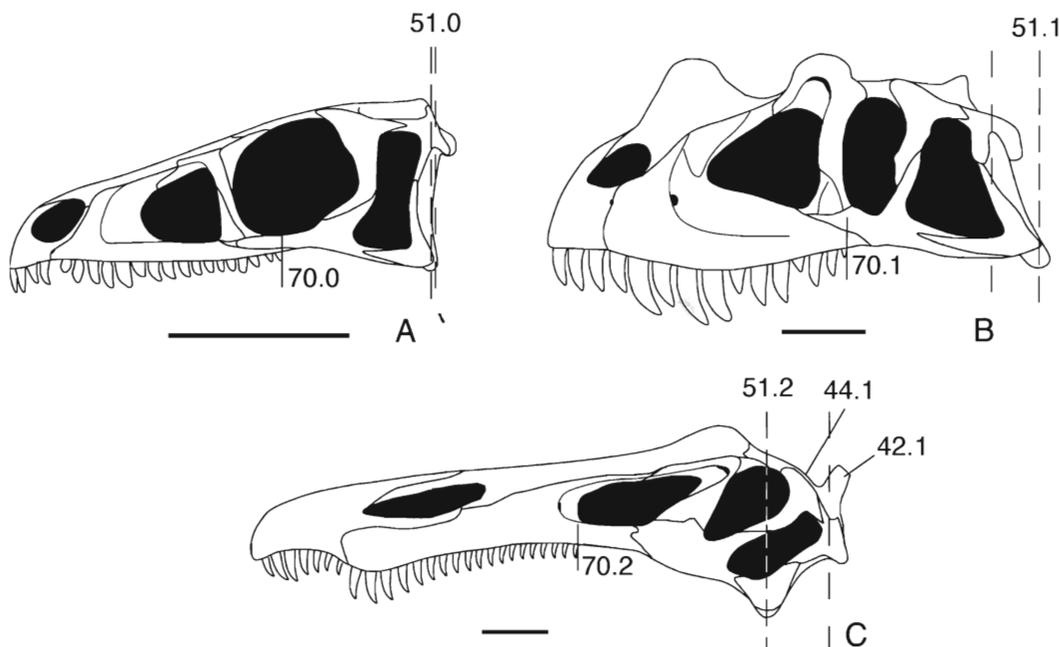
In troödontids, the situation is uncertain: the quadrate is not preserved in the articulated skull of *Saurornithoides junior* (Barsbold 1974) or in the most complete skull known for *Troödon* (Currie 1985), but the configuration of the preserved bones of the posterior part of the skull indicates that the quadrate might have been inclined anteriorly. Thus, character 51 is coded as '0/2' for troödontids.

52. Paroccipital processes: directed laterally or dorsolaterally (0); directed ventrolaterally (1); directed strongly ventrolaterally, with distal end entirely below the level of the foramen magnum (2) (modified from Rauhut 1997; ordered)

While the paroccipital processes of the opisthotic are directed strictly laterally or dorsolaterally in most crurotarsans and all ornithischians (Text-fig. 15A), they are directed ventrolaterally in all saurischians (Text-fig. 15B–C). In a few theropod taxa, including *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (BYU Mes 5583, MOR 693), and sinraptorids (Currie and Zhao 1993b), the paroccipital processes are directed very strongly ventrolaterally so that the distal ends of the processes are situated entirely below the foramen magnum (Text-fig. 15C).

The character state is uncertain in '*Chilantaisaurus*' *maortuensis* (IVPP V 2885) and *Carcharodontosaurus* (SGM-Din 1) where the distal ends of the processes are broken; however, the proximal parts of the processes are directed ventrolaterally.

Since character state 2 includes character state 1, the character is treated as ordered.



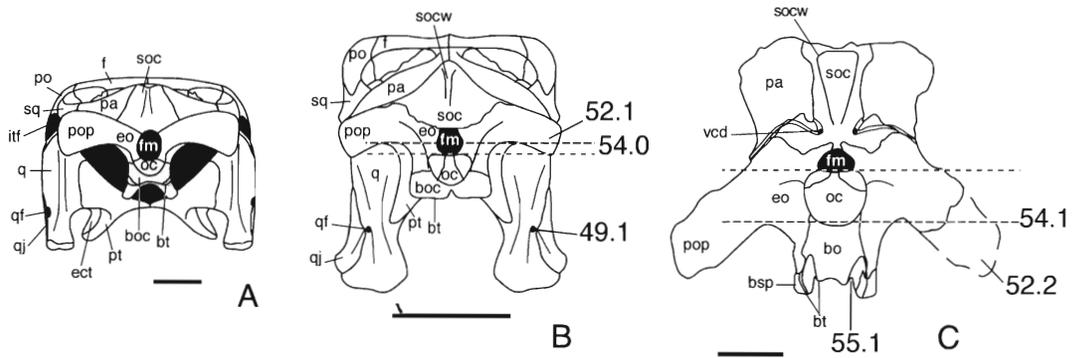
TEXT-FIG. 14. Theropod skull reconstructions in lateral view showing different character states of characters 42, 44, 51, and 70. For sources of reconstructions and identifications of the elements, see Text-figures 4–6. A, *Eoraptor lunensis*. B, *Ceratosaurus* sp. C, generalized baryonychid. Dashed lines indicate levels of quadrate-squamosal articulation (wide dash) and mandibular joint (narrow dash); strong line indicates posterior end of tooth row. Scale bars represent 50 mm (A) and 100 mm (B–C).

53. Basis of paroccipital processes: solid (0); hollowed (1) (Bakker *et al.* 1988)

The basis of the paroccipital processes is solid bone, and not pneumatized in ornithischians, sauropodomorphs, and many theropods. In a variety of theropods, including '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), birds (Witmer 1990; Currie 1995), dromaeosaurids (Currie 1995), ornithomimosaur (Makovicky and Norell 1998), oviraptorosaurs (ROM 43250), therizinosauroids (Clark *et al.* 1994), troodontids (MOR 553S, TMP 86.36.457), and tyrannosaurids (Molnar 1991), the basis of the paroccipital processes is pneumatized by a diverticulum of the posterior tympanic recess (Text-fig. 16B).

54. Ventral rim of the basis of the paroccipital processes: above or level with the dorsal border of the occipital condyle (0); situated at mid-height of occipital condyle or lower (1)

In ornithischians, sauropodomorphs, and several theropods the basis of the paroccipital process of the opisthotic is situated entirely above the occipital condyle (Text-fig. 15A–B). In many theropods, including *Magnosaurus oxoniensis* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Piatnitzkysaurus* (MACN cast of PVL 4073), *Allosaurus* (BYU Mes 5583), *Ceratosaurus* (MOR 005, 009), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), *Avimimus* (ROM 46144), abelisaurids (MACN CH 894, FMNH 96202-44C), baryonychids (BMNH R 9951), dromaeosaurids (AMNH 5356), oviraptorosaurs (ROM 43250), therizinosauroids (Clark *et al.* 1994), troodontids (MOR 553S, TMP 86.36.457), and tyrannosaurids (AMNH 973, ROM 1247), the ventral rim of the basis of the paroccipital process is situated considerably lower so that it is approximately at the level of the mid-height of the occipital condyle, or lower (Text-fig. 15c).



TEXT-FIG. 15. Occipital views of the skulls of a basal ornithischian (A) and two theropods (B–C), illustrating different character states for several cranial characters. A, basal ornithischian *Lesothosaurus diagnosticus*; redrawn from Sereno (1991b). B, *Herrerasaurus ischigualastensis*; redrawn from Sereno and Novas (1993). C, *Allosaurus fragilis* (braincase only); based on BYU Mes 5583. Abbreviations: boc, basioccipital; bsp, basisphenoid; bt, basal tuber; eo, exoccipital; f, frontal; fm, foramen magnum; itf, infratemporal fenestra; oc, occipital condyle; pa, parietal; po, postorbital; pop, paroccipital process; pt, pterygoid; q, quadrate; qf, quadrate foramen; qj, quadratojugal; soc, supraoccipital; socw, supraoccipital wedge; sq, squamosal; vcd, foramen for the entrance of the vena capitis dorsalis. Dashed lines indicate the level of the dorsal margin of the occipital condyle (wide dash) and the level of the bases of the paroccipital processes (narrow dash). Scale bars represent 10 mm (A) and 50 mm (B–C).

55. Basal tubera: equally formed by basioccipital and basisphenoid and not subdivided (0); subdivided by a lateral longitudinal groove into a medial part entirely formed by the basioccipital, and a lateral part, entirely formed by the basisphenoid (1)

In the majority of theropods the basal tubera are rather low, rounded projections formed by the basioccipital and basisphenoid. In *Allosaurus* (BYU Mes 5583, DNM 116) and sinraptorids (Currie and Zhao 1993b), the basioccipital forms the entire median part of the tubera; it is framed laterally by posteriorly extending walls of the basisphenoid, which are sharply separated from the basioccipital by deep longitudinal grooves (Text-fig. 15C).

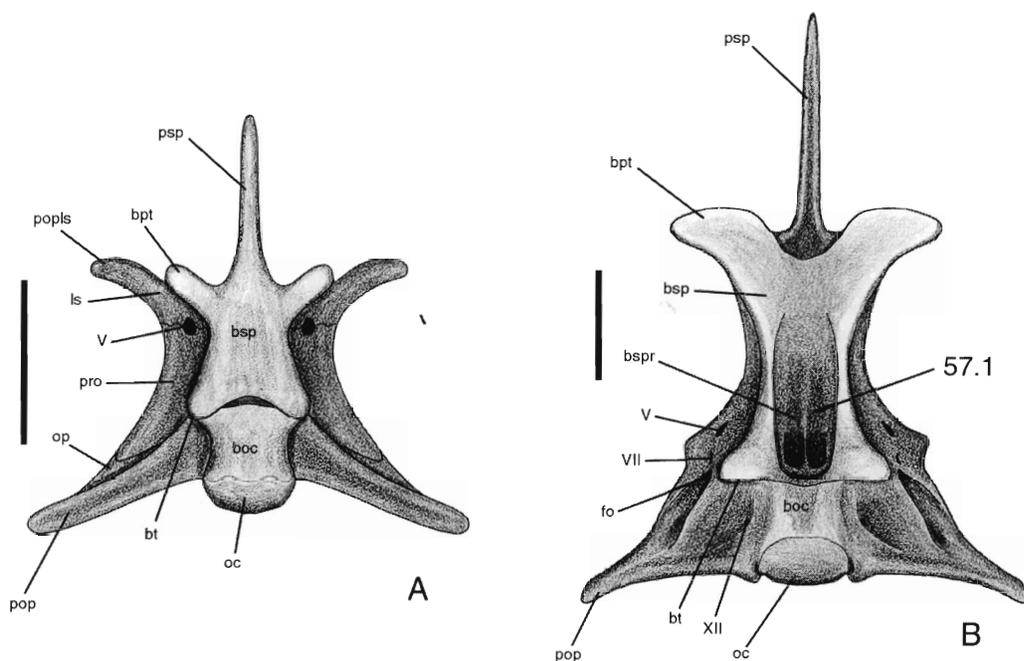
56. Basisphenoid between basal tubera and basiptyergoid processes: approximately as wide as long, or wider (0); significantly elongated, at least 1.5 times longer than wide (1)

In ornithischians, sauropodomorphs, and most theropods the basisphenoid is a rather broad element, and approximately as wide as long, or wider (Text-fig. 16A). In *Syntarsus* (QG 193), *Shuvosaurus* (TTU P 9282), and probably *Coelophysus* (Colbert 1989) the basisphenoid is markedly elongate so that it is at least 1.5 times as long as it is wide at its midpoint (Text-fig. 16B).

57. Basisphenoid recess: absent or poorly developed (0); deep, well-developed (1)

In most crurotarsans, ornithischians, sauropodomorphs, and *Herrerasaurus* there is no deep ventral depression in the main body of the basisphenoid between the basal tubera and the basiptyergoid processes. In the vast majority of theropods, a deep recess is present in this position (Text-fig. 16B). It is usually cone-shaped and leads into the interior of the basisphenoid, where it is subdivided posteriorly in many taxa. In some taxa it is connected with the eustachian system (Larsson, pers. comm. 1998). Among crown-group theropods, only troödontids, therizinosauroids, and birds lack a deep basisphenoid recess, but in these taxa the body of the basisphenoid is highly pneumatized (Currie 1985; Witmer 1990; Currie and Zhao 1993a; Clark *et al.* 1994).

A similar recess is present in a few basal crocodylomorphs (e.g. *Dibothrosuchus*; IVPP V 7907), but the phylogenetic position of these animals, and the fact that more closely related outgroups do not show this character, suggest that this recess is a development convergent to that found in most theropods.



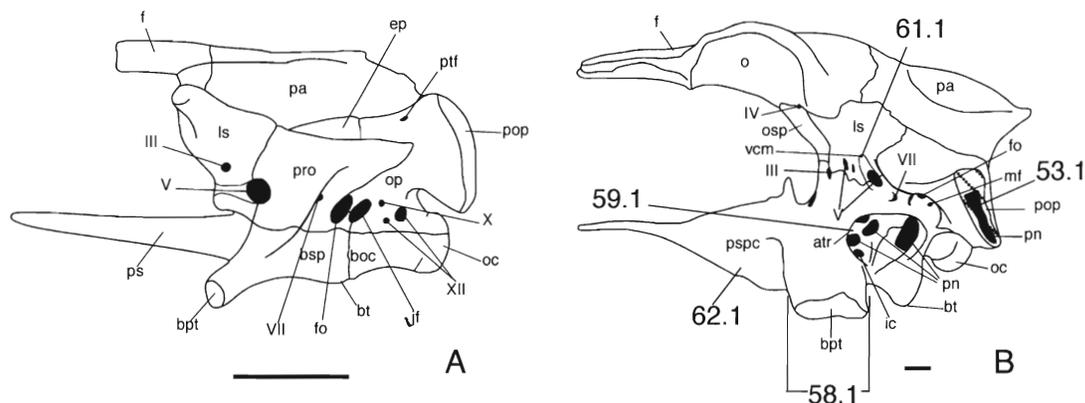
TEXT-FIG. 16. Ventral view of the braincase, showing different states for characters 56 and 57. A, basal ornithischian *Lesothosaurus diagnosticus*; based on Sereno (1991b). B, *Syntarsus rhodesiensis* based on QG 195; the postorbital processes of the laterosphenoid are broken in this specimen of *Syntarsus*; their attachments are placed above and slightly posterior to the trigeminal foramen. Abbreviations: boc, basioccipital; bpt, basipterygoid process; bsp, basisphenoid; bspr, basisphenoid recess; bt, basal tuber; fo, fenestra ovalis; ls, laterosphenoid; oc, occipital condyle; op, opisthotic; pop, paroccipital process; popls, postorbital process of the laterosphenoid; psp, parasphenoid; Roman numbers refer to the foramina for the exits of cranial nerves. Scale bars represent 10 mm.

58. Basipterygoid processes: well-developed, anteroposteriorly short and finger-like (approximately as long as wide) (0); significantly elongated anteroposteriorly (longer than wide) (1); shortened, broad, and narrow (2) (modified from Sues 1997; Makovicky and Sues 1998; unordered)

In ornithischians, sauropodomorphs, and some theropods the basipterygoid processes are usually long and finger-like, and approximately as long as they are wide at their bases (Text-fig. 17A). In many theropods, including *Allosaurus* (BYU Mes 5583, DNM 116), sinraptorids (Currie and Zhao 1993b), birds (*Archaeopteryx*: Munich specimen), baryonychids (BMNH R 9951, SMNS 58022), carcharodontosaurids (Stovall and Langston 1950), dromaeosaurids (AMNH 5356), ornithomimosaurids (Osmólska *et al.* 1972; Makovicky and Norell 1998), troodontids (Currie 1985), and tyrannosaurids (AMNH 973, ROM 1247), the bases of the basipterygoid processes are considerably elongated anteroposteriorly so that they are considerably longer than wide (Text-fig. 17B). In oviraptorosaurs (ROM 43250) and therizinosaurs (Clark *et al.* 1994) the processes are, furthermore, very low and have a transverse span narrower than that of the basal tubera.

59. Anterior tympanic recess in the braincase: absent (0); present (1) (modified from Makovicky and Sues 1998)

Basal crurotarsans, ornithischians, and sauropodomorphs lack a tympanic pneumatic system, or at least its osteological correlates in the braincase. A tympanic system is well-developed in crocodylomorphs, but recent cladistic analyses indicate that this system was acquired independently from that found in theropods, including birds (Gower and Weber 1998).



TEXT-FIG. 17. Lateral view of the braincase, illustrating states for several braincase characters. A, basal ornithischian *Lesothosaurus diagnosticus*; redrawn from Sereno (1991b). B, *Troödon formosus*; based on Currie and Zhao (1993a); the paroccipital process of *Troödon* is shown in cross-section to illustrate the internal pneumatic cavity within this bone. Abbreviations: atr, anterior tympanic recess; bpt, basipterygoid process; boc, basioccipital; bsp, basisphenoid; bt, basal tuber; ep, episthotic; f, frontal; fo, fenestra ovalis; ic, foramen for the entrance of the vidian canal for the internal carotid; jf, jugular foramen; ls, laterosphenoid; mf, metotic fissure; o, orbital facet on the frontal; oc, occipital condyle; op, opisthotic; osp, orbitosphenoid; pa, parietal; pn, pneumatic openings or cavities; pop, paroccipital process; pro, prootic; ps, parasphenoid; pspc, parasphenoid capsule; ptf, posttemporal foramen; vcm, exit of the vena capitis medialis; Roman numbers refer to the foramina for the exits of cranial nerves. Scale bars represent 10 mm.

In all theropods that are more derived than *Herrerasaurus* (Sereno and Novas 1993) a well-developed anterior tympanic recess is present, which invades the basisphenoid in the vicinity of the entrance of the vidian canal. In this area there is a large depression in which the foramen through which the internal carotid enters is placed anteriorly (Text-fig. 17B). A pneumatic foramen is usually present in the posterior part of this depression, leading into the posterior parts of the basisphenoid and the basioccipital. In some taxa, for example *Majungatholus* (FMNH 96202-44C), the anterior tympanic recess extends dorsally to a point just underneath the opening for the nervus facialis. The bony recess is especially well-developed in troödontids, where it forms a deep lateral depression in the ventrolateral wall of the braincase (Text-fig. 17B; Barsbold 1974; Currie 1985; Currie and Zhao 1993a).

The only theropod specimen examined that did not show this depression was the holotype of *Dromaeosaurus albertensis* (AMNH 5356). However, pneumatic systems are found in other dromaeosaurids (Barsbold and Osmólska 1999, and pers. obs. on undescribed specimens), and the apneumatic nature of the skull of *Dromaeosaurus* is probably apomorphic. Nevertheless, the character has been coded as uncertain in dromaeosaurids.

60. Exit of cranial nerves X and XI: laterally through the jugular foramen (0); posteriorly through a foramen lateral to the exit of the cranial nerve XII and the occipital condyle (1) (modified from Chatterjee 1993)

In basal archosaurs, the basal dinosauriform *Marasuchus*, ornithischians, and sauropodomorphs the n. vagus and n. accessorius leave the braincase laterally through the jugular foramen, together with the vena jugularis. In most theropods with the exception of *Syntarsus* (QG 193) and abelisaurids (FMNH 96202-44C), the two nerves leave the braincase through a separate foramen that opens posterolateral to the foramen for the n. hypoglossus, and is separated from the jugular foramen by a metotic strut that runs from the lateral rim of the basioccipital to the basis of the paroccipital process.

In prosauropods the foramen for the two nerves (foramen lacerticum in Gow 1990) is already displaced slightly posterior to the jugular foramen (*Plateosaurus*: GPIT Skelett 1; *Massospondylus*: Gow 1990), but it is still confluent with the latter and directed laterally rather than posteriorly.

61. Exit of mid-cerebral vein: included in trigeminal foramen (0); vein exits braincase through a separate foramen anterodorsal to the trigeminal foramen (1)

In most archosaurs, including *Euparkeria* and ornithischians, the vena cerebialis medialis leaves the braincase through the trigeminal foramen, usually through an anterodorsal notch that branches off the latter opening. In many saurischians, including sauropodomorphs (*Plateosaurus*: GPIT Skelett 1; *Massospondylus*: Gow 1990), *Dilophosaurus* (UCMP V 6468), *Allosaurus* (BYU Mes 5583, DNM 116), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), abelisaurids (FMNH 96202-44C), dromaeosaurids (AMNH 5356), oviraptorosaurs (Barsbold 1977b), and troödontids (Currie 1985), the mid-cerebral vein exits the braincase through a separate foramen that is situated anterodorsal to the trigeminal foramen (Text-fig. 17B). This foramen is placed at the proötic-laterosphenoid suture in some taxa (e.g. *Dromaeosaurus*: AMNH 5356) or it can be enclosed entirely within the laterosphenoid, as in *Troödon* (Currie 1985) or oviraptorosaurs (Barsbold 1977b).

62. Parasphenoid: forming a thin bony plate, often with a longitudinal groove ventrally (0); expanded, cone-shaped and pneumatized (1) (modified from Holtz 1994)

The parasphenoid is usually fused with the basisphenoid in archosaurs and has a long, thin cultriform process that extends anteriorly. In theropods this process may be developed as a straight, rod-like bone that points anteriorly, as in most small theropods (e.g. *Syntarsus*: QG 193, *Dromaeosaurus*: AMNH 5356), or as a rather plate-like element that is directed more dorsoanteriorly, as in many large theropods (e.g. *Majungatholus*: FMNH 96202-44C, *Allosaurus*: DNM 116). Apart from this clearly size-related difference, a special development of this process is found in ornithomimosaurids (Osmólska *et al.* 1972) and troödontids (MOR 553S; Barsbold 1974; Currie 1985). In these clades, the basis of the cultriform process is swollen into a hollow, cone-shaped structure that is pneumatized (Text-fig. 17B). The pneumatic cavity of this structure originates in the basisphenoid recess in ornithomimosaurids (Osmólska *et al.* 1972), whereas it is connected with the anterior tympanic recess in troödontids (Currie 1985), indicating that the structures might not be homologous.

63. Endocranium: small (EQ < 2.5) (0); enlarged (EQ > 2.5) (1) (modified from Holtz 1994)

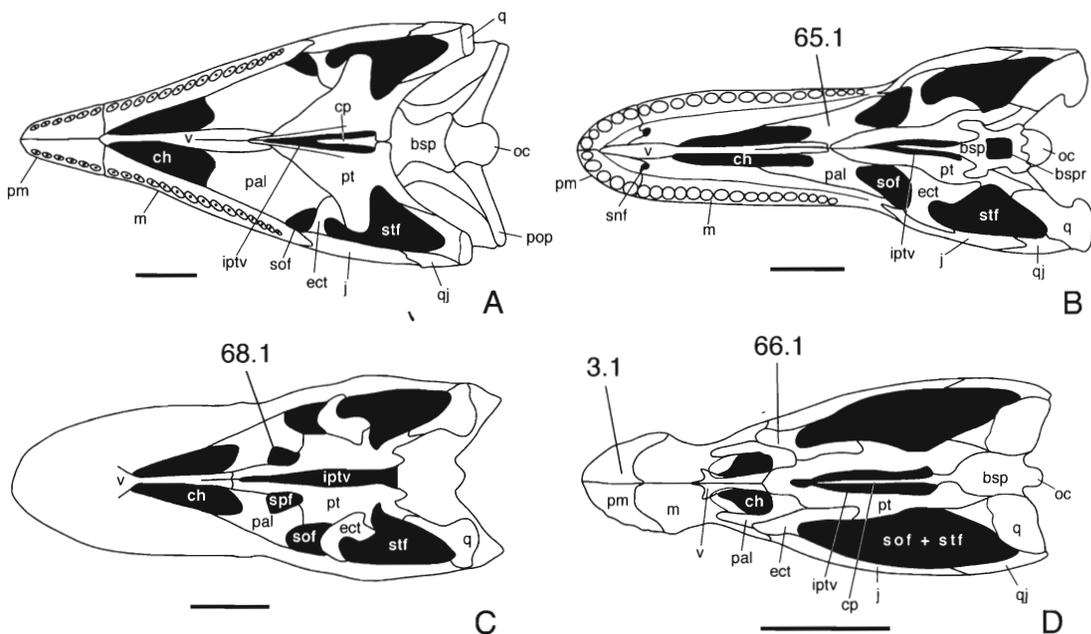
In the majority of dinosaurs the encephalization-quotient is below 2, if compared to the brain size of modern reptiles (Hopson 1980). In several theropods, including troödontids (Hopson 1977, 1980), and birds (Hopson 1977), the brain is relatively enlarged, and the encephalization quotient is above 5.

EQs have only been calculated so far for three non-avian theropods (Hopson 1977, 1980): *Allosaurus*, *Tyrannosaurus*, and *Troödon* (= *Stenonychosaurus*). However, relative brain sizes have been estimated for a number of theropods, based on comparisons with the relative brain size for the taxa mentioned above. Thus, character state '0' has been coded for *Dilophosaurus* (based on UCMP V 4214, 6468), *Syntarsus* (based on QG 193), *Ceratosaurus* (based on USNM 4735, MOR 005, 009), sinraptorids (based on Currie and Zhao 1993b), and carcharodontosaurids (based on SGM-Din 1), whereas character state '1' has been coded for dromaeosaurids (based on AMNH 5356; Currie 1995), ornithomimosaurids (based on Hopson 1979), and oviraptorosaurs (based on Osmólska 1976).

64. Brain proportions: forebrain small and narrow (0); forebrain significantly enlarged and triangular (1)

In crurotarsans, sauropodomorphs and many theropods the forebrain is not considerably widened in comparison to other parts of the brain (see e.g. Stromer 1931; Janensch 1935–36; Hopson 1979). In birds and several theropods, including *Avimimus* (ROM 46144), dromaeosaurids (TMP 74.10.5), ornithomimosaurids (Russell 1972), therizinosauroids (Currie 1992; Clark *et al.* 1994), and troödontids (AMNH 6174), the forebrain, as judged mainly from the impressions on the ventral side of the frontals or from endocasts, is markedly widened and triangular in dorsal view (Text-fig. 11B).

Although the shape of the forebrain in tyrannosaurids is conservative in terms of its general morphology (Osborn 1912a; Hopson 1979), it is relatively enlarged in comparison with more basal theropods and



TEXT-FIG. 18. Skulls of a basal ornithischian (A) and three theropods (B–D) in palatal view, showing different states for several cranial characters. A, *Lesothosaurus diagnosticus*; redrawn from Sereno (1991b). B, *Allosaurus fragilis*; redrawn from Madsen (1976). C, *Daspletosaurus torosus*; redrawn from Russell (1970). D, *Oviraptor philoceratops*; redrawn from Barsbold *et al.* (1990). Abbreviations: bsp, basisphenoid; bspr, basisphenoid recess; ch, internal choana; cp, cultriform process of the parasphenoid; ect, ectopterygoid; iptv, interpterygoid vacuity; j, jugal; m, maxilla; oc, occipital condyle; pal, palatine; pm, premaxilla; pop, paroccipital process; pt, pterygoid; q, quadrate; qj, quadratojugal; sof, suborbital fenestra; spf, subsidiary palatal fenestra; snf, subnarial foramen; stf, subtemporal fenestra; v, vomer. Scale bars represent 10 mm (A), 50 mm (D) and 100 mm (B–C).

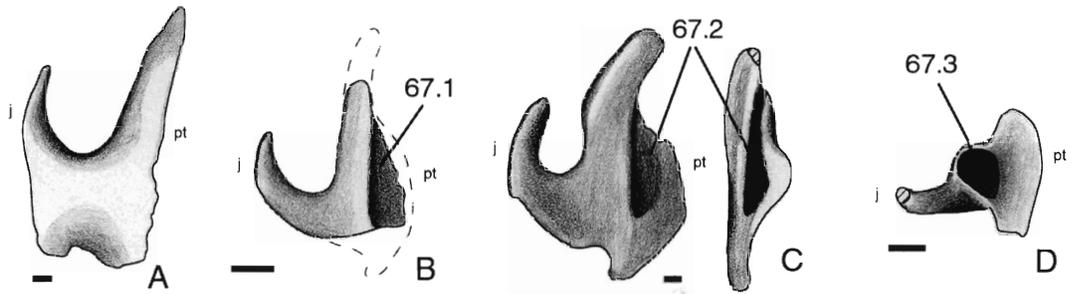
non-theropodan diapsids, thus approaching the relative dimensions found in the coelurosaurian taxa mentioned above (Larsson *et al.* 2000). However, since this does not correspond to the derived character state as described above, the character is coded as '0' for tyrannosaurids.

65. Shape of palatine in ventral view: plate-like trapezoidal or subrectangular (0); tetradiate (1); jugal process strongly reduced or absent (2) (Harris 1998; unordered)

In ventral view the palatine is a large, rather plate-like element in most crurotarsans, ornithischians, and sauropodomorphs, although it might have small processes extending towards the maxilla, vomer, pterygoid, and jugal. In all non-avian theropods with the exception of oviraptorosaurs (Osmólska 1976) and therizinosauroids (Clark *et al.* 1994), the palatine is a tetradiate element in ventral view (Text-fig. 18B), with a slender body and highly elongate processes that are subequal in length, or longer, than the main body of the bone. In birds (*Archaeopteryx*: Munich specimen), the jugal process is usually absent, and the maxillary process is strongly reduced.

66. Ectopterygoid: posterior to palatine (0); lateral to palatine (1) (Sues 1997)

In ornithischians, sauropodomorphs, and most theropods the ectopterygoid is situated entirely behind the palatine. In oviraptorosaurs (Barsbold 1983) and therizinosauroids (Clark *et al.* 1994) the ectopterygoid is at least partially situated lateral to the palatine (Text-fig. 18D).



TEXT-FIG. 19. Theropod ectopterygoids in ventral view, showing the different degrees and modes of pneumatization of this bone (character 67). A, *Majungatholus atopus*; based on FMNH 96202–44C. B, *Liliiensternus liliiensterni*; based on MB R. 2175. C, *Allosaurus fragilis*; ectopterygoid in ventral (left) and medial (right) view; based on UMNH VP 5328 (left) and 5327 (right). D, *Dromaeosaurus albertensis*; based on AMNH 5356. Abbreviations: j, contact to the jugal; pt, contact to the pterygoid. Scale bars represent 10 mm.

67. Ectopterygoid: slender, without ventral fossa (0); expanded, with a deep ventral depression medially (1); as above, but with a deep groove excavated into the body of the ectopterygoid from the medial side (2); excavated by a foramen leading from the medial side laterally into the body of the ectopterygoid (3) (modified from Gauthier 1986; Sereno *et al.* 1996; unordered)

In many crurotarsans, ornithischians and sauropodomorphs the ectopterygoid is a slender element that is not significantly expanded medially. In theropods generally, the medial part of the ectopterygoid is strongly expanded and it is usually pneumatized ventrally. The only exceptions are oviraptorosaurs, in which the ectopterygoid is strongly modified (Barsbold 1983), *Ceratosaurus* (MOR 005, 009) and abelisaurids (FMNH 96202–44C), which show the medial expansion, but no signs of pneumatization of this element (Text-fig. 19A).

The mode of pneumatization varies in different theropods. In *Liliiensternus liliiensterni* (MB R. 2175) and *Syntarsus* (QG, pers. obs., specimen number lost) a deep depression, only sharply defined laterally, is found on the ventral surface of the expanded medial part (Text-fig. 19B). This depression may occasionally invade to a small extent the lateral part of the ectopterygoid body in the form of a very shallow groove. The situation in *Allosaurus* (UMNH VP 5327, 5328), sinraptorids (Currie and Zhao 1993b), and carcharodontosaurids (Harris 1998) is similar, but here the groove that invades the lateral part of the main body of the ectopterygoid from the medial side is deep (Text-fig. 19C). In dromaeosaurids (AMNH 5356, TMP 74.10.5), ornithomimosaurs (Barsbold 1983), troödontids (MOR 553S), and tyrannosaurids (ROM 1247) the ectopterygoid is invaded by a deep foramen that extends into the lateral part of the ectopterygoid body and the lateral process of the ectopterygoid (Text-fig. 19D).

The situation in *Ornitholestes* is uncertain since the ectopterygoid is not very well preserved in the holotype (AMNH 619). However, it can be said with some certainty that either character state 2 or 3 was present.

68. Contact between pterygoid and palatine: continuous (0); discontinuous in the mid-region, resulting in a subsidiary palatal fenestra (1) (Ostrom 1969b)

The suture between the pterygoid and palatine is continuous in most crurotarsans, all ornithischians and sauropodomorphs, and many theropods. In several theropod taxa, including dromaeosaurids (Ostrom 1969b), ornithomimosaurs (TMP 90.26.1), and troödontids (Norell, pers. comm. 1999), an opening is present in the suture between the two bones (Text-fig. 18C). This opening has been termed the subsidiary palatal fenestra by Ostrom (1969b), and probably functioned as the internal choana (Norell, pers. comm. 1999).

Most reconstructions of the palate in tyrannosaurs (e.g. Osborn 1912a; Molnar 1991) do not show such an opening; however, it is present in the reconstruction of the palate of *Daspletosaurus torosus* in Russell

(1972, fig. 9; see also Text-fig. 18C). Since this reconstruction is based on the best preserved palate of any tyrannosaur described so far (Sues, pers. comm. 1998), character 68 is coded as '1' for tyrannosaurs.

Paul's (1993) claim that a subsidiary palatal fenestra is present in *Coelophysis* is not supported by existing reconstructions of the palate in this taxon (Colbert 1989), nor by my own observations of material of the closely related taxon *Syntarsus*.

69. Palatal teeth: present (0); absent (1)

The presence of palatal teeth is a primitive character for archosauromorphs, and such teeth are absent in crurotarsans and almost all dinosaurs. However, palatal teeth seem to have been present in *Eoraptor* (PVSJ 512; Sereno, pers. comm. 1996). An earlier claim that palatal teeth are present in the prosauropod *Massospondylus* (Attridge *et al.* 1985) seems to be erroneous; the elements in question were probably fish teeth that had been washed up against the palate of the specimen described by these authors prior to burial (Sereno, pers. comm. 1997).

70. Tooth row: extends posteriorly to approximately half the length of the orbit (0); ends at the anterior rim of the orbit (1); completely antorbital, tooth row ends anterior to the vertical strut of the lacrimal (2) (modified from Gauthier 1986; ordered)

In ornithischians, sauropodomorphs, and some theropods the tooth row extends posteriorly underneath the orbit to approximately half the length of this opening (Text-fig. 14A). In some theropods, including *Dilophosaurus* (UCMP V 4214, 6468), *Ceratosaurus* (USNM 4735), and abelisaurids (MACN CH 894, FMNH 36202-44C), the tooth row ends below the anterior rim of the orbit (Text-fig. 14B), whereas in other taxa, including *Magnosaurus oxoniensis* (OUM J 13558), *Proceratosaurus* (BMNH R 4860), *Allosaurus* (DNM 2560, MOR 693), *Ornitholestes* (AMNH 619), sinraptorids (Dong *et al.* 1983; Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), *Sinosauropteryx* (Chen *et al.* 1998), birds (*Archaeopteryx*: Eichstätt specimen), baryonychids (SMNS 58022), carcharodontosaurids (SGM-Din 1), dromaeosaurids (AMNH 6515, 5356), ornithomimosaurids (Pérez-Moreno *et al.* 1994), therizinosaurs (Clark *et al.* 1994), troodontids (IVPP V 9612), and tyrannosaurids (FMNH PR 308), it is completely antorbital and ends anterior to the vertical strut of the lacrimal that separates the orbit from the antorbital fenestra (Text-fig. 14C). In taxa that have lost teeth the character has been coded as '?'. The situation in *Compsognathus* (BSP A.S. I 563) is somewhat uncertain, although it seems very probable that the tooth row was completely antorbital in this taxon.

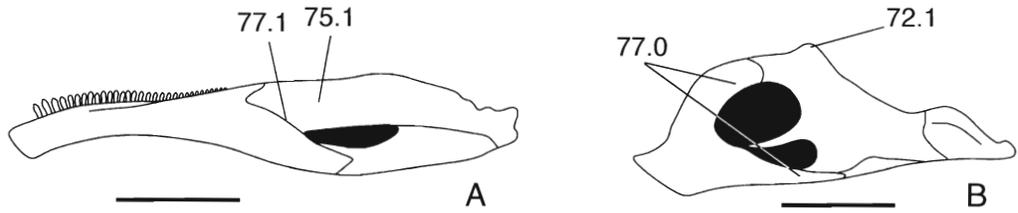
Since it seems highly unlikely that character state 2 can be reached without passing through character state 1, the character is treated as ordered.

71. Preorbital region of the skull in post-hatchling individuals: elongate, nasals considerably longer than frontals, maxilla at least twice the length of the premaxilla (0); shortened, nasals subequal in length to frontals or shorter, maxillary length less than twice the length of the premaxillary body (1)

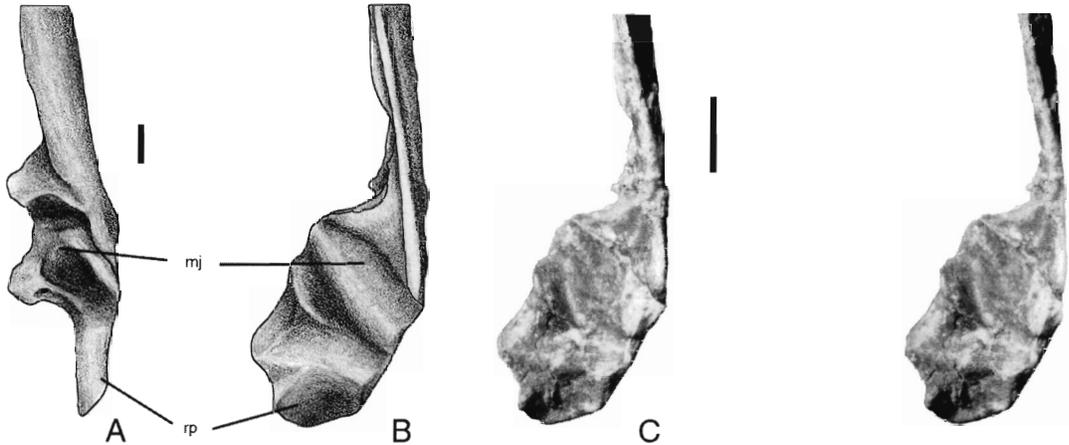
In most ornithischians, sauropodomorphs, and the majority of theropods the preorbital part of the skull forms an elongate snout, with the maxilla and the nasal being two of the longest bones of the skull roof in post-hatchling individuals. In *Caudipteryx* (Ji *et al.* 1998) and oviraptorosaurs (Barsbold *et al.* 1990) the preorbital part is considerably shortened, mainly as a result of a shortening of the nasals and maxillae (Text-fig. 7F).

72. Pronounced coronoid eminence on surangular: absent (0); present (1)

A coronoid eminence on the surangular is absent in basal ornithischians, sauropodomorphs and most theropods. Such an eminence is developed as a small, rounded dorsal projection on the anterior part of the surangular in *Avimimus* (ROM 46144) and oviraptorosaurs (Text-fig. 20B; Barsbold *et al.* 1990; Currie *et al.* 1993).



TEXT-FIG. 20. Mandible of *Erlikosaurus andrewsi* (A) and *Oviraptor philoceratops* (B) in lateral view, illustrating different states for characters 72, 75, and 77. For sources of reconstructions and identifications of the elements, see Text-figure 6. Scale bars represent 50 mm.



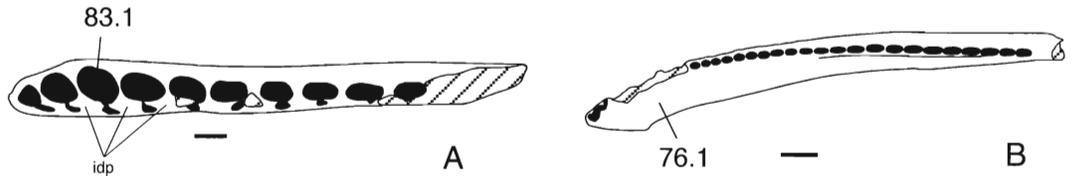
TEXT-FIG. 21. Posterior ends of the mandibles in dorsal view, illustrating different states for characters 73 and 74. A, *Plateosaurus* sp.; based on MB R. 1937. B, *Ornitholestes hermanni*; based on AMNH 619. C, same as B, stereophotographs. Abbreviations: mj, mandibular joint; rp, retroarticular process. Scale bars represent 10 mm.

73. Retroarticular process of the mandible: narrow, rod-like (0); broadened, with groove posteriorly for the attachment of the m. depressor mandibulae (1) (modified from Sereno *et al.* 1996; Harris 1998)

In ornithischians, sauropodomorphs, and several theropods the retroarticular process of the mandible is narrow (Text-fig. 21A) and the attachment area for the m. depressor mandibulae is developed as a transversely convex bulge. In a variety of theropods, including *Allosaurus* (DNM 2560, MOR 693), *Ornitholestes* (AMNH 619), *Bagaraatan* (Osmólska 1996), abelisaurids (FMNH 96202-44C), birds (Marsh 1880; Gregory 1952; Elzanowski 1977), dromaeosaurids (AMNH 5356), therizinosauroids (Clark *et al.* 1994), and tyrannosaurids (ROM 1422), the retroarticular process is transversely broadened so that it is usually broader than the mandible anterior to the mandibular joint, and the attachment area for the m. depressor mandibulae is developed as an anteroposteriorly, and sometimes also transversely concave groove (Text-fig. 21B-C).

74. Attachment of the m. depressor mandibulae on retroarticular process of mandible: facing dorsally (0); facing posterodorsally (1) (Sereno *et al.* 1996)

The attachment area for the m. depressor mandibulae faces mainly dorsally or anterodorsally in ornithischians, sauropodomorphs, and several theropods. In many theropods, including *Dilophosaurus* (UCMP V 6468), *Proceratosaurus* (BMNH R 4860), *Allosaurus* (DNM 2560, MOR 693), *Ornitholestes*



TEXT-FIG. 22. Dentaries in dorsal view, illustrating different states for characters 76 and 83. A, *Magnosaurus oxoniensis*; based on OUM J 12143. B, *Troödon formosus*; based on TMP 92.36.575. Abbreviation: idp, interdental plates. Anterior is to the left. Scale bars represent 10 mm.

(AMNH 619), sinraptorids (Currie and Zhao 1993b), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 5356, TMP 88.121.39), ornithomimosaurids (ROM 840), oviraptorosaurs (Barsbold *et al.* 1990; Currie *et al.* 1993), and tyrannosaurids (ROM 1422), the posterior end of the articular is flexed downwards, and the attachment area for the muscle faces posterodorsally (Text-fig. 21B–C).

75. Anterior portion of the surangular: less than half the height of the mandible above the mandibular fenestra (0); more than half the height of the mandible at the level of the mandibular fenestra (1) (modified from Gauthier 1986; Sereno *et al.* 1996)

In most crurotarsans, ornithischians, sauropodomorphs, and some theropods the anterior part of the surangular tapers towards the articulation with the dentary, and accounts for less than half of the total height of the mandible at the level of the mandibular fenestra. In *Dilophosaurus* (UCMP V 6468), *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (DNM 2560, MOR 693), *Compsognathus* (BSP A.S. I 563), *Ornitholestes* (AMNH 619), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (AMNH 5356), ornithomimosaurids (ROM 840), therizinosauroids (Clark *et al.* 1994), and tyrannosaurs (FMNH PR 308) the anterior portion is considerably expanded dorsoventrally and the mandibular fenestra is reduced in size so that the surangular accounts for more than half of the height of the mandible above the mandibular fenestra (Text-fig. 20A).

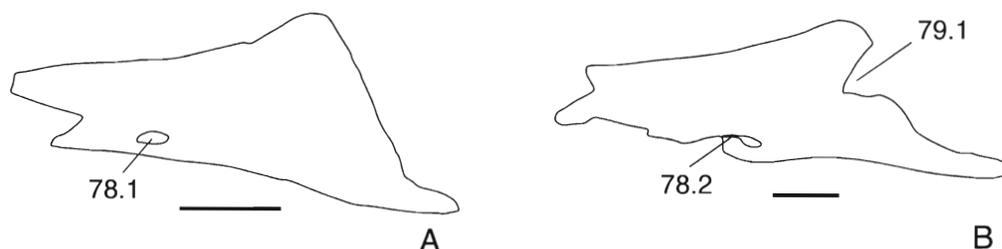
76. Dentary: almost straight in occlusal view (0); anterior portion with distinct medial curve (1) (Sues 1997)

In the majority of crurotarsans, sauropodomorphs, and theropods the dentary is an almost straight element that is not curved towards the symphysis anteriorly in occlusal view. In ornithischians, *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), ornithomimosaurids (ROM 851, TMP 90.26.1), oviraptorosaurs (TMP 90.56.6, 92.36.390), therizinosauroids (Clark *et al.* 1994), and troodontids (TMP 92.36.575) the anterior end of the mandible is bent towards the mandible symphysis (Text-fig. 22B).

Although character state '1' is present in many birds, the character has been coded as '0' for Aves, since this is the character state in the most basal representative, *Archaeopteryx* (Eichstätt and Munich specimens).

77. Posterior end of dentary: strongly forked (0); straight or only slightly concave (1) (modified from Barsbold *et al.* 1990)

The posterior end of the dentary is strongly forked to form the anterior margin of the mandibular fenestra in many crurotarsans, ornithischians, sauropodomorphs, and theropods (Text-fig. 20B). In several theropods, including *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (DNM 2560, MOR 693), birds (*Archaeopteryx*: Eichstätt specimen), baryonychids (BMNH R 9951), dromaeosaurids (AMNH 5356), ornithomimosaurids (ROM 840), therizinosauroids (Clark *et al.* 1994), and tyrannosaurs (FMNH PR 308), the posterior end of the dentary is more or less straight or only slightly concave. It usually forms an oblique border that extends further posteriorly ventrally than dorsally (Text-fig. 20A).



TEXT-FIG. 23. Outlines of theropod splenials, illustrating states for characters 78 and 79. A, *Majungatholus atopus*; left splenial in medial view; based on FMNH 96202–44C. B, *Saurornitholestes langstoni*; slightly damaged right splenial in medial view (reversed); based on TMP 88.121.39. Scale bars represent 50 mm (A) and 100 mm (B).

78. Foramen in the ventral part of the splenial: absent (0); completely enclosed in the splenial (1); opened anteroventrally (2)

No foramen is present in the splenial in *Euparkeria* (Ewer 1965), basal crurotarsans (Hungerbühler, pers. comm. 1999) and ornithischians (Serenó 1991b). In the majority of saurischians a foramen is present in the anterior half of this bone, usually very close to its ventral border (Text-fig. 23A). The foramen was interpreted as the exit of the mylohyoid nerve and termed the anterior mylohyoid foramen by Currie and Zhao (1993b). It is completely enclosed in the splenial in many taxa, including prosauropods (*Plateosaurus*: MB R. 1937), *Ceratosaurus* (USNM 4735), *Ornitholestes* (AMNH 619), *Allosaurus* (DNM 116), sinraptorids (Currie and Zhao 1993b), abelisaurids (FMNH 96202–44C), birds (*Archaeopteryx*: Munich specimen), baryonychids (BMNH R 9951), therizinosauroids (Clark *et al.* 1994), and tyrannosaurids (Molnar 1991). In *Monolophosaurus* (Zhao and Currie 1993), dromaeosaurids (AMNH 5356, TMP 88.121.39), and troödontids (Barsbold 1974) the foramen opens in a narrow notch on the ventral rim of the splenial anteriorly (Text-fig. 23B).

In ornithomimosaur the foramen seems to be absent (Osmólska *et al.* 1972), although more detailed analysis of well-preserved specimens might show this to be erroneous. In oviraptorosaurs, the splenial is highly modified and seems to lack a foramen as well (Barsbold 1983). However, more detailed descriptions of the existing material are needed to confirm this. The foramen is also absent in birds, as shown by the Munich specimen of *Archaeopteryx*.

79. Posterior end of splenial: straight (0); forked (1) (Serenó *et al.* 1996)

The posterior end of the splenial is straight in *Euparkeria* (Ewer 1965), but it is forked to form the anterior rim of the internal mandibular fenestra, or to accommodate the anterior part of the prearticular in most dinosaurs (Text-fig. 23B). Unfortunately, the splenial is usually a very thin bone and, therefore, not preserved completely in many taxa. Within theropods, a straight posterior margin of the splenial is found in *Ceratosaurus* (USNM 4735), abelisaurids (FMNH 96202–44C), birds (*Archaeopteryx*: Munich specimen), oviraptorosaurs (Barsbold 1983), and therizinosauroids (Clark *et al.* 1994).

80. Coronoid: present (0); absent (1) (Clark *et al.* 1994)

As in reptiles ancestrally, a separate coronoid ossification is present in the mandible in the majority of dinosaurs, including most theropods. However, this bone is either absent or fused with another element without any visible suture in birds (*Archaeopteryx*: Munich specimen), ornithomimosaur (Osmólska *et al.* 1972), oviraptorosaurs (Barsbold 1983; although an independent coronoid has recently been reported in the new oviraptorosaur genus *Citipati*; Clark *et al.* 2001), and therizinosauroids (Clark *et al.* 1994).

81. Premaxillary teeth: present (0); absent (1) and

82. Maxillary and dentary teeth: present (0); absent (1) (modified from Holtz 1994)

The presence of marginal teeth in the jaws is a symplesiomorphy for tetrapods that is also retained in the majority of dinosaurs. However, in many groups the dentition may be reduced or lost entirely. In

some taxa, including *Avimimus* (ROM 46144), oviraptorosaurs (ROM 43250, TMP 90.56.6, 92.36.390; Barsbold *et al.* 1990), advanced ornithomimosaur (ROM 840, 851, 1790, TMP 90.26.1), and advanced birds, all teeth are lost. In the latter two groups, however, teeth are present in the most basal members (Marsh 1880; Wellnhofer 1974; Barsbold and Perle 1984; Pérez-Moreno *et al.* 1994), so both characters are coded as '0' for them. Dentary teeth are also lost in *Microvenator* (AMNH 3041; Makovicky and Sues 1998), but the premaxilla and maxilla are unknown in this taxon. However, since I am not aware of any dinosaur in which only the dentary teeth are lost, but the maxillary dentition is retained, it seems reasonable to code character 82 as '1' in this taxon.

In therizinosauroids only the premaxillary teeth are lost, whereas the maxillary and dentary dentitions are well-developed (Clark *et al.* 1994). Premaxillary teeth are also lost in several clades of ornithischians, but since all basal members of this clade retain premaxillary dentitions (e.g. Haubold 1991; Sereno 1991b), character 81 has been coded as '0' for ornithischians.

In *Caudipteryx*, on the other hand, teeth are present in the premaxilla, but absent in the maxilla and dentary (Ji *et al.* 1998).

Holtz treated loss of maxillary and dentary teeth as two different characters (Holtz 1994, characters 56 and 120). However, as noted above, the loss of maxillary and dentary teeth always seems to be correlated in dinosaurs. Therefore, only one character is used here to avoid over-emphasizing the importance of loss of teeth in theropods.

All of the following tooth characters cannot be coded for those taxa lacking teeth; therefore, they are coded as '?' in these clades.

83. Enlarged, fang-like teeth in the anterior part of the dentary: absent (0); present (1) (reversed and modified from Gauthier 1986)

Gauthier (1986, p. 23, character 36) used this character with reversed polarity as a synapomorphy of tetanurans. However, the polarity of this character is ambiguous. Many primitive archosauromorphs and crurotarsans have enlarged anterior dentary teeth, but they are absent in *Euparkeria* (Gower, pers. comm. 1999), some crurotarsans, most ornithischians, and sauropodomorphs. Within Ornithischia only heterodontosaurids show enlarged anterior dentary teeth (Weishampel and Witmer 1990a), but their phylogenetic position indicates that these teeth are an evolutionary novelty and not homologous with the enlarged dentary teeth in many crurotarsans (Sereno 1986). In the basal theropod *Herrerasaurus* the third dentary tooth seems to be slightly enlarged, but it is not significantly larger than more posterior teeth, and the tip of the dentary is not notably expanded (Sereno and Novas 1993). Therefore, all three of the characters given above (strongly enlarged teeth, transverse and dorsoventral expansion of anterior end of dentary) should be present to code character state '1'. Finally, since the methodology outlined by Nixon and Carpenter (1993) is used here, an *a priori* determination of character polarity is unnecessary.

In *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 6468), *Syntarsus* (QG, pers. obs., specimen number lost), both species of *Magnosaurus* (OUM J 12143, 13558), and baryonychids (BMNH R 9951, MNN GDF 504) the anterior parts of the dentaries are both transversely and dorsoventrally expanded, and some of the anterior dentary teeth are significantly larger than more posteriorly placed teeth (Text-fig. 22A).

84. Serrations on premaxillary teeth: present (0); absent (1) and

85. Serrations on maxillary and dentary teeth: present (0); absent (1) (modified from Chiappe *et al.* 1996)

In archosauromorphs ancestrally, the teeth bear serrated carinae anteriorly and posteriorly, and this character is retained by many crurotarsans, most ornithischians, basal sauropodomorphs, and many theropods. However, within theropods premaxillary teeth serrations are lost in *Coelophysis* (Colbert 1989), *Syntarsus* (QG 202; in the referred snout BP/II/5278 from South Africa, the premaxillary teeth are serrated; however, the referral of this specimen to the genus *Syntarsus* might be questionable), *Compsognathus* (BSP A.S. I 563), *Ornitholestes* (AMNH 619), *Caudipteryx* (Ji *et al.* 1998), and *Sinosauropteryx* (Chen

*et al.* 1998). In tyrannosaurs the basal representative, *Aublysodon*, also lacks serrations on the premaxillary teeth (Molnar and Carpenter 1989), whereas they are present in other members of this clade. Thus character 84 is coded as uncertain for tyrannosaurs.

In birds (*Archaeopteryx*: Berlin, Eichstätt, and Munich specimens) and ornithomimosaurs (Pérez-Moreno *et al.* 1994) serrations are absent in premaxillary, maxillary, and dentary teeth. In baryonychids some of the included species lack serrations on maxillary and dentary teeth (SMNS 58022; Stromer 1915), while they are present in others (BMNH R 9951, MNN GDF 501). Therefore, character 85 is coded as uncertain in baryonychids. Unfortunately, the premaxillae of those baryonychids lacking serrations in the dentary and maxillary teeth are unknown.

86. Teeth: recurved, pointed, and with small serrations (0); leaf-shaped, with enlarged denticles (1)

In archosaurs ancestrally, the teeth are usually pointed, recurved and bear small serrations on both carinae. In some herbivorous dinosaurs, including prosauropods (*Plateosaurus*: GPIT Skelett 1, MB R. 1937; Galton 1985b, 1990) and therizinosauroids (Russell and Dong 1993a; Clark *et al.* 1994), the teeth are rather straight, leaf-shaped and have enlarged, rounded marginal denticles. In *Eoraptor* (PVSJ 512) premaxillary and posterior maxillary teeth have a conventional archosaur shape, whereas the most anterior maxillary teeth are leaf-shaped; the dentary teeth are not visible in the holotype specimen. Therefore, character 86 is coded as uncertain in *Eoraptor*.

In ornithischians the lateral teeth are triangular and show enlarged denticles. However, since this is an altogether different tooth shape, no character state of the character as defined here can be applied to ornithischians, and thus the character is coded as '?' in this clade.

87. Constriction between tooth crown and root: absent (0); present (1) (Holtz 1994)

In the many archosaurs, including most theropods, the tooth root and tooth crown are confluent, with the root often being slightly wider than the crown. In ornithischians (e.g. Sereno 1991b), basal sauropodomorphs (*Plateosaurus*: GPIT Skelett 1, MB R 1937), birds (Martin *et al.* 1980), ornithomimosaurs (Pérez-Moreno *et al.* 1994), therizinosauroids (Clark *et al.* 1994), and troodontids (Currie 1987) the teeth are slightly waisted between crown and root by a small constriction. In both *Eoraptor* (PVSJ 512) and *Compsognathus* (BSP A.S. I 563) only a few teeth show such a constriction; therefore, the character is coded as uncertain in these taxa.

### Postcranial characters

#### Axial

88. Pleurocoels in cervical vertebrae: absent (0); present (1) (Holtz 1994) and

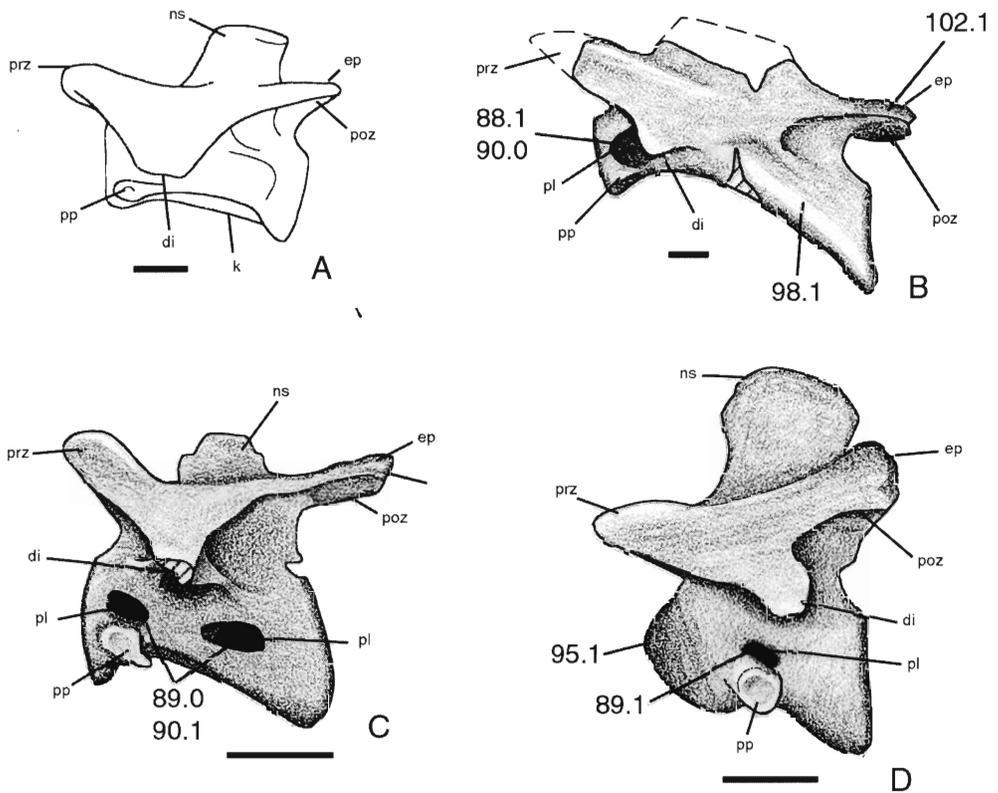
89. Number of pleurocoels in cervicals: two, arranged horizontally (0); one (1) (Gauthier 1986, as modified by Makovicky 1995) and

90. Pleurocoels developed as: deep depressions (0); foramina (1)

In the majority of crurotarsans, all ornithischians, and basal sauropodomorphs no deep depressions or foramina are present on the sides of the cervical vertebrae. In all theropods, with the exception of *Eoraptor* (ROM 44686), *Herrerasaurus* (Sereno and Novas 1993), and *Staurikosaurus* (Colbert 1970; Galton 1977), a deep recess is present above and sometimes partially behind the parapophyses on either side of the cervical vertebrae (Text-fig. 24B–D). It has been argued, repeatedly, that these pleurocoels were pneumatic and formed by diverticula connected to the lung (e.g. Janensch 1947). A detailed study of these structures by Britt (1993; cited in Makovicky 1995) has confirmed this.

Characters 89 and 90 cannot be applied to OTUs that do not have pneumatic recesses, and are therefore coded as '?' in these taxa.

In a variety of theropods, including *Coelophysis* (AMNH 7224), *Liliensternus airelensis* (CU,



TEXT-FIG. 24. Anterior theropod cervical vertebrae in lateral view, illustrating several cervical characters. A, *Herrerasaurus ischigualastensis*; redrawn from Sereno and Novas (1993). B, *Liliensternus liliensterni*; based on MB R. 2175. C, *Dilophosaurus wetherilli*; based on UCMP V 6468. D, *Allosaurus fragilis*; based on Madsen (1976) and MOR 693. Abbreviations: di, diapophysis; ep, epipophysis; k, keel; ns, neural spine; pl, pleurocoel; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis. Scale bars represent 10 mm (A-B) and 50 mm (C-D).

unnumbered), *Dilophosaurus* (UCMP V 4214, 6468), *Syntarsus* (QG 174), *Ceratosaurus* (USNM 4735, UMNH VP 5278), *Elaphrosaurus* (MB dd unnumbered), *Microvenator* (AMNH 3041), abelisaurids (MACN CH 894, FMNH/UA field #96300), oviraptorosaurs (Makovicky 1995), and therizinosauroids (Makovicky 1995), a second pair of pneumatic recesses is present on the posterior part of the centrum, behind the more anterior one (Text-fig. 24C). In *Avimimus* (ROM 46144) a second pair of recesses is present only in some vertebrae; therefore, character 89 has been coded as uncertain in this taxon. Rowe and Gauthier (1990) and Holtz (1994) obviously considered the presence of two pneumatic recesses as the derived character state, but Britt (1993, cited in Makovicky 1995) argued that this was the primitive state, based on ontogenetic data from modern birds (Britt, pers. comm. 1995).

The pleurocoels in the cervical vertebrae are developed as deep, but superficial depressions in *Coelophysis* (AMNH 7224), both species of *Liliensternus* (Text-fig. 24B; CU unnumbered, MB R. 2175), and *Syntarsus* (QG 174), whereas foramina piercing the bone and leading into internal pneumatic chambers are present in all other theropods (Text-fig. 24C-D). *Elaphrosaurus* (MB dd unnumbered) shows a transitional model in which some pleurocoels are developed as superficial depressions, whereas others show foramina within the depressions; therefore, the character state is coded as uncertain in this taxon.

Although pneumatisation patterns in the postcranial skeleton can vary greatly in modern birds, this variation is usually greater in the appendicular skeleton than in the vertebral column (see e.g. Starck 1979).

Since the distribution and development of pleurocoels in theropods seems to be rather constant, these features are used as characters here.

91. Pleurocoel in axis: absent (0); present (1) (reversed from Rowe and Gauthier 1990)

No pneumatic openings or deep pleurocentral grooves are found in the axis of the vast majority of crurotarsans, and in no ornithischian or primitive sauropodomorph. In most theropods, with the exception of *Coelophysis* (Rowe and Gauthier 1990), *Dilophosaurus* (UCMP V 4214), *Syntarsus* (QG 174), *Magnosaurus oxoniensis* (OUM J 13558), *Piatnitzkysaurus* (Bonaparte 1986), and *Afrovenator* (UC OBA 1), the axis shows a large, deep depression or a large foramen posterodorsal of the axial parapophyses (Text-fig. 25c). Axial pleurocoels are also present in advanced sauropods, but their absence in more basal members of Sauropodomorpha indicates that these pleurocoels have evolved independently from the pleurocoels of theropods.

The absence of axial pleurocoels has been used by Rowe and Gauthier (1990) and Holtz (1994) to define a ceratosaurian ingroup, termed *Coelophysoidea* by Holtz. This assumes that axial pleurocoels were originally present in primitive theropods, but secondarily lost in this group. However, in modern birds, the pneumatisation of the cervical vertebral column during ontogeny starts at the cervical/dorsal transition and then continues anteriorly (e.g. Baer 1896; Müller 1907). Furthermore, no saurischian dinosaur is known in which just the anteriormost cervical vertebrae, but not the more posterior ones are pneumatised. Thus, it seems more likely that in theropods the pneumatisation of the cervical vertebral column by diverticula of a cervical air sac also occurred from the cervical/dorsal transition forwards. Consequently, the presence of axial pleurocoels is regarded as a derived character here.

Since there is the strong possibility that the pneumatisation of the vertebral column in non-avian theropods followed the same ontogenetic pattern as that found in birds, the character has only been coded as '0' in taxa for which abundant material is available (*Coelophysis*, *Syntarsus*), or in animals where all postaxial cervicals, including the third cervical, have well-developed pleurocoels.

92. Epipophyses on axis: absent (0); present as small ridges (1); strongly pronounced (overhanging the postzygapophyses) (2) (modified from Gauthier 1986; ordered)

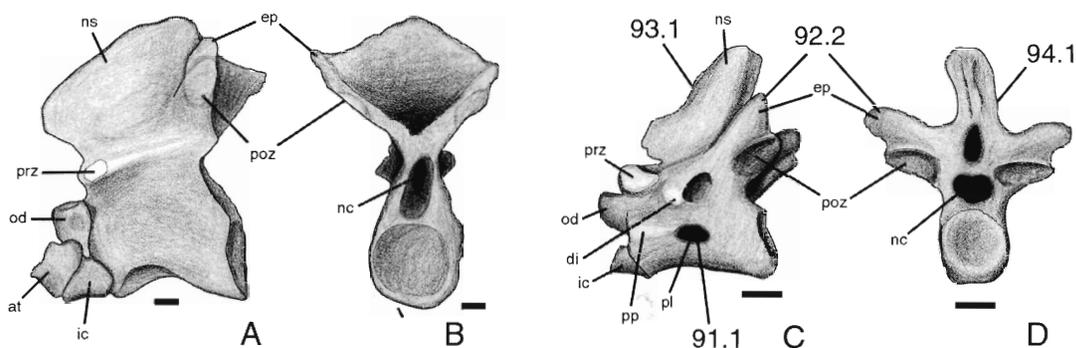
In many crurotarsans, the basal dinosauriform *Marasuchus*, and ornithischians no epipophyses are present on the axial postzygapophyses. In all theropods an elongate, posterolaterally pointing epiphysis is present. It is uncertain if such a process is also present in sauropodomorphs ancestrally; it is absent in an axis of *Plateosaurus* from the Knollenmergel of Trossingen (SMNS 13200), but present in the same element of an individual from equivalent beds in Halberstadt (MB Skelett 25).

In some theropods and MB Skelett 25 the epiphysis is developed as a small ridge on the postzygapophysis that ends in a point posteriorly. In many theropods, including *Dilophosaurus* (UCMP V 4214), *Magnosaurus* (OUM J 13558), *Piatnitzkysaurus* (Bonaparte 1986), *Allosaurus* (AMNH 5767, DNM 116), *Ceratosaurus* (USNM 4735, UMNH VP 5278), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), abelisaurids (MACN CH 894), baryonychids (BMNH R 9951), carcharodontosaurids (Harris 1998), dromaeosaurids (MOR 660, YPM 5204), troodontids (Makovicky 1995), and tyrannosaurids (Makovicky 1995), the epipophyses are high, cone-shaped and overhang the postzygapophyses considerably posteriorly (Text-fig. 25).

Since character state 2 includes character state 1, the character is treated as ordered.

93. Axial neural spine: sheet-like (0); anteroposteriorly reduced and rod-like (1) (Molnar *et al.* 1990)

In ornithischians, sauropodomorphs, and several theropods the axial neural spine is anteroposteriorly long and the dorsal margin rises in a convex slope from the anterior end towards the posterior end; thus, the spine forms a dorsally convex sheet of bone in lateral view (Text-fig. 25A). In *Monolophosaurus* (Zhao and Currie 1993), *Piatnitzkysaurus* (Bonaparte 1986), *Allosaurus* (AMNH 5767), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), baryonychids (BMNH R 9951), carcharodontosaurids (Harris 1998), dromaeosaurids (MOR 660, YPM 5204), troodontids (Makovicky 1995), and tyrannosaurids (Makovicky 1995) the axial neural spine is



TEXT-FIG. 25. Axes of two theropods, illustrating several axial characters. A–B, *Dilophosaurus wetherilli*; left lateral and posterior view; based on UCMP V 4214. C–D, *Deinonychus antirrhopus*; left lateral and posterior view; based on YPM 5204. Abbreviations as in Text-figure 24, and: at, atlantal intercentrum; ic, axial intercentrum; nc, neural canal; od, odontoid. Scale bars represent 10 mm.

anteroposteriorly reduced, restricted to the posterior part of the neural arch, and rises abruptly in a concave arc from the roof of the neural canal (Text-fig. 25c).

94. Large groove excavated into posterior base of axis: present (0); absent (1) (Makovicky 1995)

In ornithischians, sauropodomorphs, and many theropods the posterior end of the axial neural spine is strongly widened transversely and hollowed posteriorly by a large groove that is deepest between the postzygapophyses and becomes shallower dorsally (Text-fig. 25B). In *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), birds (Marsh 1880), dromaeosaurids (MOR 660, YPM 5204), ornithomimosaurs (Makovicky 1995), and troodontids (Makovicky 1995) the posterior end of the axial neural spine is not widened transversely and the posterior groove is absent or reduced to a small, deep pit between the postzygapophyses (Text-fig. 25D).

95. Cervical vertebral centra: amphi- to platycoelous (0); strongly opisthocoelous (1) (Gauthier 1986)

In crurotarsans, basal dinosauriforms, basal ornithischians, basal sauropodomorphs, and many theropods the cervical vertebrae are amphiplatycoelous, whereas they are strongly opisthocoelous in *Magnosaurus oxoniensis* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (Text-fig. 24D; DNM 116, MOR 693, USNM 4734), *Compsognathus* (BSP A.S. I 563), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), baryonychids (BMNH R 9951, MNN GDF 500), and carcharodontosaurids (Stromer 1931; Stovall and Langston 1950). This character is only coded as '1' for taxa that have a well-rounded anterior 'ball' on the cervical centra; in several other theropod taxa, including *Piatnitzkysaurus* (Bonaparte 1986), *Ceratosaurus* (UMNH VP 5278), abelisaurids (MACN CH 894, FMNH/UA field #96300), and tyrannosaurs (AMNH 5468, FMNH PR 308), the anterior articular surface of the cervical vertebrae might be very slightly convex.

This character was first proposed by Gauthier (1986, p. 10) as a synapomorphy of a supposedly monophyletic Carnosauria. Gauthier (1986) and Molnar *et al.* (1990) expressed the suspicion that the character might be size-related, and it was therefore omitted in later analyses (e.g. Holtz 1994). However, as pointed out by Rauhut (1995) and Harris (1998), opisthocoelous cervical vertebrae are not found in all large theropods, nor are they restricted to large forms. The tyrannosaurids, which include some of the largest known theropod taxa, have cervical vertebrae that are posteriorly concave and anteriorly flat to very slightly convex, whereas the small theropod *Compsognathus* shows strongly convex cervical vertebrae. That *Compsognathus* is not necessarily an exception is shown by reported small opisthocoelous theropod cervical vertebrae from the Upper Jurassic Morrison Formation of the USA (YPM 1996, 1997; Makovicky 1997) and the Barremian of the Isle of Wight (type of *Calamospondylus foxi*, BMNH R 901; Lydekker 1889).

96. Interior pneumatic spaces in cervicals: absent (0); present, structure camerate (1); present, structure camellate (2) (Britt 1993)

Whereas internal pneumatic cavities are unknown in ornithischians and basal sauropodomorphs, they are common in theropods. According to Britt (1993, cited in Makovicky 1995; Britt 1995, and pers. comm. 1995), two fundamentally different types of internal pneumatic cavities can be recognized: a camerate and a camellate type. In the camerate type the cavities in the cervical vertebrae consist of several large chambers that are not further subdivided, whereas in the camellate type the internal cavities are subdivided by a large number of delicate bony lamellae (Britt, pers. comm. 1995). Since the internal architecture of cervical vertebrae is rarely visible in specimens without the use of invasive techniques or technical equipment, character codings for this character are based on Britt (1995), Makovicky (1995), and Harris (1998), unless otherwise indicated.

Internal pneumatic cavities of the camerate type are present in *Coelophysis*, *Piatnitzkysaurus* (based on Bonaparte 1986, figs 9, 11), *Allosaurus*, sinraptorids, *Torvosaurus*, and dromaeosaurids, whereas the camellate type is present in *Ceratosaurus*, birds, carcharodontosaurids, ornithomimosaurs, oviraptorosaurs, troodontids, and tyrannosaurids.

97. Ventral keel in anterior cervicals: present (0); absent (1) (Makovicky 1995)

In ornithischians, sauropodomorphs, and several theropod taxa the axis and postaxial anterior cervical vertebrae bear a faint longitudinal ventral keel (Text-fig. 24A), which is usually best developed towards the posterior end of the centrum. Such a ventral keel is absent in *Magnosaurus oxoniensis* (OUM J 13558), *Coelurus* (YPM 1993), *Elaphrosaurus* (MB dd unnumbered), *Ornitholestes* (Makovicky 1995), sinraptorids (Currie and Zhao 1993b), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), abelisaurids (MACN CH 894, FMNH/UA field #96300), birds (Makovicky 1995), dromaeosaurids (MOR 660, YPM 5204, 5210), ornithomimosaurs (AMNH 6570, 21786, ROM 840, TMP 93.62.1), oviraptorosaurs (ROM 43250; Makovicky 1995), therizinosauroids (Makovicky 1995), and troodontids (MOR 553S). In tyrannosaurs a true ventral keel is absent, but a small ventral projection is found on the ventral sides of the anterior cervical vertebral centra (Makovicky 1995); therefore, this character is coded as '?' for tyrannosaurs.

98. Broad ridge from the diapophyses to the ventral rim of the posterior end of the vertebral centra in cervical vertebrae: absent (0); present (1)

In *Liliensternus airelensis* (CU unnumbered) and *Liliensternus liliensterni* (MB R. 2175) a broadly rounded ridge connects the posterior margin of the diapophyses with the ventral rim of the posterior end of the vertebral centrum in the anterior and mid-cervical vertebrae (Text-fig. 24B). The ridge is better developed in *Liliensternus airelensis*, where it separates the anterior cervical pleurocoel from the slightly more dorsally placed posterior pleurocoel, than in *Liliensternus liliensterni*. Such a ridge is unknown in any other dinosaur taxon.

99. Prezygapophyses in anterior cervicals: transverse distance between prezygapophyses less than width of neural canal (0); prezygapophyses situated lateral to the neural canal (1) (Makovicky 1995)

In sauropodomorphs and several theropods the prezygapophyses of the anterior cervical vertebrae are situated close together so that the distance between their median margins is less than the width of the neural canal. In ornithischians and many theropods, including *Magnosaurus oxoniensis* (OUM J 13558), *Piatnitzkysaurus* (Bonaparte 1986), *Allosaurus* (DNM 116, MOR 693), *Coelurus* (YPM 1993), *Ornitholestes* (Makovicky 1995), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), abelisaurids (FMNH/UA field #96300), birds (Marsh 1880), baryonychids (BMNH R 9951), carcharodontosaurids (Harris 1998), dromaeosaurids (MOR 660, YPM 5204, 5210), ornithomimosaurs (Makovicky 1995), oviraptorosaurs (Makovicky 1995), troodontids (MOR 553S), and tyrannosaurs (AMNH 5468), the prezygapophyses are relatively enlarged and placed entirely lateral to the neural canal.

100. Prezygapophyses in anterior postaxial cervicals: straight (0); anteroposteriorly convex, flexed ventrally anteriorly (1) (modified from Gauthier 1986)

In crurotarsans, ornithischians, sauropodomorphs, and many theropods the articular surface of the prezygapophyses is more or less straight. In a variety of theropods, including *Coelurus* (YPM 1993), *Ornitholestes* (Makovicky 1995), birds (*Archaeopteryx*: Berlin and Eichstätt specimens), dromaeosaurids (MOR 660, YPM 5204, 5210), ornithomimosaurs (ROM 840), and oviraptorosaurs (Makovicky 1995), the anterior part of the articular surface is flexed ventrally, reflecting the more pronounced curvature of the neck in these animals.

101. Anterior articular facet of anterior cervical vertebrae: approximately as high as wide or higher (0); significantly wider than high (1); wider than high and higher laterally than medially (kidney-shaped) (2) (modified from Gauthier 1986)

In basal ornithischians, all sauropodomorphs, and some theropods the anterior cervical vertebrae show a round to high oval anterior intervertebral articular facet. In many theropods this facet is significantly wider than high, and its shape can be broadly oval, as in *Staurikosaurus* (Galton 1977), *Dilophosaurus* (UCMP V 4214, 6468), *Magnosaurus oxoniensis* (OUM J 13558), *Piatnitzkysaurus* (Bonaparte 1986), *Elaphrosaurus* (MB dd unnumbered), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), *Microvenator* (AMNH 3041), abelisaurids (MACN CH 894, FMNH/UA field #96300), baryonychids (BMNH R 9951), and carcharodontosaurids (Sereno *et al.* 1996), or the lateral sides might be higher than the medial part, thus giving the facet a kidney-like outline (Gauthier 1986, fig. 3G-1). The latter character state is found in *Ornitholestes* (AMNH 619), birds (Marsh 1880), dromaeosaurids (MOR 660, MOR 5204), ornithomimosaurs (Osmólska *et al.* 1972), oviraptorosaurs (Makovicky 1995), and troödontids (MOR 553S).

102. Epipophyses in anterior cervical vertebrae: absent or poorly developed (0); well-developed (1); pronounced, strongly overhanging the postzygapophyses (2) (modified from Gauthier 1986; ordered)

Epipophyses are absent in the anterior cervicals of the basal dinosauriform *Marasuchus* (Sereno and Arcucci 1994) and a few theropods, including *Staurikosaurus*, *Elaphrosaurus* (MB dd unnumbered), and oviraptorosaurs (Makovicky 1995). In other ornithischians, sauropodomorphs, and theropods epipophyses are well-developed in the anterior cervicals.

As for the axial epipophyses (character 92), the processes in the anterior cervical vertebrae can be developed as a rather small ridge that ends in a posterior point (Text-fig. 24B) or as large, massive processes that considerably overhang the postzygapophyses (Text-fig. 24C). The latter character state is found in *Dilophosaurus* (UCMP V 6468), *Magnosaurus* (OUM J 133558), *Monolophosaurus* (Zhao and Currie 1993), *Piatnitzkysaurus* (Bonaparte 1986), *Allosaurus* (DNM 116, MOR 693), *Ceratosaurus* (UMNH VP 5278), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), abelisaurids (MACN CH 894, FMNH/UA field #96300), baryonychids (BMNH R 9951), carcharodontosaurids (Harris 1998), dromaeosaurids (MOR 660, YPM 5204, 5210), troödontids (MOR 553S), and tyrannosaurs (FMNH PR 308).

The morphology of these processes may be quite different in different taxa. Whereas the epipophyses in the majority of the taxa listed above are developed as rather cone-shaped, massive, dorsoposteriorly pointing processes, they are transversely thin and anteroposteriorly elongated in abelisaurids, where their height exceeds that of the neural spine. In dromaeosaurids and troödontids, the epipophyses are stout, rather low and curve laterally posteriorly.

Although the development of the cervical epipophyses might be at least partially size-dependent, the character is used here, since even character state 2 is not entirely restricted to large taxa.

As in character 92, character state 2 includes character state 1; thus the character is treated as ordered.

103. Hyposphene-hypantrum articulation in dorsal vertebrae: absent (0); present (1) (Gauthier 1986) and
104. Shape of hyposphene-hypantrum articulation: hyposphene developed as a single sheet of bone (0); hyposphene wide, formed by the ventrally bowed medial parts of the postzygapophyses, and only connected by a thin horizontal lamina of bone (1)

Accessory vertebral articulations are absent in basal dinosauriforms and ornithischians. In saurischians an accessory articulation, the hyposphene-hypantrum articulation, is present in the dorsal (Text-figs 26A, 27), and sometimes also the posterior cervical and anterior caudal vertebrae. The hyposphene is usually developed as a vertical wall of bone that extends ventrally from between the postzygapophyses and slots into a notch between the prezygapophyses of the next vertebra. In many taxa the ventral end of the hyposphene is slightly expanded transversely. This additional articulation obviously prevented torsion between the elements of the vertebral column.

Gauthier (1986, p. 16) claimed that such an articulation is absent in herrerasaurids. However, Novas (1993) clearly showed that these articulations are present in *Herrerasaurus*. A hyposphene-hypantrum articulation is also absent in advanced birds (Gauthier 1986), but it is present in basal forms including *Rahonavis* (UA 8656).

In some taxa, including *Unenlagia* (MCF PVPH 78), basal birds (*Rahonavis*: UA 8656), dromaeosaurids (MOR 660, YPM 5204, 5210), and troodontids (MOR 553S), the hyposphene is broad and consists of two vertical bony lamellae which are separated by a deep vertical groove in posterior view. Ventrally, the two lamellae are connected by a small horizontal lamella. In dromaeosaurids and troodontids the accessory articulations are, furthermore, restricted to the posterior two-thirds of the dorsal vertebral column. It cannot be determined if this is also the case in *Unenlagia* and *Rahonavis* because of the fragmentary preservation of the specimens.

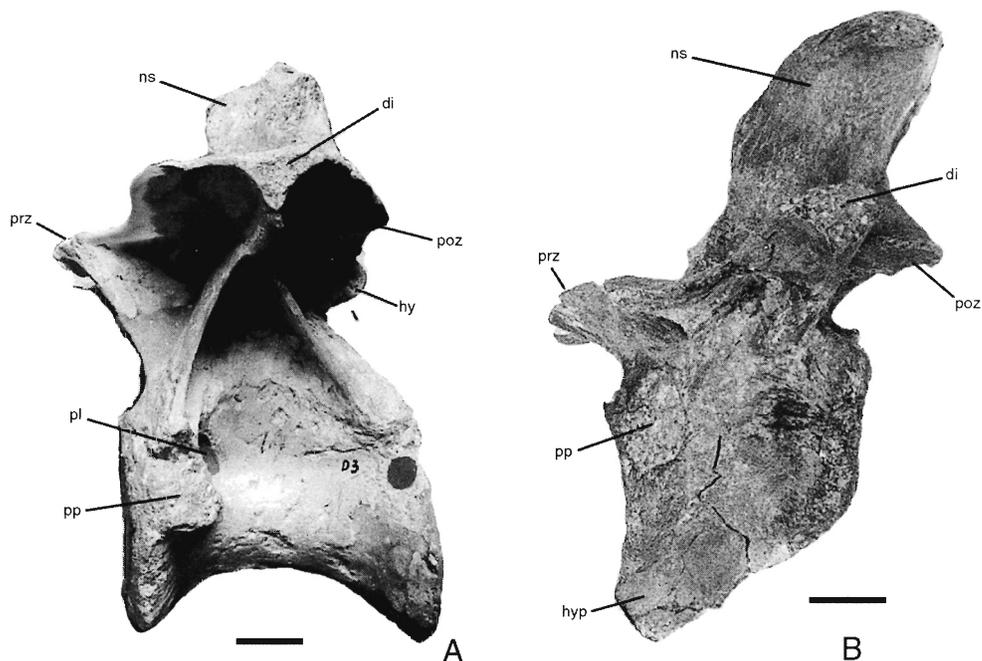
105. Shape of dorsal centra in anterior view: subcircular or oval (0); significantly wider than high (1) (Makovicky and Sues 1998)

In ornithischians, sauropodomorphs, and most theropods the intervertebral articular facets of the dorsal vertebral centra from the posterior half of the dorsal vertebral column have a subcircular to high oval outline. In *Microvenator* (AMNH 3041) and oviraptorosaurs (Makovicky 1995) the intervertebral articular facets are considerably wider than high. Within dromaeosaurids, *Deinonychus* (YPM 5204, 5210) and *Saurornitholestes* (MOR 660) have posterior dorsals in which the intervertebral articular facets are subcircular in outline, while they are broadly oval in *Velociraptor* (IGM 100/986). Therefore, this character is coded as uncertain in dromaeosaurids.

106. Pleurocoels in dorsal vertebrae: absent (0); present in anterior dorsals ('pectorals') (1); present in all dorsals (2) (Holtz 1994, as modified by Harris 1998; ordered)

In basal dinosauriforms, ornithischians, and basal sauropodomorphs the dorsal vertebrae do not show any deep pneumatic recesses in the vertebral centrum. The majority of theropods that possess cervical pleurocoels have similar deep recesses or pneumatic foramina in at least the anterior dorsal vertebrae (Text-fig. 26A), a pattern that is consistent with the mode of pneumatization of the vertebral column in the ontogeny of birds (see character 91). It is, therefore, interesting that dorsal pleurocoels are entirely absent in a few taxa that have cervical pleurocoels; these include *Elaphrosaurus* (MB dd unnumbered) and *Avimimus* (ROM 46144).

In several theropod taxa, including *Torvosaurus* (Britt 1991), *Microvenator* (AMNH 3041), *Neovenator* (Hutt *et al.* 1996), *Unenlagia* (MCF PVPH 78), carcharodontosaurids (Stromer 1931; Harris 1998), oviraptorosaurs (Barsbold *et al.* 1990), and tyrannosaurids (FMNH PR 308), all dorsal vertebrae are pleurocoelous. In dromaeosaurids all dorsal vertebrae are pleurocoelous in *Deinonychus* (YPM 5204, 5210) and *Saurornitholestes* (MOR 660), while the posterior dorsals lack pleurocoels in *Velociraptor* (IGM 100/986); therefore, the character is coded as '1/2' in dromaeosaurids. This character is coded as '0/1' for many taxa in which only apneumatic posterior dorsals are known.



TEXT-FIG. 26. Anterior dorsal vertebrae of two theropods in left lateral view, illustrating states for several vertebral characters. A, *Liliensternus liliensterni*; MB R. 2175. B, *Troödon formosus*; TMP 94.12.438. Abbreviations as in Text-fig. 24, and: hy, hyosphene; hyp, hypapophysis. Scale bars represent 10 mm.

The pleurocoels in the anterior dorsal vertebrae are similar in position to those of the cervical vertebrae, situated above and partially behind the parapophyses in the anterior half of the centrum (Text-fig. 26A). In more posterior dorsals in which the parapophyses are situated on the neural arch, the pleurocoels are placed more medially on the vertebral centrum. In many archosaurs, including crurotarsans, sauropodomorphs, and many theropods in which the posterior dorsals are not pleurocoelous, large pleurocentral grooves are present in the posteriormost dorsal vertebral centra. However, these pleurocentral grooves differ from true pleurocoels in that their margins are not as sharply defined and they are not as deep as the pleurocoels.

Since no theropods are known in which only the posterior dorsals, but not the anterior ones are pneumatised, the character is treated as ordered.

107. Hypapophyses in anterior dorsals: absent or poorly developed (0); strongly pronounced (1) (Gauthier 1986)

In basal dinosauriforms, ornithischians, sauropodomorphs, and a variety of theropods prominent hypapophyses in the anterior dorsal vertebrae are absent. Prominent hypapophyses are present in at least dorsal 2 and 3 in *Ornitholestes* (Makovicky 1995), sinraptorids (Currie and Zhao 1993b), *Avimimus* (ROM 46144), birds (*Rahonavis*: UA 8656), dromaeosaurids (MOR 660, YPM 5204, 5210), oviraptorosaurs (ROM 43250), and troodontids (Text-fig. 26B; MOR 553S). Hypapophyses are also present in eusuchian crocodiles (Gauthier 1986), but this condition certainly arose independently in crocodile evolution.

108. Ventral keel in anterior dorsals: absent or very poorly developed (0); pronounced (1)

In many ornithischians, sauropodomorphs, and theropods a very weak, rounded ventral keel is present in the otherwise ventrally rather rounded anterior dorsal vertebrae. In a variety of theropods, including

*Monolophosaurus* (Zhao and Currie 1993), *Piatnitzkysaurus* (Bonaparte 1986), *Xuanhanosaurus* (IVPP V 6729), '*Szechuanosaurus*' *zigongensis* (Gao 1993), *Allosaurus* (DNM 116, MOR 693), *Coelurus* (YPM 2010), *Ornitholestes* (Makovicky 1995), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Avimimus* (ROM 46144), birds (UA 8656), baryonychids (BMNH R 9951, MNN GDF 500), carcharodontosaurids (Harris 1998), dromaeosaurids (MOR 660, YPM 5204, 5210), oviraptorosaurs (ROM 43250), troodontids (MOR 553S), and tyrannosaurids (FMNH PR 308), the anterior dorsal vertebral centra narrow rapidly directly below the parapophysis and form a deep, sharp ventral keel.

109. Neural spine of posterior dorsals: broadly rectangular and approximately as high as long (0); high rectangular, significantly higher than long (1)

In basal dinosauriforms, ornithischians, sauropodomorphs, and some theropods the posterior dorsal neural spines are anteroposteriorly elongate and rather low so that they are approximately as high as long or lower (Text-fig. 27B). In many theropods, including *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Gojirasaurus* (Carpenter 1997), *Dilophosaurus* (UCMP V 4214), *Magnosaurus oxoniensis* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Piatnitzkysaurus* (MACN CH 895), *Allosaurus* (DNM 116, USNM 4734), *Ceratosaurus* (UMNH VP 5278), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Unenlagia* (MCF PVPH 78), abelisaurids (MACN CH 894), birds (*Archaeopteryx*: Munich specimen), baryonychids (BMNH R 9951), carcharodontosaurids (Stovall and Langston 1950), dromaeosaurids (MOR 660, YPM 5204, 5210), oviraptorosaurs (Makovicky 1995), therizinosauroids (Russell and Dong 1993a), troodontids (MOR 553S), and tyrannosaurids (FMNH PR 308), the neural spines of the posterior dorsal vertebrae are considerably higher than long (Text-fig. 27A).

110. Neural spine in posterior dorsals: of subequal length throughout its height or tapering dorsally (0); significantly expanded dorsally, fan-shaped (1) (Chen *et al.* 1998)

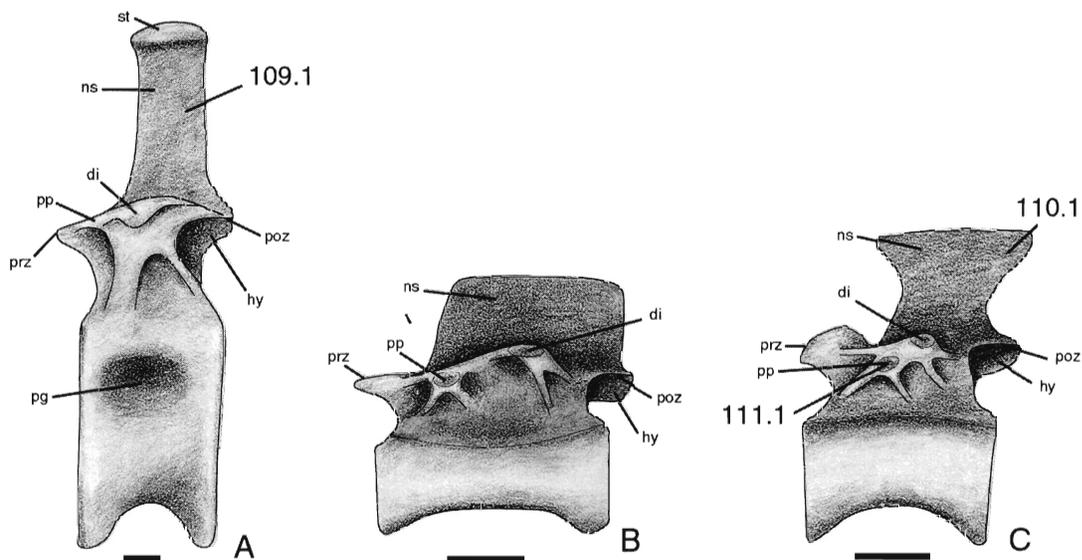
In ornithischians, sauropodomorphs, and most theropods the neural spines of the posterior dorsal vertebrae taper dorsally or are of subequal anteroposterior length throughout their height in lateral view. In *Compsognathus* (BSP A.S. I 563), *Elaphrosaurus* (MB dd unnumbered), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), and *Sinosauropteryx* (Chen *et al.* 1998) the posterior dorsal neural spines are significantly anteroposteriorly expanded dorsally so that they are longer anteroposteriorly at their tip than at their base (Text-fig. 27c).

111. Parapophyses in posteriormost dorsals: on the same level as transverse process (0); distinctly below transverse process (1) (Makovicky 1995)

In archosaurs the parapophyses are situated at the mid-height of the centrum in anterior dorsals, but migrate dorsally in more posterior dorsal vertebrae. In ornithischians, sauropodomorphs, and several theropods they are on the same level as the transverse processes in the posteriormost dorsals so that the tuberculum and capitulum of the ribs attached to this vertebra are only offset horizontally, but not vertically (Text-fig. 27B). In many theropods, including *Allosaurus* (DNM 116), *Coelurus* (Makovicky 1995), *Ornitholestes* (Makovicky 1995), sinraptorids (Currie and Zhao 1993b), *Avimimus* (ROM 46144), *Unenlagia* (MCF PVPH 78), birds (Makovicky 1995), baryonychids (BMNH R 9951), dromaeosaurids (MOR 660), ornithomimosaurids (Makovicky 1995), therizinosauroids (Makovicky 1995), troodontids (Makovicky 1995), and tyrannosaurids (FMNH PR 308), the parapophyses remains below the transverse process even in the posteriormost rib-bearing dorsal vertebra (Text-fig. 27c), and the capitulum and tuberculum of the ribs are offset vertically as well as horizontally.

112. Posterior dorsal vertebrae: strongly shortened, centra much shorter than high (0); relatively short, centra approximately as high as long, or only slightly longer (1); significantly elongated, much longer than high (2) (ordered)

In ornithischians, sauropodomorphs, and many theropods the posterior dorsal vertebral centra are approximately as high as long. In *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), and *Allosaurus* (DNM 116) the centra are strongly shortened and considerably higher than long (Text-fig. 27A).



TEXT-FIG. 27. Posterior dorsal vertebrae of three theropod dinosaurs in left lateral view, showing states for several axial characters. A, *Herrerasaurus ischigualastensis*; penultimate dorsal vertebra; redrawn (reversed) from Novas (1993). B, *Syntarsus rhodesiensis*; reconstruction of the eleventh dorsal vertebra; based on QG 1. C, unnamed compsognathine from the Lower Cretaceous of Brazil; reconstruction of the posteriormost dorsal vertebra; based on SMNK 2349 Pal. Abbreviations as in Text-figures 24 and 26, and: pg, pleurocentral groove; st, spine table. Scale bars represent 10 mm.

In a variety of other theropods, including *Coelophysis* (AMNH 7224), *Gojirasaurus* (Carpenter 1997), both species of *Liliensternus* (CU unnumbered, MB R. 2175), *Dilophosaurus* (UCMP V 4214), *Syntarsus* (QG 1), *Magnosaurus oxoniensis* (OUM J 13558), *Elaphrosaurus* (MB dd unnumbered), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Avimimus* (ROM 46144), and ornithomimosaur (ROM 852), the posterior dorsal vertebrae are considerably elongated so that they are much longer than high. This is especially striking in *Coelophysis* and *Syntarsus* where they are more than twice as long as they are high (Text-fig. 27B).

113. Number of sacral vertebrae: two (0); three (1); more than three (2); more than five (3) (modified from Gauthier 1986) (ordered)

In archosaurs ancestrally, the number of sacral vertebrae is two, as is the case in *Euparkeria*, most crurotarsans, and basal dinosauriforms (Sereno and Arcucci 1993, 1994). Most dinosaurs have more than two sacral vertebrae, and the incorporation of a third vertebra into the sacrum was considered a dinosaurian synapomorphy by Gauthier (1986). Ornithischians primitively have five sacral vertebrae (Sereno 1986), whereas Gauthier (1986) assumed the primitive number of sacral vertebrae for saurischians to be three. However, there is some confusion about the sequence of incorporation of vertebrae into the sacrum. Novas (1996a) and Wilson and Sereno (1998) argued that the third sacral in saurischians is a dorsosacral vertebra, mainly based on the South American prosauropod *Riojasaurus*, but several specimens of the prosauropods *Plateosaurus* (GPIT Skelett 1, SMNS 1986, 13200) and *Sellosaurus* (SMNS 5715, 17928) clearly show that the third sacral in these taxa is a caudosacral vertebra. This difference in the derivation of the third sacral vertebra in prosauropods may indicate that the incorporation of this vertebra happened independently in different groups of saurischians (see Galton 1999). This interpretation would be in general accordance with the interpretation of herrerasaurids as theropods (Sereno and Novas 1992, 1993; Novas 1993; Sereno 1993) since the number of sacral vertebrae in both *Herrerasaurus* and *Staurikosaurus* is two (Galton 1977; Novas 1993). However, the possibly even more basal theropod *Eoraptor* (Sereno *et al.* 1993) has three sacral vertebrae.

In all other theropods the number of sacral vertebrae is at least five. In several theropod taxa, including *Elaphrosaurus* (MB dd unnumbered), *Unenlagia* (MCF PVPH 78), abelisaurids (MACN CH 894), ornithomimosaurids (ROM 852, 01790), oviraptorosaurs (ROM 43250; Barsbold *et al.* 1990; Currie 1990), and troödontids (Barsbold 1974), the number of sacral vertebrae is further increased to up to seven.

In birds the basal form *Archaeopteryx* retained five sacral vertebrae (Wellnhofer 1974, 1992, 1993), but more derived members of this clade have increased the number of sacra considerably. Therefore, the character is coded as '2/3' in birds.

In dromaeosaurids the number of sacral vertebrae is usually given as five (Ostrom 1976b; Makovicky 1995), although Ostrom (1976b) noted that a sixth vertebra was fused to the sacrum in a specimen of *Deinonychus*. Only five fused elements are present in *Sauromitholestes* (MOR 660, TMP 92.36.129), but in *Velociraptor* (IGM 100/985, 100/986), the ilium covers seven vertebrae and six vertebrae contact the ilium in IGM 100/986. Thus, the character is coded as '2/3' in dromaeosaurids. The same coding has been applied to therizinosauroids, where the number of sacral vertebrae is five in *Alxasaurus* and *Nanshiungosaurus brevispinus*, but six in *Segnosaurus* (Makovicky 1995).

114. Sacral centra: rounded or keeled ventrally (0); flattened ventrally (1) (Makovicky 1995)

The sacral vertebrae are usually relatively high and ventrally rounded or keeled in basal dinosauriforms, ornithischians, sauropodomorphs, and many theropods. In a number of theropods, including *Syntarsus* (QG 1, BP/II 5246), *Elaphrosaurus* (MB dd unnumbered), *Ornitholestes* (AMNH 619), *Unenlagia* (MCF PVPH 78), birds (UA 8656), dromaeosaurids (IGM 100/985, 100/986, MOR 660), ornithomimosaurids (AMNH 21790, ROM 852, 01790, USNM 4736), oviraptorosaurs (ROM 43250), therizinosauroids (Makovicky 1995), and troödontids (Barsbold 1974), the sacral vertebrae are dorsoventrally flattened and have a broad, flat, ventral surface that usually bears a shallow longitudinal sulcus.

115. Pleurocoels in sacral vertebrae: absent (0); present (1) (Holtz 1994)

Sacral pleurocoels are absent in basal dinosauriforms, ornithischians, basal sauropodomorphs, and many theropods. Pleurocoels are present in at least some sacral vertebrae in carcharodontosaurids (Harris 1998), ornithomimosaurids (AMNH 21790, USNM 4736), and oviraptorosaurs (ROM 43250, Barsbold *et al.* 1990). In dromaeosaurids pleurocoels are present in the first sacral vertebra in some specimens (e.g. MOR 660), but not all (see Norell and Makovicky 1997). Claims that pleurocoels are present in the sacral vertebrae of *Allosaurus* and tyrannosaurs (Molnar *et al.* 1990; Holtz 1994) were not confirmed in this study (*Allosaurus*: MOR 693; *Albertosaurus*: ROM 807).

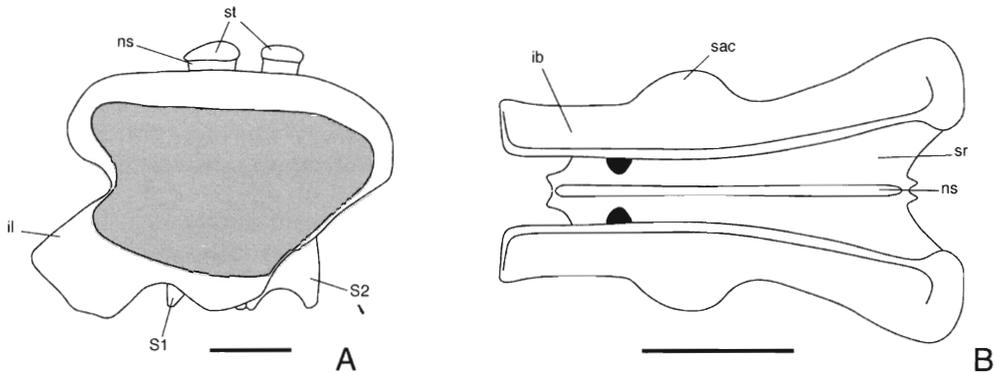
116. Sacral ribs: slender and well separated (0); forming a more or less continuous sheet in ventral or dorsal view (1); very massive and strongly expanded (2) (modified from Rowe and Gauthier 1990; unordered)

In basal dinosauriforms, ornithischians, most sauropodomorphs, and many theropods the sacral ribs are distinct, well separated, and usually not considerably expanded. In a number of theropods, including *Coelophysis* (Colbert 1989), *Syntarsus* (QG 1), *Ceratosaurus* (Gilmore 1920), *Elaphrosaurus* (MB dd unnumbered), abelisaurids (MACN CH 894), and birds (Marsh 1880), the sacral ribs and transverse processes are fused to each other and with their centra and the ilium to form almost continuous sheets of bone between the sacral vertebrae and the ilium when viewed from above or below (Text-fig. 28B).

In *Herrerasaurus* (Novas 1993) and *Staurikosaurus* (Galton 1977) the sacral ribs are very massive; they are especially expanded laterally and cover almost the entire medial side of the ilium (Text-fig. 28A; Novas 1993, 1996a). In a few sauropodomorphs (e.g. *Plateosaurus*: SMNS 13200) the sacral ribs are similarly expanded.

117. Number of caudal vertebrae: 41 or more (0); fewer than 41 caudals (1); fewer than 36 caudals (2) (modified from Chiappe *et al.* 1996; ordered)

The number of caudal vertebrae is variable in ornithischians and sauropodomorphs, but it is generally over 40 in well-preserved specimens of at least the basal members of these groups (Colbert 1981; Galton 1990;



TEXT-FIG. 28. Sacra of theropod dinosaurs, illustrating different states for character 116. A, sacrum and ilium of *Herrerasaurus ischigualastensis* in lateral view; the shaded area indicates the attachment area of the very massive sacral ribs on the medial side of the ilium; modified from Novas (1993). B, sacrum and ilia of *Syntarsus rhodesiensis* in dorsal view, showing the almost continuous sheet of bone formed by the sacral ribs between the sacrum and the iliac blades; based on Raath (1990) and QG1. Abbreviations: ib, iliac blade; il, ilium; ns, neural spine; S1, S2, sacral vertebrae; sac, supraacetabular crest; sr, sacral ribs; st, spine table. Scale bars represent 50 mm.

Sues and Norman 1990). A high caudal count is retained in a number of theropods, most notably in *Sinosauropteryx*, where the total number of caudals exceeds 59 (Chen *et al.* 1998).

However, the number of caudal vertebrae is reduced in several theropod taxa. In ornithomimosaurs (Makovicky 1995) and tyrannosaurs (Makovicky 1995) it is fewer than 41, and in *Caudipteryx* (NGMC 97-9-A), birds (*Archaeopteryx*: Eichstätt and Munich specimens), and troödontids (IVPP V 9612) fewer than 36 vertebrae are present in the tail.

Ostrom (1969b, 1990) gave the number of caudal vertebrae in dromaeosaurids as 36–40, but in a well-preserved tail of *Velociraptor* (IGM 100/986), only 26 elements are present, and, based on the morphology of the last vertebrae preserved, it is estimated that fewer than ten vertebrae are missing. The caudal vertebral count for oviraptorosaurs was given as ‘about 40’ by Barsbold *et al.* (1990), but new finds indicate that it might have been considerably lower (Norell and Makovicky, pers. comm. 1999).

Since character state 2 includes state 1, the character is treated as ordered.

118. Number of caudal vertebrae bearing transverse processes: 16 or more (0); fewer than 16 (1); 11 or fewer (2) (Gauthier 1986, as modified by Makovicky and Sues 1998; ordered)

The transverse processes in the caudal vertebrae serve as the attachment area for the *m. caudofemoralis longus*, which is the main propulsion muscle in most reptiles (Gatesy 1990), either aquatic or terrestrial. Therefore, transverse processes are usually well-developed in archosaurs and are often present in at least the proximal two-thirds of the tail. In theropods there is the trend towards a reduction of the *caudofemoralis longus* musculature, and consequently, the transverse processes in the tail are reduced (Gatesy 1990). Thus, more than 15 caudal vertebrae bear transverse processes in crurotarsans, ornithischians, sauropodomorphs, and several theropods, but the processes are present only in 15 or fewer caudals in *Caudipteryx* (NGMC 97-9-A), *Bagaraatan* (Osmólska 1996), ornithomimosaurs (Russell 1972; Barsbold and Osmólska 1990), therizinosauroids (Russell and Dong 1993a), and tyrannosaurids (Molnar *et al.* 1990). In birds (*Archaeopteryx*: Berlin and Munich specimens), dromaeosaurids (IGM 100/986), and troödontids (IVPP V 9612) 11 or fewer caudal vertebrae bear transverse processes.

119. Number of caudal vertebrae with well-developed neural spines: 11 or more (0); fewer than 11 (1)

The neural spines usually decrease rather gradually in size throughout the tail in crurotarsans, ornithischians, sauropodomorphs and many theropods, and are present over at least half the length of

the caudal vertebral column, although a marked reduction might occur distal to the transition point in theropods. In birds (*Archaeopteryx*: Eichstätt and Munich specimens; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986), and troödontids (IVPP V 9612) neural spines are restricted to, at most, the first ten caudal vertebrae, and subsequently they disappear abruptly.

120. Ventral groove in anterior caudals: absent (0); present (1) (Rowe and Gauthier 1990)

In basal ornithischians and sauropodomorphs, the anterior caudal vertebrae are rounded ventrally and do not have a longitudinal ventral groove. Such a groove is found in the majority of theropods with the exception of *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Magnosaurus oxoniensis* (OUM J 13558), *Elaphrosaurus* (MB dd unnumbered), '*Chilantaisaurus*' *maortuensis* (IVPP V 2885), abelisaurids (MACN CH 894), baryonychids (MNN GDF 510), and ornithomimosaurids (USNM 4736). Rowe and Gauthier (1990) considered the presence of this groove as a possible synapomorphy of Ceratosauria, but it has a much wider distribution within theropods. It is well developed in many supposedly ceratosaurian taxa, including *Ceratosaurus* (UMNH VP 5278; Gilmore 1920), but is also unquestionably present in many other taxa, although it might be narrow and shallow, as, for example, in *Allosaurus* (DNM 116, MOR 693). A well-developed longitudinal ventral groove is also present in mid- and posterior caudal vertebrae in the vast majority of theropods.

121. Ventral surface of anterior caudals: rounded (0); with a distinct keel bearing a narrow, shallow groove on its midline (1)

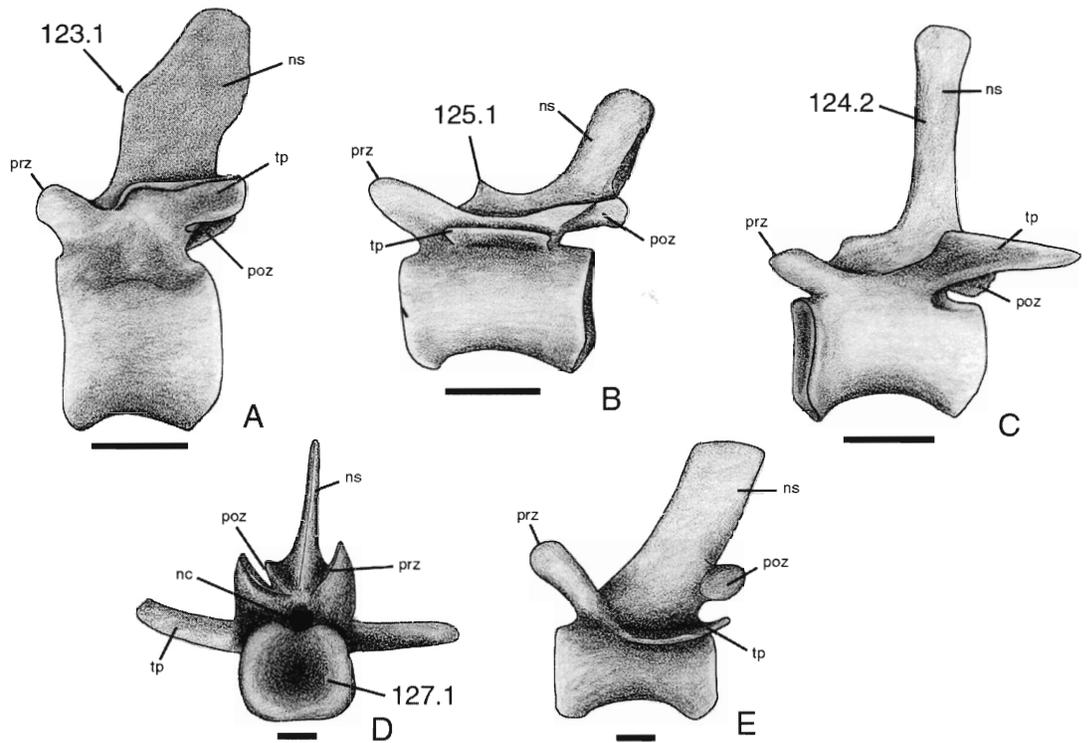
In ornithischians, sauropodomorphs, and many theropods the ventral surface of the anterior caudal vertebrae is more or less well rounded or broadly flattened. In a variety of theropods, including *Allosaurus* (DNM 116, MOR 693), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), and carcharodontosaurids (Rauhut 1999), the vertebral centra narrow considerably ventrally, but the lateral sides are not strongly convex dorsoventrally. Ventrally, the lateral sides are abruptly bent medially to form a narrow, flat, ventral surface that bears a narrow, shallow, longitudinal groove.

122. Prezygapophyses of distal caudal vertebrae: not elongated (0); strongly elongated, overhanging at least one-quarter of the length of the preceding centrum (1) (modified from Gauthier 1986)

In crurotarsans, basal dinosauriforms, ornithischians, sauropodomorphs, and some theropods the prezygapophyses of the distal caudal vertebrae are short, and do not permit strong interlocking of the distal caudal vertebral column. In most theropods with the exception of *Coelophysis* (AMNH 7224), *Dilophosaurus* (UCMP V 4214), *Ceratosaurus* (USNM 4735), *Coelurus* (YPM 1991, 1992, 1994, 1995), *Caudipteryx* (NGMC 97-9-A), *Microvenator* (Makovicky and Sues 1998), oviraptorosaurs (Makovicky 1995), and therizinosaurs (Russell and Dong 1993a; Makovicky 1995), the prezygapophyses of the distal caudal vertebrae are elongated and overlap at least one-quarter, often more than one-third, of the length of the preceding vertebra (see Text-fig. 30). They are tightly appressed to the lateral sides of the preceding vertebra, where shallow grooves are usually developed for the reception of the zygapophyses. In most birds elongate prezygapophyses are absent, but they still seem to be present in *Archaeopteryx*, based on faint impressions in the rock in the Berlin specimen; therefore the character is coded as uncertain in Aves. This character is used instead of Gauthier's (1986, p. 19, character 20) 'transition point in tail', since it seems to be a good indication of the presence of a pronounced transition point, and is easier to determine. Determination of a true transition point depends on examination of more or less complete caudal vertebral columns, whereas the presence of elongated prezygapophyses can be shown with a single element.

123. Anterior margin of neural spines of anterior mid-caudal vertebrae: straight (0); with distinct kink, dorsal part of anterior margin more strongly inclined posteriorly than ventral part (1)

The anterior to anterior mid-caudal vertebrae usually have well-developed neural spines with a straight, continuous anterior margin in ornithischians, sauropodomorphs, and the majority of theropods. In some theropods, including *Allosaurus* (MOR 693), *Siamotyrannus* (Buffetaut *et al.* 1996), and carcharodontosaurids (Stovall and Langston 1950), the anterior margin of the neural spines of these vertebrae arises



TEXT-FIG. 29. Anterior and mid-caudal vertebrae of several theropods, illustrating character states of several axial characters. A–B, *Allosaurus fragilis*; fourth and nineteenth caudal vertebra, left lateral view; based on Madsen (1976). C, *Majungatholus atopus*; mid-caudal vertebra, left lateral view; based on FMNH/UA 96313. D–E, *Deinonychus antirrhopus*; anterior caudal vertebra (?fifth), anterior and left lateral view; based on YPM 5210 and Ostrom (1969b). Abbreviations: nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process. Scale bars represent 50 mm (A–C) and 10 mm (D–E).

almost vertically from the roof of the neural arch, but shows a pronounced kink at mid-height, or higher, so that the dorsal part of the margin is more strongly inclined posteriorly than the ventral part (Text-fig. 29A).

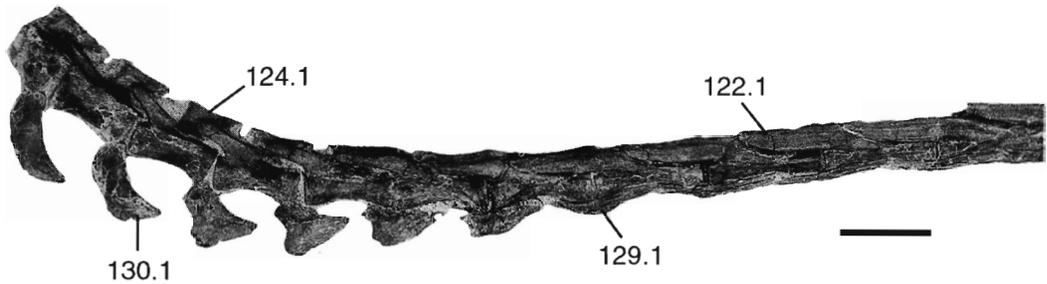
124. Neural spines of mid-caudals: rod-like and posteriorly inclined (0); subrectangular and sheet-like (1); rod-like and vertical (2) (unordered)

In ornithischians, sauropodomorphs, and many theropods the neural spines of the mid-caudal vertebrae are anteroposteriorly short, posteriorly inclined, and placed on the posterior end of the neural arch. In a number of theropods, including *Coelurus* (YPM 991, 1992, 1994, 1995), *Elaphrosaurus* (MB dd unnumbered), *Sinosauropteryx* (NGMC 65), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), ornithomimosaurs (TMP unnumbered, USNM 4736), and tyrannosaurs (AMNH 5226), the neural spines of the mid-caudals are elongate, broadly rectangular, lower than long, and extend over approximately two-thirds of the length of the neural arch (Text-fig. 30).

In contrast to this morphology, the neural spines of the mid-caudals are very slender, placed on the posteriormost part of the neural arch, and are vertical or even slightly inclined anteriorly in *Ceratosaurus* (UMNH VP 5278) and abelisaurids (Text-fig. 29c; FMNH/UA field #96313).

125. Anterior spur in front of neural spine in mid-caudals: absent (0); present (1) (reversed from Makovicky 1995)

In ornithischians, sauropodomorphs, and most theropods the mid-caudal vertebrae have only one neural spine that is placed on the posterior half of the neural arch. In some taxa, including *Allosaurus* (DNM 116),



TEXT-FIG. 30. Undetermined ornithomimosaur; mid-caudal vertebral column; Judith River Formation, southern Alberta; TMP unnumbered. Scale bar represents 50 mm.

sinraptorids (Gao 1992), *Afrovenator* (UC OBA 1), *Siamotyrannus* (Buffetaut *et al.* 1996), and carcharodontosaurids (Stovall and Langston 1950), a small additional spur is found anterior to the neural spine (Text-fig. 29B). Welles (1984, fig. 22) figured an anterior mid-caudal of *Dilophosaurus* with a similar, but not as well-developed, spur in front of the neural spine. However, this feature is not mentioned in the description, and it is not found in other mid-caudals of the holotype (UCMP V 4214); therefore, the character is coded as '0' for *Dilophosaurus*.

Makovicky (1995) used *Dilophosaurus* and *Allosaurus* as successively closer outgroups for his analysis of coelurosaurian interrelationships. Based on the alleged presence of the anterior spur in these two taxa, he considered the absence of this character as a coelurosaurian synapomorphy. However, theropodan outgroups do not show this character, and it has a very restricted distribution within Theropoda, indicating that the presence of the spur is the apomorphic character state.

126. Relative length of distal caudal centra: significantly elongated in relation to centrum height (0); not elongated in relation to centrum height (1) (Sues 1997)

In basal dinosauriforms, ornithischians, many sauropodomorphs, and the majority of theropods the distal caudal vertebral centra are considerably elongated in relation to centrum height, and they are often subequal in length or even longer than more anterior caudal vertebrae. In some sauropodomorphs (e.g. *Plateosaurus*: GPIT Skelett 1) and several theropods, including *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), oviraptorosaurs (Makovicky 1995), and therizinosauroids (Sues 1997; Makovicky and Sues 1998), the distal caudal vertebrae are smaller than more anterior vertebrae, but closely resemble them in their proportions.

127. Shape of anterior caudal centra: oval (0); subrectangular and box-like (1) (Gauthier 1986)

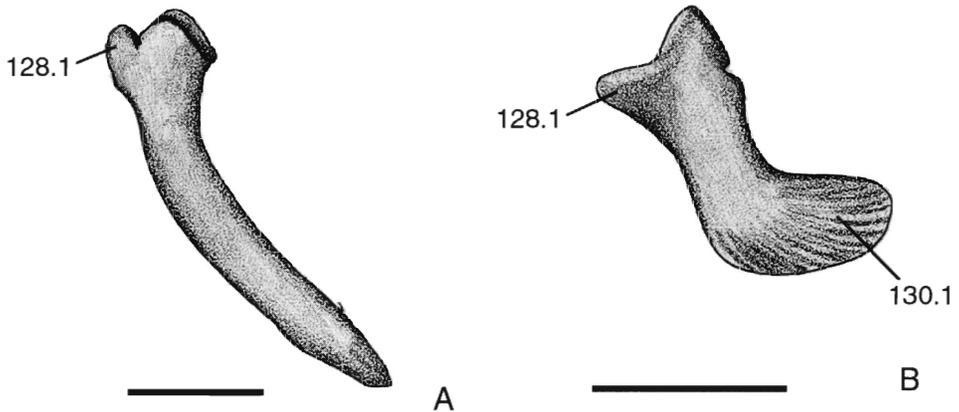
In basal ornithischians, sauropodomorphs, and many theropods, the anterior caudal vertebrae resemble the posterior dorsal vertebrae in their outline, which is usually high oval. In some theropods, including birds (*Archaeopteryx*: Eichstätt and Munich specimens; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/985, 100/986, YPM 5210), and troodontids (IVPP V 9612), the anterior caudal vertebrae are rather short and show a subrectangular outline (Text-fig. 29D).

128. Cranial process at base of chevrons: absent (0); present (1) (modified from Sereno *et al.* 1996)

In basal dinosauriforms, ornithischians, and sauropodomorphs the chevrons usually bear two articular facets for articulation with the anterior and posterior articulation facet of the caudal vertebrae. In all theropods examined the chevrons have a process anterior to the anterior articulation facet that does not articulate with the vertebrae (Text-fig. 31).

129. Distal chevrons: rod-like or L-shaped (0); skid-like (1)

In ornithischians, sauropodomorphs, and many theropods the distal caudal haemapophyses are a simple rod of bones or only flexed posteriorly distally. In a number of theropods, including *Caudipteryx* (NGMC



TEXT-FIG. 31. Mid-caudal chevrons, illustrating states for characters 128 and 130. A, *Majungatholus atopus*; based on FMNH/UA 96313. B, *Allosaurus fragilis*; redrawn from Madsen (1976). Scale bars represent 50 mm.

97-9-A), *Sinosauropteryx* (NGMC 65), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), birds (*Archaeopteryx*: Berlin specimen; *Rahonavis*: UA 8656), dromaeosaurids (YPM 5203, 5204, IGM 100/986), ornithomimosaurs (AMNH 5355, TMP unnumbered), troödontids (NMC 12340, IVPP V 9612), and tyrannosaurids (AMNH 5226), the distal chevrons are dorsoventrally elongated, and form a skid-like ventral process between their adjacent vertebrae (Text-fig. 30). In many taxa (e.g. *Velociraptor* IGM 100/986, *Struthiomimus* AMNH 5355, *Rahonavis* UA 8656), the haemapophyses are widened, plate-like in ventral view, and forked anteriorly.

130. Mid-caudal chevrons: rod-like or only slightly expanded ventrally (0); L-shaped (1) (Sereno *et al.* 1996)

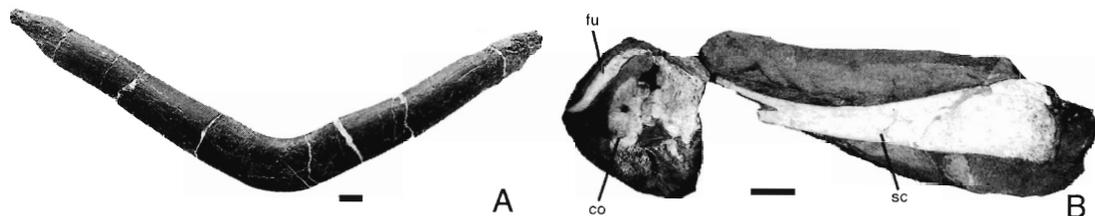
The mid-caudal chevrons are simple, rod-like structures in ornithischians, sauropodomorphs, and several theropods (Text-fig. 31A). In *Poekilopleuron* (Eudes-Deslongchamps 1838), *Allosaurus* (Madsen 1976), *Ornitholestes* (AMNH 619), sinraptorids (Gao 1992), *Caudipteryx* (NGMC 97-9-A), *Sinosauropteryx* (NGMC 65), *Deltadromeus* (SGM-Din 2), birds (*Archaeopteryx*: Eichstätt specimen, *Rahonavis*: UA 8656), dromaeosaurids (YPM 5244), ornithomimosaurs (TMP unnumbered, USNM 4736), and tyrannosaurids (Lambe 1917) the chevrons are expanded and usually flexed backwards ventrally so that they are roughly L-shaped (Text-fig. 31B).

#### *Pectoral girdle*

131. Furcula: absent (0); present (1) (Gauthier 1986)

Clavicles are primitively present in archosaurs, but they are not fused into a single element, the furcula, in crurotarsans, ornithischians, and sauropodomorphs (Bryant and Russell 1993). A true furcula is known in several theropod taxa, including *Segisaurus* (UCMP V 338), *Allosaurus* (DNM 116, UMNH VP 7411, 7408), *Caudipteryx* (NGMC 97-9-A), birds (*Archaeopteryx*: e.g. Owen 1863), dromaeosaurids (Norell *et al.* 1997), oviraptorosaurs (IGM 100/9/72), and tyrannosaurids (Makovicky and Currie 1998). The element is usually developed as a boomerang-shaped bone (Text-fig. 32A) that attaches to the acromion process of the scapulae and curves medially across the coracoids.

The distribution of true furculae in theropods was poorly understood until recently. The absence of ossified clavicles in all dinosaurian taxa then known was the main argument for the rejection of the theropod origin of birds in the highly influential work of Heilmann (1926). In 1936, Camp first noted the presence of a clavicle in the small Early Jurassic theropod, *Segisaurus*, but it was not until 1983 that a true furcula was described in a non-avian theropod (Barsbold 1983).



TEXT-FIG. 32. Furculae of theropod dinosaurs. A, *Allosaurus fragilis*; UMNH VP 7408; anterior view. B, *Segisaurus halli*; UCMP V 338; pectoral girdle as preserved in lateral view. Abbreviations: co, coracoid; fu, furcula; sc, scapula. Scale bars represent 10 mm.

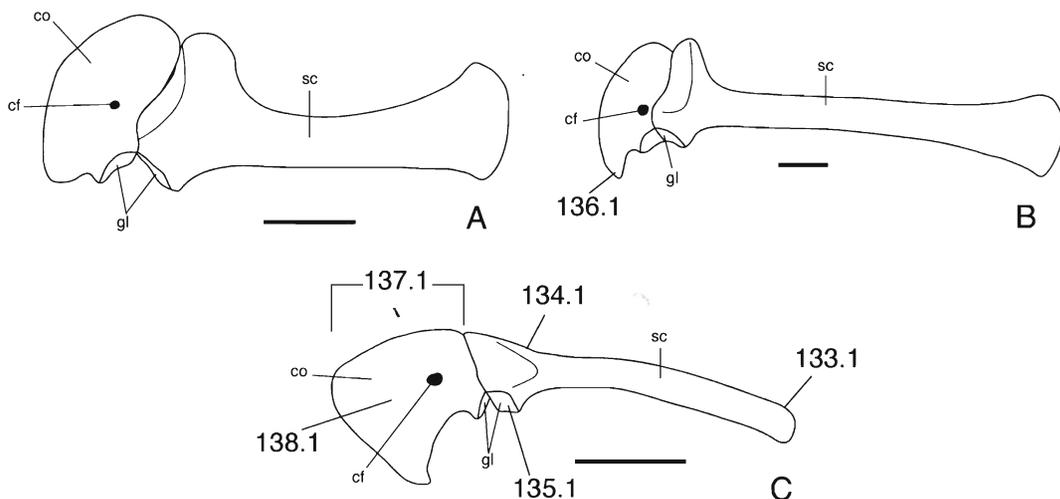
In 1986, Gauthier reviewed the distribution of furculae in theropods and concluded that the presence of a true furcula is a coelurosaurian synapomorphy. He also considered the possibility that the furcula of birds is not homologous with the clavicles of more basal archosaurs but a neomorphic element of advanced theropods. The latter idea was supported by Bryant and Russell (1993), who again reviewed the distribution of clavicles and furculae in dinosaurs and concluded that the interpretation of the furcula as either a neomorph or a homologue with the clavicles is equally parsimonious. However, the discovery of furculae in more theropod taxa (Chure and Madsen 1996; Norell *et al.* 1997; Makovicky and Currie 1998) rather supports the conventional view of this element being homologous with the clavicles of basal archosaurs (Makovicky and Currie 1998).

My own observations of *Segisaurus* (UCMP V 338) confirm that the bone that is usually considered to be a clavicle in this animal (e.g. Camp 1936; Bryant and Russell 1993) really represents a true furcula. As in other theropods that possess a furcula, the supposed clavicle in *Segisaurus* is attached to the acromion process of the left scapula and then curves medially over the left coracoid towards the right side. The right branch of the bone is missing in the specimen, but the mid-part, in which the bone starts to curve backwards towards the other side of the pectoral girdle, is still preserved (Text-fig. 32B). As in other theropods, the furcula of *Segisaurus* seems to have been broadly boomerang-shaped.

Unfused clavicles have so far only been described in two theropods: the abelisaurids *Carnotaurus* (Bonaparte *et al.* 1990) and the small troodontid *Sinornithoides* (Russell and Dong 1993b). In *Carnotaurus*, Bonaparte *et al.* (1990, p. 24) tentatively identified a small, rod-like element as the right clavicle, mainly because it was found lying on the coracoid. The accuracy of this identification can only be shown by new specimens of this species. In *Sinornithoides* Russell and Dong (1993b, p. 2169) stated that 'It appears that the medial extremity of one clavicle is pointed; the elements were probably not coossified into a furculum'. However, the clavicles in *Sinornithoides* (IVPP V 9612) are extremely slender, and only the posterior (lateral) ends are preserved in articulation with the acromion processes of the scapulae. The medial parts are broken and only one small fragment is present between the coracoids. This fragment is even more slender than the lateral parts of the clavicular and is not notably pointed at any end. Furthermore, it cannot be ruled out that it might represent a fragment of a cervical or gastral rib. Thus, unless the specimen has been damaged since the original description, nothing can be said concerning medial fusion of the clavicles.

132. Scapula: short and broad (ratio length/minimal height of shaft <9) (0); slender and elongate (ratio >10) (1) (modified from Pérez-Moreno *et al.* 1993)

In archosaurs ancestrally, the scapula is rather broad and short, with a total length that is less than nine times the length of the minimal height of the shaft (Text-fig. 33A). This condition is retained in ornithischians, sauropodomorphs, and several theropods. In a variety of theropods, including *Allosaurus* (MOR 693), *Compsognathus* (BSP A.S. I 563), *Caudipteryx* (MGMC 97-9-A), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids (TMP 88.121.39), ornithomimosaur (ROM 851), therizinosauroids (Russell and Dong 1993a), and tyrannosaurids (Lambe 1917), the scapula is significantly more slender and more than ten times longer than it is high at the minimal height of the shaft (Text-fig. 33B-C).



TEXT-FIG. 33. Pectoral girdles of a basal sauropodomorph and two theropods in left lateral view, illustrating states for several pectoral characters. A, basal sauropodomorph *Plateosaurus* sp.; based on SMNS F 65. B, *Allosaurus fragilis*; based on MOR 693. C, *Saurornitholestes langstoni*; based on TMP 88.121.39. Abbreviations as in Text-figure 32, and: cf, coracoid foramen; gl, glenoid facet. Scale bars represent 100 mm (A–B) and 50 mm (C).

Pérez-Moreno *et al.* (1993, p. 177, character 1) stated this character as ‘scapular blade . . . Short and broad (0). Slender (1)’. The character as defined here is essentially the same, but a more precise definition, as presented here, seems desirable.

133. Distal end of scapula: expanded (0); not expanded (1) (Gauthier 1986)

In ornithischians, sauropodomorphs, and many theropods the shaft of the scapula ends in a usually funnel-shaped expansion distally (Text-fig. 33A–B). In *Herrerasaurus* (Serenó 1993), *Ceratosaurus* (UMNH VP 5278), sinraptorids (Currie and Zhao 1993b), *Unenlagia* (MCF PVPH 78), abelisaurids (MACN CH 894), birds (*Archaeopteryx*: Berlin specimen), dromaeosaurids (TMP 88.121.39), ornithomimosaurids (ROM 851), therizinosauroids (Russell and Dong 1993a), and troodontids (IVPP V 9612) the shaft of the scapula is of subequal height throughout its length, or only very slightly and gradually widening distally (Text-fig. 33C).

134. Acromion process of scapula: significantly and abruptly expanded dorsally (0); small, dorsal rim of proximal scapula slopes gently downwards (1) (reversed and modified from Molnar *et al.* 1990)

In basal dinosauriforms, ornithischians, sauropodomorphs, and many theropods the acromion process of the scapula arises abruptly from the scapular blade. In these taxa the posterior margin of the acromion process usually projects at an angle of 60 degrees or more towards the scapular blade and is at least as high as the blade (Text-fig. 33A–B). In *Caudipteryx* (NGMC 97-9-A), *Unenlagia* (MCF PVPH 78), abelisaurids (MACN CH 894), birds (*Archaeopteryx*: Berlin specimen; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, TMP 88.121.39), and troodontids (IVPP V 9612) the acromion process rises gradually from the scapular blade and is relatively much lower than in the above-mentioned taxa (Text-fig. 33C), or even absent. Ornithomimosaurids show an intermediate state: the acromion process is rather long and low (AMNH 5355, ROM 85), but it arises abruptly from the blade. Thus, the character is coded as uncertain in this clade.

Molnar *et al.* (1990) considered the abruptly expanded acromion process as a carnosaurian synapomorphy. However, it is present in sauropodomorphs (e.g. *Plateosaurus*: SMNS F 65) and all basal

theropods for which the scapula is known; therefore, this morphology represents the plesiomorphic character state.

135. Glenoid facet on scapula: facing ventrally (0); facing ventrolaterally (1) (Novas and Puerta 1997)

In dinosaurs ancestrally, the glenoid facet faces downwards and backwards (Benton 1990), and this character is retained in ornithischians, sauropodomorphs, and many theropods. In birds the glenoid facet of the scapula faces more laterally than ventrally, and a similar orientation of the facet is found in *Unenlagia* (MCF PVP 78), dromaeosaurids (Text-fig. 33c; IGM 100/986, TMP 88.121.39), and troödontids (IVPP V 9612, MOR 553S).

136. Ventral part of coracoid anterior to the glenoid facet: approximately level with the rim of the facet (0); with tapering posteroventral process (1) (Gauthier 1986)

In ornithischians, sauropodomorphs, and a number of theropods the coracoid is semicircular in outline and the ventral margin in front of the glenoid facet is not expanded beyond the rims of the facet. In many theropods, including *Piatnitzkysaurus* (Bonaparte 1986), *Xuanhanosaurus* (IVPP V 6729), *Allosaurus* (DNM 116, MOR 693), *Elaphrosaurus* (MB dd unnumbered), *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), *Sinosauropteryx* (Currie, pers. comm. 1999), *Deltadromeus* (SGM-Din 2), abelisaurids (MACN CH 894), birds (*Archaeopteryx*: Berlin and Munich specimens), baryonychids (MNN GDF 500), carcharodontosaurids (Stovall and Langston 1950), dromaeosaurids (IGM 100/986, YPM 5236), ornithomimosaurs (AMNH 5355, ROM 851), oviraptorosaurs (IGM 100/9/72), therizinosauroids (Barsbold 1976c), troödontids (IVPP V 9612), and tyrannosaurids (ROM 807), the coracoid has a well-developed, usually tapering process anterior to the glenoid facet (Text-fig. 33B-C). This process probably served as an attachment area for the m. coracobrachialis (Ostrom 1974).

137. Coracoid: higher than long (0); longer than high (1)

In most basal archosaurs, ornithischians, sauropodomorphs and many theropods the coracoid is a high oval element that is considerably higher than long (Text-fig. 33A-B). In advanced theropods there is a general trend towards the elongation of this bone, which culminates in the strap-like coracoid of modern birds (see Ostrom 1976c). Thus, the coracoid is longer than high in *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), birds (*Archaeopteryx*: Munich specimen), dromaeosaurids (Text-fig. 33c; YPM 5236), oviraptorosaurs (IGM 100/9/72), therizinosauroids (Barsbold 1976c), and troödontids (IVPP V 9612). The height of the element, as used here, excludes the anterior ventral process.

138. Shape of coracoid: semicircular (0); subrectangular (1) (Gauthier 1986)

As pointed out by Gauthier (1986), the coracoid is a semicircular element in basal archosaurs, and this rounded shape is retained in ornithischians, sauropodomorphs, and many theropods despite the presence of a well-developed ventral anterior process in some of these taxa. In a variety of theropods, including basal birds (*Archaeopteryx*: Munich specimen), dromaeosaurids (TMP 88.121.39, YPM 5236), oviraptorosaurs (IGM 100/9/72), and troödontids (IVPP V 9612), the coracoid is rather subrectangular to trapezoidal in shape (Text-fig. 33c). In *Therizinosaurus*, the coracoid exhibits an intermediate condition and might best be described as roughly parallelogram-shaped (Barsbold 1976c); therefore, the character is coded as uncertain in therizinosauroids.

#### *Forelimb*

139. Ratio femur/humerus: more than 2.5 (0); between 1.2 and 2.2 (1); less than 1 (2) (ordered)

In the majority of archosaurs, including many theropods, the femur is considerably longer than the humerus. Individual values vary between species and even within one species, but in the vast majority of animals examined the ratio femur/humerus was between 1.2 and 2.2. This was chosen as the interval of

normal variation of this ratio for the definition of this character. Two extreme deviations from this state are found in theropods: in *Allosaurus* (DNM 116, MOR 693), abelisaurids (MACN CH 894), and tyrannosaurs (Lambe 1917; Maleev 1974) the forelimb is considerably shortened and the ratio is higher than 2.5. By contrast, birds have strongly elongated forelimbs, an adaptation for flight, and in most taxa (*Archaeopteryx*: Berlin, Eichstätt and Munich specimen) the humerus is longer than the femur.

Since a transformation from character state 0 to character state 2 has to pass through state 1, the character is treated as ordered.

140. Outline of proximal articular facet of humerus: broadly oval (more than twice as broad transversely than anteroposteriorly) (0); distinctly rounded (less than twice as broad anteroposteriorly than transversely) (1)

In ornithischians, sauropodomorphs, and most theropods the proximal facet of the humerus for the articulation with the glenoid facet is transversely broad, rather flat, and broadly oval in outline. In *Elaphrosaurus* (MB dd unnumbered) and especially abelisaurids (MACN CH 894), this facet is strongly expanded anteroposteriorly so that it is rather round in outline. Notably in abelisaurids the facet forms an expanded ball that fits into the transversely broad and very clearly defined glenoid facet on the scapulacoracoid; the situation in *Elaphrosaurus* is similar but less strikingly developed.

141. Shape of internal tuberosity on humerus: triangular, often rounded (0); rectangular (1)

In most dinosaurs the internal tuberosity is a well-developed process on the medial side of the proximal end of the humerus. It is usually directed medially and slightly posteriorly, and is often confluent with the articular facet in proximal view. In anterior or posterior view the process is triangular or rounded in outline (Text-fig. 34A–B).

In *Caudipteryx* (NGMC 97-9-A), *Avimimus* (ROM 46144), birds (*Archaeopteryx*: Munich specimen), dromaeosaurids (TMP 88.121.39), oviraptorosaurs (IGM 100/9/72), therizinosauroids (Barsbold 1976c), and troödontids (IVPP V 9612) the tuberosity is proximodistally elongated and has a rather rectangular outline (Text-fig. 34D).

142. Deltopectoral crest: extending over at least one-third of the length of humerus and well developed (0); strongly reduced, only developed as a small, triangular eminence (1) (Gauthier 1986)

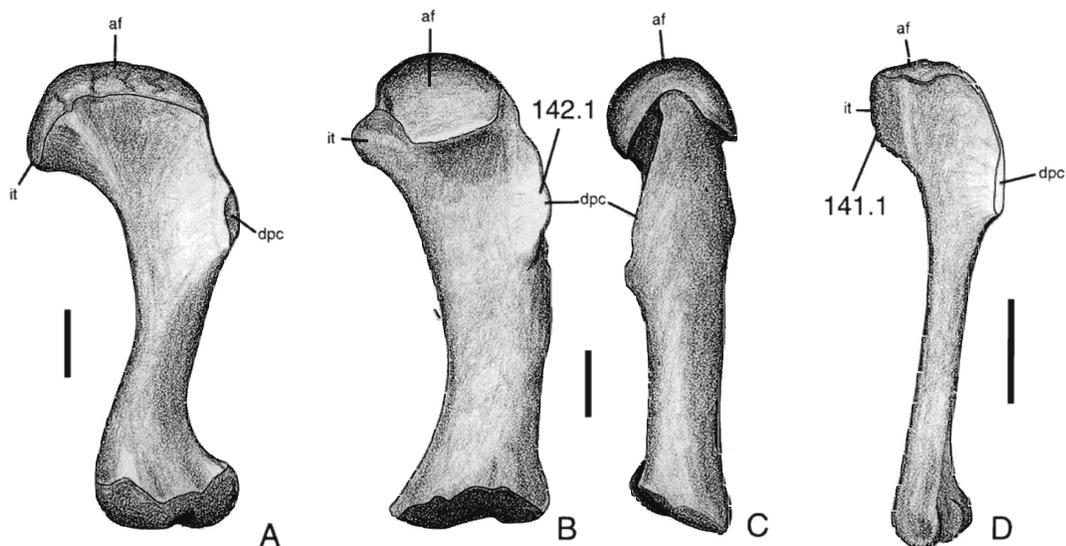
In dinosaurs ancestrally, the deltopectoral crest of the humerus is well-developed and extends over at least one-third of the length of the humeral shaft (Benton 1990). This character state is retained in most theropods, but in some members of this clade, including *Elaphrosaurus* (MB dd unnumbered), abelisaurids (MACN CH 894), ornithomimosaurids (AMNH 6570, ROM 840), and tyrannosaurids (Lambe 1917; Maleev 1974), the deltopectoral crest is strongly reduced and only developed as a low, usually roughly triangular eminence (Text-fig. 34B–C). Gauthier (1986) considered this character to be a synapomorphy of ornithomimosaurids. However, as noted above, it has a wider distribution amongst theropods.

143. Humerus in lateral view: sigmoidal (0); straight (1) (Holtz 1994)

In ornithischians, sauropodomorphs, and most theropods the proximal articular facet for the glenoid is directed slightly posteroproximally, and the distal end of the humerus is bent anteriorly so that the bone has a slightly sigmoidal shape. In *Ceratosaurus* (UMNH VP 5278), *Elaphrosaurus* (MB dd unnumbered), *Torvosaurus* (Galton and Jensen 1979), *Chilantaisaurus* (IVPP V 2884), *Deltadromeus* (SGM-Din 2), abelisaurids (MACN CH 894), baryonychids (MNN GDF 500), ornithomimosaurids (AMNH 6570, ROM 840), and tyrannosaurids (FMNH PR 308, ROM 807) the humerus is straight (Text-fig. 34c).

144. Olecranon process of ulna: well-developed (0); strongly reduced or absent (1) (Novas 1998)

In ornithischians, sauropodomorphs, and many theropods the proximal end of the ulna is strongly expanded and has a well-developed olecranon process. The proximal expansion is usually at least twice



TEXT-FIG. 34. Left theropod humeri in anterior (A–B, D) and lateral (C) views, illustrating several forelimb characters. A, *Allosaurus fragilis*; redrawn from Madsen (1976). B–C, *Carnotaurus sastrei*; based on MACN CH 894. D, *Deinonychus antirrhopus*; redrawn (reversed) from Ostrom (1969b). Abbreviations: af, articular facet on head of humerus; dpc, deltopectoral crest; it, internal tuberosity. Scale bars represent 50 mm.

as wide anteroposteriorly as the shaft at its narrowest part. In *Microvenator* (AMNH 3041), *Deltadromeus* (SGM-Din 2), birds (*Archaeopteryx*: Berlin specimen, *Rahonavis*: UA 8656), dromaeosaurids (MOR 660, YPM 5220), oviraptorosaurs (IGM 100/9/72), therizinosauroids (Barsbold 1976c), and troödontids (IVPP V 9612, NMC 12433) the proximal end of the ulna is not considerably expanded, and the olecranon process is poorly developed or absent (Text-fig. 3G).

In ornithomimosaurs the proximal end of the ulna is not considerably expanded, but the olecranon process is usually well-developed (e.g. TMP 93.104.1); therefore, the character is coded as uncertain.

145. Radius: more than half the length of humerus (0); less than half the length of humerus (1)

Whereas the radius is more than half the length of the humerus in ornithischians, sauropodomorphs, and most theropods, it is strongly shortened in *Torvosaurus* (Galton and Jensen 1979; Britt 1991), abelisaurids (MACN CH 894), baryonychids (MNN GDF 500), and tyrannosaurs (FMNH PR 308; Lambe 1917; Maleev 1974) where it is less than half the length of the humerus.

146. Large distal carpal, capping Mc I and parts of Mc II: absent (0); present (1); present, showing the shape and morphology of a semilunate carpal in proximal view, but rectangular rather than semilunate in palmar view (2); typical semilunate carpal present (3) (modified from Gauthier 1986; ordered)

In saurians ancestrally, the distal carpals are restricted to the bases of their respective metacarpals, and this situation seems to be retained in crurotarsans, ornithischians, and sauropodomorphs (Gauthier 1986), and it is also present in *Herrerasaurus* (Sereno 1993). In all theropods with the exception of ornithomimosaurs (Osborn 1916), the distal carpal I is enlarged and overlaps the proximal articular facet of metacarpal I and parts of the proximal articular facet of metacarpal II. The situation in ornithomimosaurs is almost certainly a secondary reduction. Barsbold (1983) stated that the distal carpals are also reduced in tyrannosaurids; however, an enlarged distal carpal that overlaps metacarpals I and II is at least present in *Albertosaurus* (FMNH PR 308). As discussed by Gauthier (1986), distal carpal II fuses with distal carpal I during ontogeny in theropods.

Whereas the enlarged distal carpal is a broad, rather unstructured disc of bone in many theropods (e.g. *Syntarsus*: QG 1, *Afrovenator*: UC OBA 1, *Xuanhanosaurus*: IVPP V 6729), it is developed as a semilunate carpal in the theropods listed below. In these taxa the element is subrectangular in proximal view and shows slightly raised, rounded ridges on the dorsal (plantar) and ventral (palmar) margins. A rounded process for the distal facet for metacarpal I is developed on the medial side dorsally (Text-fig. 35).

In *Coelurus* (YPM 2010), and to a slightly lesser degree in *Allosaurus* (DNM 116), the distal carpal I exhibits the morphology described above, but it is somewhat rectangular or flattened rather than truly semilunate in ventral view. A true semilunate carpal is present in *Caudipteryx* (Ji *et al.* 1998), *Avimimus* (ROM 46144), birds (*Archaeopteryx*: Berlin specimen), dromaeosaurids (YPM 5208, 5217), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), therizinosaurs (IVPP V 11559), and troodontids (IVPP V 9612).

Since higher character states include lower ones, the character is treated as ordered.

147. Metacarpus: relatively short and broad (ratio length/width of Mc I–III < 2) (0); slender and elongated (ratio > 2.2) (1)

The metacarpus of ornithischians, sauropodomorphs, and many theropods is rather short and broad. In *Ornitholestes* (Osborn 1916), birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens), dromaeosaurids (YPM 5206), oviraptorosaurs (IGM 100/9/72), and troodontids (IVPP V 9612) the metacarpus is very slender and elongated (Text-fig. 35B).

Note that only metacarpals I–III have been used to calculate the ratio for this character to exclude the effects of reduction of the number of digits in the hand.

148. Contact between Mc I and Mc II: metacarpals contact each other at their bases only (0); Mc I closely appressed to proximal half of Mc II (1) (Gauthier 1986)

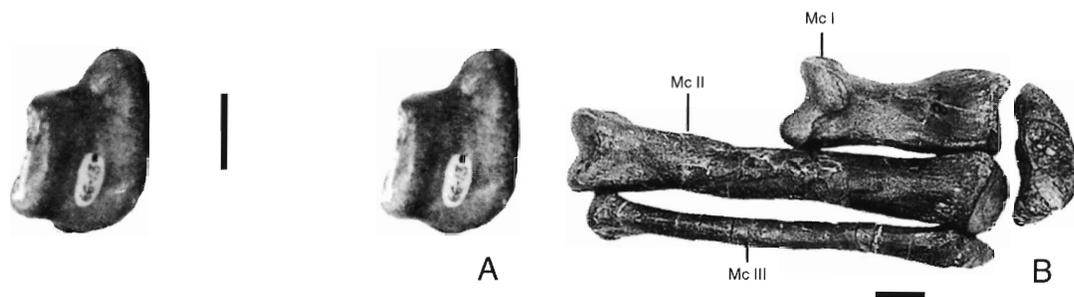
In ornithischians, sauropodomorphs, and some theropods all metacarpals are clearly separated and only contact at their bases, where they slightly overlap each other. In these animals the proximal part of the lateral side of metacarpal I is dorsoventrally rounded, or might only be flattened in its most proximal part. In many theropods, including *Poekilopleuron* (Eudes-Deslongchamps 1838), *Xuanhanosaurus* (IVPP V 6729), *Allosaurus* (DNM 116, MOR 693), *Ornitholestes* (Osborn 1916), *Torvosaurus* (Galton and Jensen 1979), *Afrovenator* (UC OBA 1), birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens), dromaeosaurids (YPM 5206), ornithomimosaurs (AMNH 6569, TMP 93.104.1), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), troodontids (IVPP V 9612), and tyrannosaurids (FMNH PR 308, ROM 807), at least the proximal half, and often almost all of the shaft of metacarpal I, is closely appressed to the basal half of metacarpal II (Text-figs 36, 37). Thus, the lateral side of metacarpal I is flattened, and usually has a medial flange ventrally that is overlapped by metacarpal II.

149. Distal end of Mc I: condyles more or less symmetrical (0); condyles strongly asymmetrical, the medial condyle being positioned more proximally than the lateral (1)

In crurotarsans and ornithischians metacarpal I has a more or less symmetrical distal end, with both condyles of the gynglimoidal articular facet showing a subequal distal extension. In all saurischians with the exception of *Herrerasaurus* (Sereno 1993), the distal end of metacarpal I is pronouncedly asymmetrical (e.g. Text-fig. 36). The medial condyle is lower, but wider, and positioned more proximally than the lateral condyle; thus, the articular surface is directed medioproximally instead of strictly proximally. Together with the correspondingly asymmetrical morphology of the proximal articulation of phalanx I-1, and a twist in the shaft of this phalanx, this morphology enables the opposability of the pollex in many taxa (e.g. Galton 1971).

150. Medial side of Mc II: expanded proximally (0); not expanded (1)

In ornithischians, sauropodomorphs and many theropods the medial side of metacarpal II is expanded medially at its proximal end (Text-fig. 36). Such an expansion is absent in *Herrerasaurus* (Sereno 1993), *Liliensternus liliensterni* (MB R. 2175), *Ornitholestes* (Osborn 1916), birds (*Archaeopteryx*: Berlin and



TEXT-FIG. 35. *Deinonychus antirrhopus*. A, semilunate carpal; proximal view (stereophotographs); YPM 5208. B, left metacarpals (YPM 5206) and semilunate carpal (YPM 5208), dorsal (plantar) view. Scale bars represent 10 mm.

Eichstätt specimens), dromaeosaurids (YPM 5206), ornithomimosaurids (AMNH 6569, TMP 93.104.1), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), therizinosauroids (IVPP V 11559), troödontids (IVPP V 9612), and tyrannosaurids (FMNH PR 308, ROM 807), where the medial side of metacarpal II is more or less straight (Text-fig. 35B).

It might be suspected that this character may be correlated with character 148; however, this is not the case. In many theropods where metacarpal I is closely appressed to the medial side of metacarpal II, a proximal medial expansion of the latter is nevertheless present, although reduced when compared to taxa that show character state 0 for character 148.

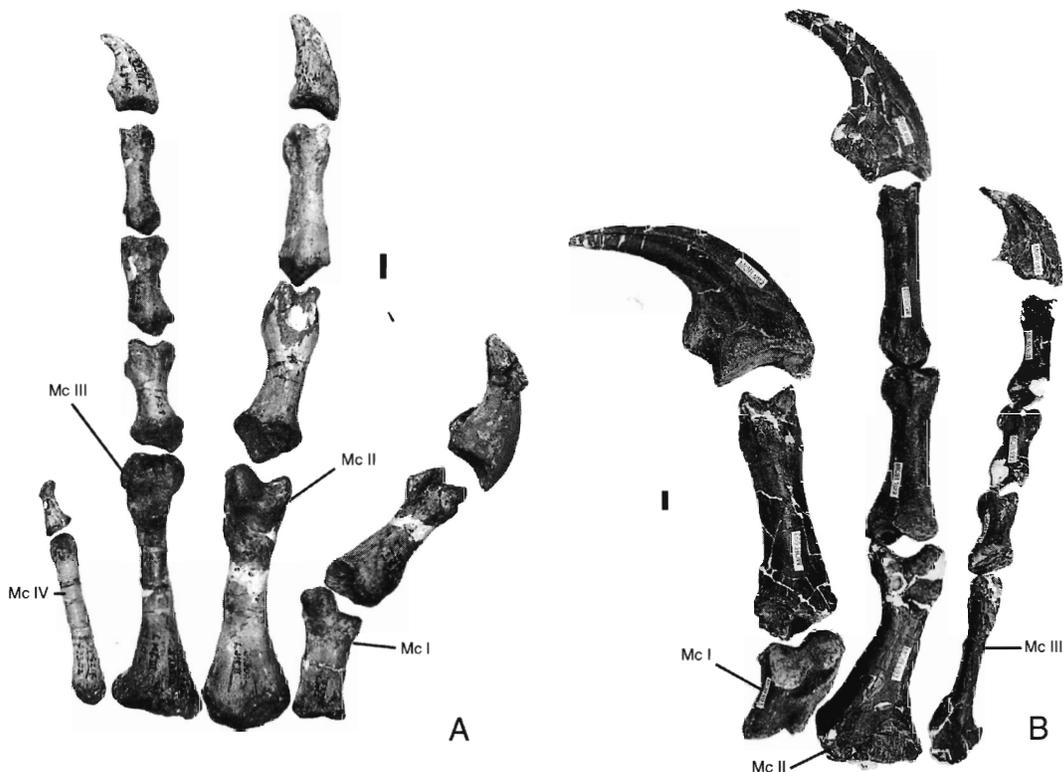
151. Shaft of Mc III: subequal in width to Mc II (0); considerably more slender than Mc II (less than 70 per cent of the width of Mc II) (1) and
152. Proximal articular end of Mc III: expanded and similar in width to Mc I and II (0); not expanded, very slender when compared to Mc I and II (1) (modified from Gauthier 1986)

In crurotarsans, ornithischians, and sauropodomorphs metacarpal III is subequal in width to metacarpal II or even wider. As pointed out by Gauthier (1986, p.17), the manus of saurischians is generally asymmetrical, mainly because digits are reduced only from the lateral side of the hand, a pattern that seems to be unique in tetrapods (Holder 1983). Thus, metacarpal III is reduced in width in all theropods with the exception of *Herrerasaurus* (Sereno 1993), and its shaft is considerably more slender than that of metacarpal II (Text-figs 36B, 37).

The especially slender appearance of metacarpal III in maniraptorans is mainly caused by the lack of a proximal (and distal) expansion of the metacarpal (Text-fig. 35B), whereas such an expansion is present in many other theropods, even though the shaft of the metacarpal may be very slender (Text-fig. 36). Thus, a proximal expansion of the metacarpal is absent in *Ornitholestes* (Osborn 1916), *Caudipteryx* (NGMC 97-9-A), birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens), dromaeosaurids (YPM 5206), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), and troödontids (IVPP V 9612).

153. Five fingers present (0); fifth finger absent and fourth finger reduced to a metacarpal with only one phalanx (1); fourth finger absent (2) (modified from Gauthier 1986; ordered)

As noted above, there is a tendency towards reduction of the lateral fingers of the hand in saurischian dinosaurs. Thus, in saurischians ancestrally, the fifth finger is still present, but it is reduced and does not bear an ungual. Digit V retains two phalanges in basal sauropodomorphs (Galton 1990), but is reduced to a metacarpal only in *Eoraptor* and *Herrerasaurus*, and completely absent in all other theropods. Metacarpal 4 is also strongly reduced and usually bears no more than one phalanx in theropods (Text-fig. 36A). In a variety of theropods, including *Allosaurus* (DNM 116), *Ornitholestes* (Osborn 1916), *Caudipteryx* (NGMC 97-9-A), *Sinosauropteryx* (Chen *et al.* 1998), birds (*Archaeopteryx*: all specimens examined),



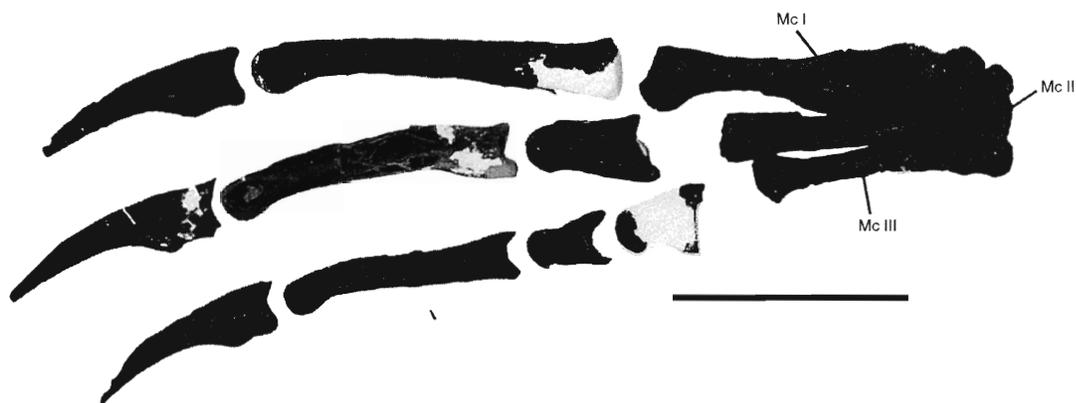
TEXT-FIG. 36. Theropod mani in dorsal view, illustrating several manual characters. A, *Dilophosaurus wetherilli*; left manus; UCMP V 4214. B, *Allosaurus fragilis*; right manus; MOR 693. Scale bars represent 10 mm.

dromaesaurids (YPM 5206), ornithomimosaur (AMNH 6569, TMP 93.104.1), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), therizinosauroids (IVPP V 11559), troodontids (IVPP V 9612), and tyrannosaurids (FMNH PR 308), the fourth finger is absent and the metacarpal is only represented by a vestige (Osborn 1916), or is also absent (Text-figs 35B, 36B, 37).

The question concerning which digits are preserved in birds has been a matter of heated debate. Whereas it is usually believed to be digits 1–3, based on digit morphology (e.g. Starck 1979), there have been repeated claims that the digits of birds represent digits 2–4, based on embryological evidence (e.g. Hinchliffe 1977; Hinchliffe and Hecht 1984; Burke and Feduccia 1997), and the latter argument has played a major role in the rejection of the theropod origin of birds by several authors (e.g. Burke and Feduccia 1997; Hinchliffe 1997).

However, the whole argument seems to be imbalanced, since different lines of evidence (and different criteria of homology) are being compared. The interpretation of the digits of advanced theropods as digits 1–3 is based on detailed anatomical comparisons and character congruence in phylogenetic analyses. If the same criteria are applied to the manus of birds, then the digits can only be identified as 1–3, based on the detailed morphological similarities with the digits of advanced theropods and the high number of other characters that indicate a close relationship between them.

If the validity of the morphological evidence in birds is questioned because of the embryological data, then the identification of the homology of the digits in advanced theropods may also be questioned. No embryological data for theropods exist; therefore, it is not possible to evaluate whether interpretations of theropod digit homology would be supported by this evidence. Thus, while the morphological evidence supports the homology of the digits of birds and advanced theropods, the embryological data is



TEXT-FIG. 37. Left manus of an undetermined ornithomimosaur (probably *Ornithomimus edmontonicus*; TMP 93.104.1), illustrating states for several manual characters; metacarpals in dorsal view, phalanges in lateral view. Scale bar represents 50 mm.

non-comparable and, therefore, useless for the discussion of whether birds were derived from theropod dinosaurs or some other group.

154. Third finger of the hand: longer than second finger (0); shorter than second finger (1) (Gauthier 1986)

In archosaurs ancestrally, the third digit is the longest digit in the manus (Gauthier 1986), and this character state is retained in ornithischians and *Herrerasaurus* (Serenó 1993). In all other animals studied for this paper the second digit of the manus is longer than the third (Text-figs 36–37).

155. Extensor pits on the dorsal surface of the distal end of metacarpals: absent or poorly developed (0); deep, well-developed (1) (Serenó *et al.* 1993)

The dorsal grooves for the attachment of the extensor tendons on the distal ends of the metacarpals are poorly developed in ornithischians and sauropodomorphs, where they are simple, shallow depressions or even absent. In contrast, the pits are developed as deep, often crater-like depressions on the distal ends of the metacarpals of many theropods (e.g. Text-fig. 36A), including *Eoraptor* (Serenó *et al.* 1993), *Herrerasaurus* (Serenó 1993), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), *Syntarsus* (QG 1), *Poekilopleuron* (Eudes-Deslongchamps 1838), *Xuanhanosaurus* (IVPP V 6729), '*Szechuanosaurus*' *zigongensis* (Gao 1993), *Allosaurus* (DNM 116, MOR 693), *Ceratosaurus* (Gilmore 1920), *Elaphrosaurus* (MB dd unnumbered), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Galton and Jensen 1979), *Afrovenator* (UC OBA 1), and baryonychids (MNN GDF 500). In several groups of mainly Cretaceous theropods, the pits are shallow or absent.

156. Proximal outline of Mc III: subrectangular (0); triangular, apex dorsal (1)

In ornithischians the proximal outline of metacarpal III is subrectangular. In sauropodomorphs, *Herrerasaurus*, *Syntarsus*, and *Dilophosaurus* the only significant modification is the presence of a lateral flange dorsally that overlaps the proximal end of metacarpal IV, which is moved to the palmar surface of digit three (Gauthier 1986). In all other theropods the dorsal side of the articular facet is reduced in width and the proximal outline is roughly triangular, with the apex positioned dorsally.

157. Shaft of Mc III: straight (0); bowed laterally (1) (Gauthier 1986)

In ornithischians, sauropodomorphs, and many theropods the shaft of metacarpal III is straight. In birds (*Archaeopteryx*: Munich specimen), dromaeosaurids (YPM 5206) and troodontids (Barsbold *et al.* 1987)

the shaft of metacarpal III is slightly bowed laterally so that its lateral side is convex. This flexure is only slight in dromaeosaurids, troodontids and early birds, and seems to be mainly caused by a slight medial twist of the distal articular facet.

Russell and Dong (1993b, p. 2172) believed that a flexure of metacarpal III was absent in troodontids, based on the holotype of *Sinornithoides* (IVPP V 9612) and illustrations of the hand of an unnamed Early Cretaceous theropod in Barsbold *et al.* (1987). However, in the type specimen of *Sinornithoides*, both metacarpals III are covered at least partially by other parts of the hand or matrix, making it difficult to determine if the metacarpal is bowed or not. In the illustrations of the hand of the unnamed troodontid in Barsbold *et al.* (1987, fig. 2A–B, pl. 50), a slight medial twist of the distal articular end is clearly visible.

158. Ratio phalanx I-1/Mc I: 1 or less (0); between 1 and 1.5 (1); more than 1.5 (2) (ordered) and
159. Penultimate phalanx of the second finger: shorter than first phalanx (0); longer than first phalanx (1) and
160. Penultimate phalanx of the third finger: as long as, or shorter than, more proximal phalanges (0); longer than each of the more proximal phalanges (1); longer than both proximal phalanges taken together (2) (modified from Gauthier 1986; ordered)

As pointed out by Gauthier (1986), the manus of theropods shows a tendency towards relative enlargement if compared to the size of the complete forelimb during theropod evolution. Apart from a lengthening of the metacarpus (character 146), this enlargement is mainly caused by relative elongation of the manual phalanges.

Thus, in dinosaurs ancestrally, the first phalanx of manual digit I is shorter or subequal in length to metacarpal I, and the penultimate phalanges of digits II and III are shorter than more proximal phalanges. In all theropods, the penultimate phalanx of the second finger is longer than the first phalanx, and in all theropods with the exception of *Eoraptor* (ROM 44686), phalanx I-1 is longer than metacarpal I, and the penultimate phalanx of the third digit is longer than more proximal phalanges of this finger (Text-figs 36–37).

In several theropod taxa, including *Xuanhanosaurus* (IVPP V 6729), *Allosaurus* (DNM 116), *Afrovenator* (UC OBA 1), *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), *Sinosauropteryx* (Currie, pers. comm. 1999), birds (*Archaeopteryx*: Berlin and Eichstätt specimen), dromaeosaurids (YPM 5206), oviraptorosaurs (IGM 100/9/72), troodontids (IVPP V 9612), and tyrannosaurids (ROM 807), digit I-1 is further elongated and is more than 1.5 times the length of metacarpal I (Text-fig. 36B). In advanced ornithomimosaurids, metacarpal I is apomorphically elongated and sometimes longer than metacarpal II. However, this is not the case in the basal ornithomimosaur *Harpymimus* (Barsbold and Perle 1984). Since the digit is also very long and slender in all advanced members of this group (e.g. TMP 93.104.1), the character is coded as '2' for ornithomimosaurids.

In all of the taxa that show character state 2 for character 158, with the exception of *Allosaurus* and oviraptorosaurs, the penultimate phalanx of digit III is longer than the combined length of the two more proximal phalanges (Text-fig. 37). This is also the case in *Ornitholestes* (Osborn 1916), in which phalanx I-1 is unknown. In tyrannosaurids the third digit of the manus is completely absent; thus, the character state for this taxon cannot be determined. In *Caudipteryx* and *Sinosauropteryx* no measurements could be taken, but the phalanx is clearly significantly longer than more proximal ones, and character state 2 might be present in these taxa.

161. Manual ungual I: less than half the length of the radius (0); more than two-thirds of the length of the radius (1) (modified from Sereno *et al.* 1998)

The pollex is enlarged in saurischians ancestrally (Gauthier 1986), but the length of its ungual, as measured perpendicular to the articular facet, is less than one-half the length of the radius in sauropodomorphs and most theropods. In *Torvosaurus* (Galton and Jensen 1979), *Sinosauropteryx* (Chen *et al.* 1998), and baryonychids (BMNH R 9951, MNN GDF 500) the length of the ungual is more than two-thirds the length

of the radius. In *Chilantaisaurus tashuikouensis* (IVPP V 2884) the radius is not preserved. However, the length of manual ungual I in this species is approximately half the length of the humerus; unless *Chilantaisaurus tashuikouensis* had an unusually long radius, manual ungual I was most probably more than two-thirds the length of the latter bone. Therefore, the character is tentatively coded as 1 in this species.

Therizinosauroids exhibit an intermediate state in respect to the ratio of the length of manual ungual I and the radius. In *Alxasaurus*, the ungual is slightly more than half the length of the radius (Russell and Dong 1993a); therefore, the character is coded as uncertain in this clade.

162. Dorsal lip at proximal articular end of manual unguals: absent (0); present (1) (Currie and Russell 1988)

In ornithischians, sauropodomorphs, and many theropods the dorsal curve of the manual unguals is continuously convex towards the proximal articular end. In *Microvenator* (AMNH 3041), birds (*Archaeopteryx*: Berlin specimen), dromaeosaurids (TMP 74.10.5, YPM 5206), oviraptorosaurs (IGM 100/9/72, TMP 12.06.88–9), and troodontids (MOR 553S) the dorsal margin is convex over a short section directly anterior to the articular facet so that the dorsal proximal end of the ungual bears a proximodorsally directed lip (Text-fig. 38B). This feature is usually best developed in manual unguals II and III, and only faint or absent in ungual I.

163. Flexor tubercle on manual unguals: less than half the height of the articular facet (0); more than half the height of the articular facet (1)

The insertion area of the flexor tendons on the manual unguals is usually developed as a well-formed ventral tubercle in saurischians, but this tubercle is lower than one-half the height of the articular facet in sauropodomorphs and many theropods (Text-fig. 38A). In birds (*Archaeopteryx*: Berlin and Munich specimens), dromaeosaurids (TMP 74.10.5, YPM 5206), and troodontids (MOR 553S), the height of the tubercle exceeds half the height of the articular facet (Text-fig. 38B).

164. Mc I: significantly longer than broad (0); very stout, approximately as broad as long (1)

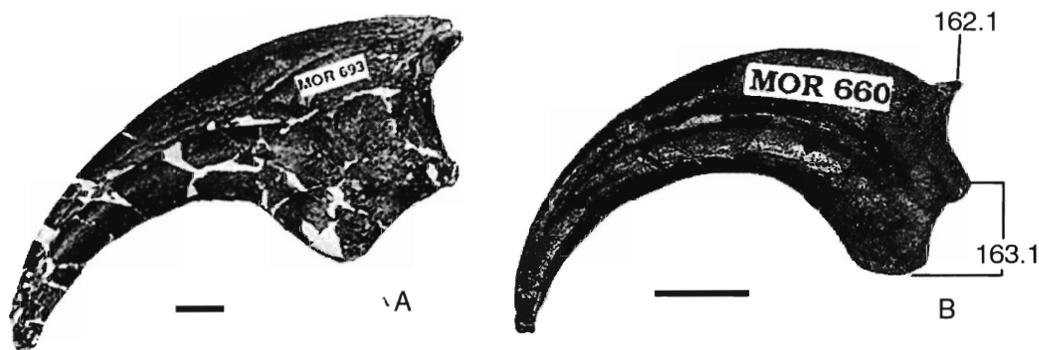
The first metacarpal is usually the shortest phalanges-bearing metacarpal in the hand of archosaurs. This condition is retained throughout theropods, with the exception of some advanced ornithomimosaurids. However, in most theropods, the bone is significantly longer than broad and a well-developed 'neck' between the articular ends is present. In some theropods, including *Poekilopleuron* (Eudes-Deslongchamps 1838), *Allosaurus* (DNM 116, MOR 693), *Torvosaurus* (Galton and Jensen 1979), and *Afrovenator* (UC OBA 1), metacarpal I is approximately as broad as long, and is block-like or roughly parallelogram-shaped in dorsal view (Text-fig. 36B).

### *Integument*

165. Contour feathers: absent (0); present (1)

With the growing acceptance of the theropod origin of birds, the question of when true contour feathers first appeared during theropod evolution has become of interest. Feduccia (1985) considered feathers as being primarily adapted for flight and thus argued that for this reason, no non-flying theropod could have had feathers. Other authors argued that feathers evolved primarily for thermoregulation in theropods and only later became adapted for flight (e.g. Thulborn 1987; Paul 1988a).

With the discovery of integumentary filaments in the small non-avian theropod *Sinosauropteryx* (Chen *et al.* 1998), the discussion concerning the possible presence of feathers in theropods has been revived. Although the filaments in *Sinosauropteryx* are difficult to interpret and cannot be shown to be protofeathers with certainty (Unwin 1998), they are certainly some kind of integumentary covering. The recent description of certainly non-avian dinosaurs with true contour feathers (Ji *et al.* 1998) strengthens the view that feathers arose before the evolution of flight. Given the difficult interpretation of the filaments of *Sinosauropteryx*, the character is focused on the occurrence of true contour feathers, consisting of a central rachis and marginal barbs.



TEXT-FIG. 38. Manual ungual II of two theropod dinosaurs in lateral view, illustrating states for characters 162 and 163. A, *Allosaurus fragilis*; MOR 693. B, *Sauromitholestes langstoni*; MOR 660. Scale bars represent 10 mm.

Certainly the distribution of integumentary structures, such as feathers, in extinct taxa is difficult to evaluate since these structures are almost never preserved. However, several theropods are known from deposits that might conserve feathers, so it might be possible to narrow down the first appearance of these structures in theropods. Because of the preservational difficulties, the distribution of feathers within dinosaurs will be discussed at greater length than usual.

No feathers have been described in any specimen of ornithischians, although skin impressions are known from several species (e.g. Osborn 1912*b*). Therefore, the character is coded as 0 in this clade.

The small, Late Jurassic theropod *Compsognathus* is known from two specimens, both of which come from very fine grained lithographic limestone deposits (Bidar *et al.* 1972; Ostrom 1978). The fact that not the slightest impression of any integumentary structures could be found in any of them (Ostrom 1978), whereas feather impressions are present in all specimens of *Archaeopteryx* (Ostrom 1985; Wellnhofer 1992, 1993), which come from the same deposits as the holotype of *Compsognathus*, indicates that probably no contour feathers were present in this animal. Likewise, *Sinosauropteryx* is now known from several specimens (Chen *et al.* 1998; Currie, pers. comm. 1999), all from the fine-grained volcanoclastic deposits of the Yixian Formation of China. None of the specimens shows any signs of contour feathers, although such structures are found in other fossils from the same deposits (e.g. Hou *et al.* 1995; Ji *et al.* 1998, 1999). The basal ornithomimosaur *Pelecanimimus* is represented by a partial skeleton from the Barremian lithographic limestones of Las Hoyas, Spain. Although skin impressions are preserved in the holotype (Pérez-Moreno *et al.* 1994), no feathers could be found. Again, feather impressions are known from the same deposits (Sanz *et al.* 1988; Sanz and Buscalioni 1992).

True contour feathers have been described in the Late Jurassic basal bird *Archaeopteryx* (e.g. Owen 1863; Rietschel 1985) and the non-avian theropods *Protarchaeopteryx* and *Caudipteryx* (Ji *et al.* 1998).

#### *Pelvic girdle*

166. Ilium: brachyiliac (0); dolichoiliac (1) (Colbert 1964)

Colbert (1964) first commented on differences between the ilia of theropods and basal sauropodomorphs. He termed the sauropodomorph condition the 'brachyiliac pelvis' and the theropod condition the 'dolichoiliac pelvis'. The brachyiliac ilium is characterized by a low, short, preacetabular process that is usually rounded or tapers anteriorly and does not extend to the level of the anterior end of the pubic peduncle (Text-fig. 39A). This iliac morphology is found in crurotarsans, basal dinosauriforms, basal sauropodomorphs, *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus*. The ilium in sauropods is a modified version of the brachyiliac ilium of basal sauropodomorphs (Colbert 1964).

The dolichoiliac condition is found in all other theropods. It is characterized by an elongated and

dorsoventrally expanded, blade-like preacetabular process that usually overhangs the pubic peduncle anteriorly to a considerable extent (Text-fig. 39B–F).

In ornithischians the preacetabular process is also elongated but rather low, and there are enough differences to indicate that the ornithischian ilium was modified independently from the brachyiliac condition.

167. Pelvis: propubic (0); opisthopic (1) (Seeley 1887)

In archosaurs ancestrally, the pelvis is triradiate, with the pubis pointing anteroventrally. This condition is retained in basal dinosauriforms, sauropodomorphs, and many theropods (e.g. Text-fig. 39B). In ornithischians and a variety of theropods, including *Herrerasaurus* (Novas 1993), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/985, 100/986), and therizinosauroids (Barsbold and Maryanska 1990), the pubis is retroverted, so that in the articulated pelvis the distal part of the shaft is positioned more posterior than the more proximal regions (Text-fig. 39A, E–F).

The retroverted pubis of ornithischians shows several structural differences from the condition found in most theropods, indicating that it is not homologous with the opisthopic condition found in some theropods. Whereas the pubis in opisthopic pelvises in theropods is rather stout and has a suture with the element of the other side distally, that of ornithischians is a very slender, rod-like bone that lacks a median suture. Among theropods, only advanced birds show a similar pubic morphology.

The degree of retroversion is different in different taxa: the pubis is almost vertical in *Herrerasaurus*, *Unenlagia*, and *Archaeopteryx*, but strongly inclined posteriorly in ornithischians, dromaeosaurids, therizinosauroids, and advanced birds.

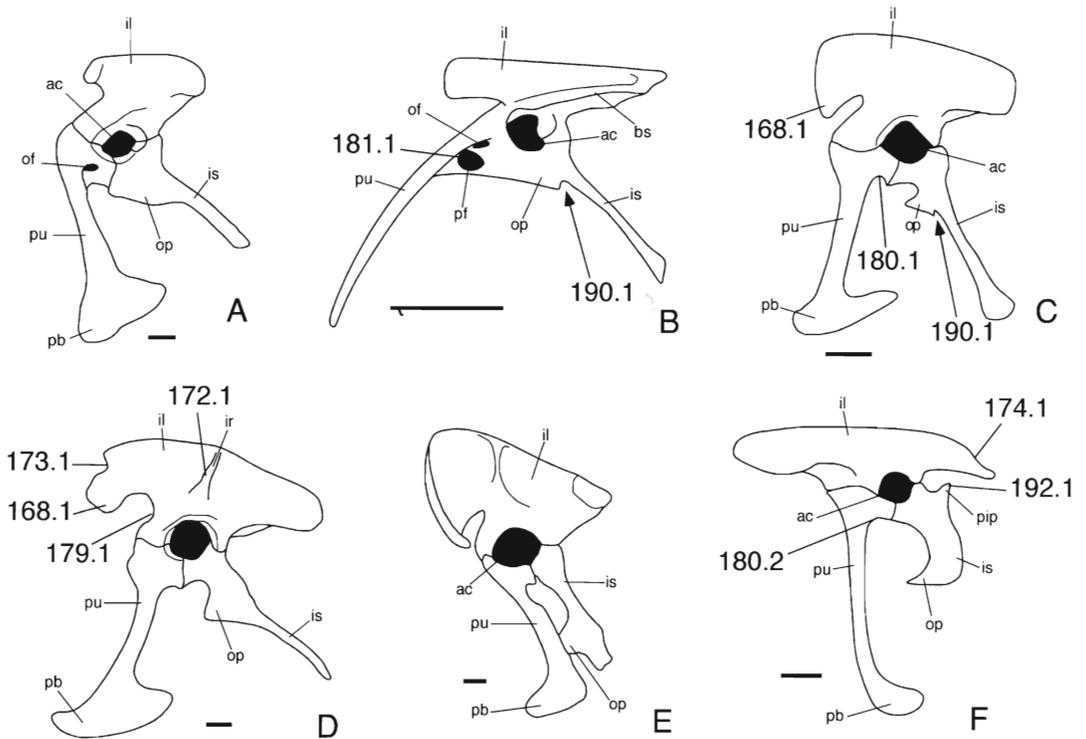
168. Pronounced ventral ‘hook’ on anterior expansion of ilium: absent (0); present (1) (modified from Gauthier 1986)

In ornithischians, basal sauropodomorphs, *Eoraptor*, *Herrerasaurus*, *Coelophysis*, *Liliensternus liliensterni*, *Syntarsus*, *Unenlagia*, and birds the preacetabular process of the ilium is not expanded dorsoventrally anteriorly if compared with the basal part of this process, and the anterior end is more or less rounded (Text-fig. 39A–B, F). In all other theropods, the anterior end of the process is dorsoventrally expanded and the anterior margin forms an acute angle with the ventral margin (Text-fig. 39C–E). It is questionable whether this ventral ‘hook’ served as an anteroventral enlargement for the insertion of the m. iliobtibialis (Romer 1923a) because this muscle is usually restricted to the dorsal rim of the ilium in crocodiles (Romer 1923b) and birds (McGowan 1979; see character 172 below).

169. Preacetabular part of ilium: significantly shorter than postacetabular part (0); subequal in length to postacetabular part (1); significantly longer than postacetabular process (modified from Currie and Russell 1988; Hutchinson 2001a)

As noted above under character 165, the preacetabular process of the ilium is short in archosaurs ancestrally, and it is much shorter than the postacetabular process in sauropodomorphs, *Eoraptor*, *Herrerasaurus*, and even many theropods with a dolichoiliac ilium (Text-fig. 39A–C).

In several theropods the preacetabular process of the ilium is elongated, and it is subequal in length to the postacetabular process (Text-fig. 39D) in *Compsognathus* (BSP A.S. I 563), *Elaphrosaurus* (MB dd unnumbered), *Ornitholestes* (AMNH 619), *Stokesosaurus* (UMNH VP 7434, IPFUB Gui Th 1), *Caudipteryx* (NGMC 97-9-A), *Sinosauropteryx* (Currie, pers. comm. 1999), ornithomimosaurs (Osmólska *et al.* 1972), oviraptorosaurs (Barsbold *et al.* 1990), and tyrannosaurids (ROM 807), and significantly longer than the postacetabular process (Text-fig. 39F) in *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin and Munich specimens), and dromaeosaurids (IGM 100/985, 100/986, MOR 660). Because of the strongly modified ilium in therizinosauroids (Text-fig. 39E; Barsbold and Maryanska 1990), the character state in these animals is coded as uncertain; however, the preacetabular process is at least as long as the postacetabular process.



TEXT-FIG. 39. Theropod pelvis in left lateral view, illustrating several pelvic characters. A, *Herrerasaurus ischigualastensis*; redrawn (reversed) from Novas (1993). B, *Syntarsus rhodesiensis*; based on QG 1, QG 691, and Raath (1990). C, *Allosaurus fragilis*; modified from Molnar *et al.* (1990). D, generalized tyrannosaurid; based on Osborn (1916) and ROM 807. E, *Segnosaurus galbinensis*; redrawn from Barsbold and Maryanska (1990). F, *Rahonavis ostromi*; based on UA 8656. Abbreviations: ac, acetabulum; bs, brevis shelf; il, ilium; ir, iliac ridge; is, ischium; of, obturator foramen; op, obturator process; pf, pubic fenestra; pip, posterior ischial process; pu, pubis. Scale bars represent 50 mm (A–B), 100 mm (C–E), and 10 mm (F).

170. Preacetabular part of ilium: approximately as high as postacetabular part (excluding the ventral expansion) (0); significantly higher than postacetabular part (1) (Makovicky and Sues 1998)

In archosaurs ancestrally, and also in ornithischians, basal sauropodomorphs and most theropods the preacetabular part of the ilium (excluding the ventral expansion) is subequal in height to the basal part of the postacetabular process (Text-fig. 39B–D, F). In *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), and therizinosauroids (Barsbold and Maryanska 1990) the height of the iliac blade increases anteriorly and the preacetabular process is considerably higher than the basal part of the postacetabular process (Text-fig. 39E).

Within oviraptorosaurs, the same modification is found in caenagnathids (Currie and Russell 1988) and *Oviraptor* (Barsbold *et al.* 1990), but not in *Ingenia* (Barsbold *et al.* 1990). Although it seems probable that the situation in *Ingenia* represents a reversal (Makovicky and Sues 1998), the character is thus coded as uncertain.

171. Articulation of iliac blades with sacrum: vertical, well separated above sacrum (0); strongly inclined mediadorsally, almost contacting each other or sacral neural spines at the midline (1) (Holtz 1994)

In archosaurs ancestrally, the lateral sides of the iliac blades are vertical or even slightly ventrally directed. Thus, the medial sides of the iliac blades are well separated from the sacral neural spines. This situation is

retained in ornithischians, sauropodomorphs, and many theropods. In birds (*Rahonavis*: UA 8656; Marsh 1880), ornithomimosaurs (AMNH 21790, ROM 852, 01790), oviraptorosaurs (Sues, pers. comm. 1998), and tyrannosaurids (ROM 807) the iliac blades are inclined medially and contact the sacral neural spines; their lateral sides face at least slightly dorsally. As discussed by Hutchinson (2001a), this inclination might indicate a separation of the epaxial musculature above the sacrum.

In *Stokesosaurus* (UMNH VP 7434, IPFUB Gui Th 1) and *Microvenator* (AMNH 3041) where the sacral neural spines are not preserved, the inclination of the iliac blades can be deduced from the relative orientation of the pubic and ischial peduncle; thus, the character is coded as 1 in these two taxa.

In dromaeosaurids (IGM 100/985, 100/986) the pelvis is relatively broad and the iliac blades are clearly separated from the sacral neural spines. However, the ventral parts of the iliac blades are expanded laterally so that at least parts of the blade also face slightly dorsally; thus, dromaeosaurids resemble the taxa listed above in this respect. Unfortunately, it cannot be said whether the dromaeosaurid condition is derived from the condition seen in other coelurosaurs.

172. Vertical ridge on iliac blade above acetabulum: absent or poorly developed (0); well-developed (1) (Molnar *et al.* 1990)

The lateral surface of the iliac blade is not subdivided into an anterior and a posterior part in ornithischians, sauropodomorphs and many theropods. In some theropods a vertical ridge is present on the lateral side of the iliac blade above the acetabulum and forms such a subdivision (Text-fig. 39E). A faint reminder of this ridge is present in several theropods (e.g. *Liliensternus airelensis*, *Piatnitzkysaurus*), but a well-developed, sharply defined ridge is only present in *Stokesosaurus* (UMNH VP 7434), *Siamotyrannus* (Buffetaut *et al.* 1996), and tyrannosaurids (ROM 807).

The significance of this ridge is uncertain. According to Romer (1923a) and Colbert (1964), the entire area above the acetabulum and below the insertion area of the superficial m. iliobtibialis, served as the insertion site of the m. iliofemoralis in theropods; in this case the reason for the presence of the ridge in some theropod taxa is not obvious. To account for this separation in the muscle attachment areas, Russell (1972) reconstructed the m. iliofemoralis with two separate heads in ornithomimosaurs.

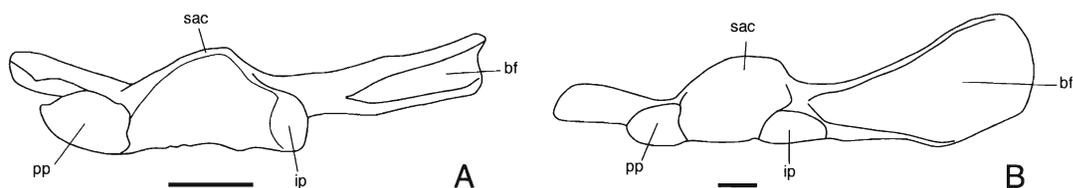
However, in birds the posterior limit of the m. iliiochantericus posterior is found in approximately the same position as the ridge in theropods, and this limit is marked by a faint ridge in some taxa (McGowan 1979). The crocodylian homologue of this muscle, the m. pubo-ischio-femoralis internus pars I, arises from the posteriormost dorsal vertebrae in crocodiles (Romer 1923b). In connection with the development of the dolichoiliac condition in theropods, this muscle might have been moved onto the preacetabular part of the ilium; thus, the pelvic muscles of theropods were probably more bird-like than reconstructed by Romer (1923a). As in birds (Hudson *et al.* 1959; McGowan 1979), the preacetabular process of the ilium might have served as the insertion area of the m. iliiochantericus posterior (= m. pubo-ischio-femoralis internus pars I), whereas the postacetabular process was the attachment area of the m. piriformis pars iliofemoralis (probably homologous with the m. iliofemoralis of crocodiles), and the separation between these two muscles was marked by a vertical ridge in some taxa. If this interpretation is correct, then the ventral 'hook' on the anterior end of the ilium probably served as the attachment area for the m. iliiochantericus anterior, as is the case in birds (McGowan 1979). However, it should be noted that some uncertainty remains about the significance of this character (Hutchinson 2001a).

173. Anterior rim of ilium: convex or straight (0); distinctly concave dorsally (1)

In most theropods the anterior rim of the preacetabular blade of the ilium is broadly rounded dorsally. In *Stokesosaurus* (UMNH VP 7434, IPFUB Gui Th 1) and tyrannosaurids (ROM 807) the dorsal part of the anterior margin is concave (Text-fig. 39D). Since this character can only be observed in taxa with a dolichoiliac ilium, it is coded as '?' in taxa with brachyiliac ilia.

174. Posterior end of ilium: rectangular (0); sloping downwards (1) (Gauthier 1986)

The posterior end of the ilium is high and often rectangular in lateral view in ornithischians, sauropodomorphs, and many theropods. In *Ornitholestes* (AMNH 619), *Caudipteryx* (NGMC 97-9-A),



TEXT-FIG. 40. Left theropod ilia in ventral view, illustrating the differences in the development of the brevis fossa (character 176). A, *Sinraptor dongi*; redrawn from Currie and Zhao (1993b). B, *Syntarsus rhodesiensis*; based on QG 1. Abbreviations: bf, brevis fossa; ip, ischial peduncle; pp, pubic peduncle; sac, supraacetabular crest. Scale bars represent 100 mm (A) and 10 mm (B).

*Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin specimen; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, MOR 660), oviraptorosaurs (Currie and Russell 1988; Barsbold *et al.* 1990), therizinosauroids (Barsbold and Maryanska 1990), and troödontids (IVPP V 9612) the posterodorsal margin of the ilium slopes gently downwards (Text-fig. 39F).

175. Pubic peduncle of ilium: transversely broad and roughly triangular in outline (0); anteroposteriorly elongated and narrow (1)

The pubic peduncle of the ilium is anteroposteriorly rather short and transversely wide in ornithischians, sauropodomorphs, and several theropods. The outline of the peduncle is roughly triangular or semi-oval, with the apex directed anterior to anteromedially. Its anteroposterior length approximately equals its transverse width, or only slightly exceeds it.

In *Ornitholestes* (AMNH 619), *Stokesosaurus* (UMNH VP 7434, IPFUB Gui Th 1), *Microvenator* (AMNH 3041), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids (MOR 660), ornithomimosaur (AMNH 21790, ROM 852, 01790), and tyrannosaurids (ROM 807), the pubic peduncle of the ilium is transversely narrow, strongly elongated anteroposteriorly, and more than twice as long as wide. The situation in oviraptorosaurs is uncertain: whereas the pubic peduncle in caenagnathids seems to be narrow and elongate (Currie and Russell 1988), the peduncle in oviraptorids is rather short (Barsbold *et al.* 1990).

176. Brevis fossa: narrow and with subparallel margins (0); very strongly expanded posteriorly (1) (reversed and modified from Molnar *et al.* 1990)

The presence of a lateral shelf on the postacetabular blade of the ilium for the attachment of the m. caudofemoralis brevis is a synapomorphy of dinosaurs (Novas 1996a), probably linked with a lateral shift of this muscle on the line from basal archosaurs to extant birds (Hutchinson 2001a). The muscle inserts in a longitudinal ventral groove that is bounded by the iliac blade laterally and the brevis shelf medially.

In basal ornithischians, sauropodomorphs, and many theropods this groove is rather narrow and its margins are subparallel or diverge slightly posteriorly (Text-fig. 40A). In *Coelophysis* (AMNH 7224), *Lilienstermus liliensterni* (MB R. 2175), *Segisaurus* (UCMP V 338), *Syntarsus* (QG 1), *Elaphrosaurus* (MB dd unnumbered), and ornithomimosaur (AMNH 21790, ROM 852, 01790), the margins diverge strongly posteriorly and the fossa is funnel-shaped and notably broad at its posterior end (Text-fig. 40B).

This character is coded as '?' in non-dinosaurian outgroups, in which it is not applicable.

177. Pubic peduncle: subequal in length to ischial peduncle (0); significantly longer than ischial peduncle, ischial peduncle tapering ventrally and without clearly defined articular facet (1)

In ornithischians, sauropodomorphs, and some theropods the pubic peduncle of the ilium is subequal in anteroposterior length to the ischial peduncle and the latter has a well-developed, flat, articular facet for the ischium. This facet is reduced, the ischial peduncle tapers, and the peduncle is less than half as long as the pubic peduncle in many theropods (Text-fig. 39C–D, F), including *Staurikosaurus* (Galton

1977), *Magnosaurus oxoniensis* (OUM J 13558), *Monolophosaurus* (Zhao and Currie 1993), *Allosaurus* (DNM 116, MOR 693, USNM 4734), *Compsognathus* (BSP A.S. I 563), *Ornitholestes* (AMNH 619), *Stokesosaurus* (UMNH VP 7434, IPFUB Gui Th 1), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), *Neovenator* (Hutt *et al.* 1996), *Sinosauropteryx* (NGMC 65), *Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin specimen; *Rahonavis*: UA 8656), baryonychids (BMNH R 9951), dromaeosaurids (IGM 100/985, 100/986, MOR 660), ornithomimosaurids (AMNH 21790, ROM 852, 01790), and tyrannosaurids (ROM 807). The character is polymorphic in oviraptorosaurs: character state 1 is present in caenagnathids (Currie and Russell 1988), while character state 0 is present in oviraptorids (Barsbold *et al.* 1990).

This character resembles character 175, but the characters are not completely correlated: all theropods that have character state 1 for character 175 also have state 1 for character 177, but not all theropods that exhibit the derived state for the latter character have character state 1 for the former character.

178. Articulation facet of pubic peduncle of ilium: facing more ventrally than anteriorly, and without pronounced kink (0); with pronounced kink and anterior part facing almost entirely anteriorly (1)

The articulation of the pubic peduncle of the ilium for the pubis is a relatively simple, usually concave, mainly ventrally directed facet in ornithischians, sauropodomorphs, and most theropods. In some theropods, including *Coelophysis* (AMNH 7224), both species of *Liliensternus* (CU unnumbered, MB R. 2175), *Syntarsus* (QG 1), and ornithomimosaurids (AMNH 21790), the articular facet is subdivided into a small, ventrally oriented posterior part, and a larger, more anteriorly oriented, anterior part; both parts lie at a wide angle towards each other. A similar situation is found in *Dilophosaurus* (UCMP V 4214), but in this taxon, the anterior part is considerably smaller than the posterior one.

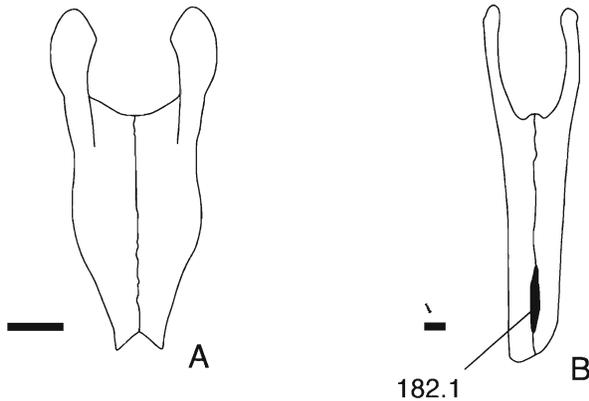
179. Anterior margin of pubic peduncle: straight or convex (0); concave (1)

The anterior margin the pubic peduncle of the ilium is dorsoventrally straight or slightly convex in most dinosaurs. Only in *Ornitholestes* (AMNH 619), *Stokesosaurus* (UMNH VP 7434), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), and tyrannosaurids (ROM 807) is the articular end of the peduncle expanded anteriorly, and thus the anterior margin of the peduncle is dorsoventrally concave in lateral view (Text-fig. 39D).

180. Obturator foramen in pubis: completely enclosed (0); open ventrally (1); absent (2) (modified from Holtz 1994; ordered)

The foramen for the obturatorius is completely enclosed by the pubis in archosaurs ancestrally, and this condition is retained in basal ornithischians, sauropodomorphs, and several theropods. In many theropod groups there is a tendency towards the reduction of the bony plate that encloses the foramen, and thus it is open ventrally in *Magnosaurus oxoniensis* (OUM J 13558), *Allosaurus* (DNM 116, MOR 693, USNM 4734), *Coelurus* (YPM 2010), sinraptorids (Currie and Zhao 1993b), *Siamotyrannus* (Buffetaut *et al.* 1996), carcharodontosaurids (Rauhut 1995), and ornithomimosaurids (AMNH 5201), where it is developed as a more or less narrow ventral notch in the ischial peduncle of the pubis (Text-fig. 39C). The foramen is absent and the ventral border of the ischial peduncle of the pubis is straight or only very slightly concave (Text-fig. 39E-F) in *Elaphrosaurus* (MB dd unnumbered), *Ornitholestes* (AMNH 619), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin and Munich specimens; *Rahonavis*: UA 8656), dromaeosaurids (IGM 100/985, 100/986), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (Barsbold and Maryanska 1990), and troodontids (Russell 1969). Baryonychids (MNN GDF 500) and tyrannosaurids (Osborn 1916; Maleev 1974) show an intermediate state (Text-fig. 39D), with a very broad obturator notch in the ischial peduncle, and are therefore coded as uncertain (1/2). The same coding has been applied to *Neovenator*, in which the obturator foramen is not enclosed by the pubis (Hutt *et al.* 1996), but the exact situation is undescribed.

An interesting taxon in respect to this character is an unnamed compsognathine from the Lower



TEXT-FIG. 41. Articulated pubes of two theropods in anterior view, illustrating different states of character 182. A, *Herrerasaurus ischigualastensis*; redrawn from Novas (1993). B, unnamed compsognathine from the Lower Cretaceous of Brazil; SMNK 2349 Pal. Scale bars represent 50 mm (A) and 10 mm (B).

Cretaceous of Brazil (SMNK 2349 Pal). In this specimen, an enclosed foramen is present on the right side, and a ventrally open notch on the left side. It should be noted, though, that the character seems to be consistent in other taxa: for example, no specimens of *Allosaurus* or tyrannosaurids with an enclosed foramen are known, although both taxa are represented by dozens of individuals.

Since it seems reasonable to assume that character state 2 cannot be reached without passing through character state 1, the character is treated as ordered.

181. Pubic fenestra below obturator foramen: absent (0); present (1) (Gauthier 1986)

In archosaurs ancestrally, the pubis has an expanded, thin bony plate that extends from the ischial peduncle of this bone towards the pubic shafts, and this plate is also found in sauropodomorphs and some theropods. This plate is usually pierced by the obturator foramen directly below the ischial peduncle, but no additional openings are present in basal dinosauriforms, sauropodomorphs, and many theropods. In *Coelophysis* (Rowe and Gauthier 1990), *Gojirasaurus* (MB 1985.G.1-3), *Segisaurus* (UCMP V 338), and *Syntarsus* (QG 1, BP/1/5246) the pubic plate is perforated by a large fenestra below the obturator foramen (Text-fig. 39B).

Rowe and Gauthier (1990) argued that this fenestra was also present in *Ceratosaurus*, but it was opened ventrally in this taxon. However, it is questionable if the broad notch in the ventral rim of the pubic plate of *Ceratosaurus* represents the same structure as the fenestra found in other theropods, or if it results from the ventral expansion of the ischial peduncle close to the suture with the ischium (Gilmore 1920). An alternative explanation might be that a pubic fenestra was present in theropods ancestrally, but is absent in more derived taxa due to the reduction of the pubic plate (see also Hutchinson 2001a).

182. Pubic apron: completely closed (0); with medial opening distally above the pubic boot (1) (modified from Rauhut 1995)

In archosaurs ancestrally, the pubis is a plate-like element. The articulated pubes form a broad apron in anterior view and the suture between the elements is continuous (Text-fig. 41A) in basal dinosauriforms, sauropodomorphs, *Eoraptor* (ROM 44686), *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Coelophysis* (Colbert 1989), *Gojirasaurus* (MB 1985.G.1-3), *Liliensternus liliensterni* (MB R. 2175), *Syntarsus* (QG 1), and *Torvosaurus* (Britt 1991). In all other theropods an elongate oval opening is present between the conjoined pubes above their distal ends (Text-fig. 41B). This opening might have served as the passage of a diverticulum of possible abdominal air sacs (Frey, pers. comm. 1998).

183. Pubic shafts in lateral view: straight (0); anteriorly convex (1); anteriorly concave (2) (modified from Harris 1998)

The pubic shafts are more or less straight in lateral view in basal dinosauriforms, ornithischians, sauropodomorphs, and most theropods. They are anteriorly convex (Text-fig. 39B) in *Coelophysis*

(AMNH 7224), *Syntarsus* (QG 1), *Monolophosaurus* (Zhao and Currie 1993), *Ceratosaurus* (USNM 4735), *Coelurus* (YPM 2010), and *Avimimus* (ROM 46144), whereas they are anteriorly concave in *Allosaurus* (DNM 116), *Microvenator* (AMNH 3041), carcharodontosaurids (Stromer 1931; Harris 1998), oviraptorosaurs (Barsbold *et al.* 1990), and tyrannosaurids (Text-fig. 39D; Osborn 1916; Lambe 1917). In *Compsognathus* (Bidar *et al.* 1972), the pubic shafts are straight proximally but anteriorly convex distally.

184. Strongly expanded pubic boot: absent (0); present (1) (Gauthier 1986)

In basal dinosauriforms, ornithischians, sauropodomorphs, *Eoraptor* (ROM 44686), *Coelophysis* (AMNH 7224), *Gojirasaurus* (MB 1985.G.1-3), *Liliensternus liliensterni* (MB R. 2175), *Segisaurus* (UCMP V 338), *Syntarsus* (QG 1), *Torvosaurus* (Galton and Jensen 1979; Britt 1991), and baryonychids (MNN GDF 500) the distal ends of the pubes are not significantly anteroposteriorly expanded. In all other theropods the distal ends of the pubes are expanded to at least twice the anteroposterior length of the pubic shafts and form a well-developed pubic boot (Text-fig. 39A, C–F). A pubic boot is absent in advanced birds, but its presence in the basal birds *Archaeopteryx* (Berlin, Eichstätt, and Munich specimens) and *Rahonavis* (UA 8656) indicates that it is the primitive character state for Aves.

185. Pubic boot in ventral view: broadly triangular (0); narrow, with subparallel margins (1) (reversed and modified from Holtz 1994)

The pubic boot in theropods is broadly triangular, with the apex oriented posteriorly in ventral view in some theropod taxa, including *Dilophosaurus* (UCMP V 6468), *Magnosaurus oxoniensis* (OUM J 13558), *Allosaurus* (DNM 116, MOR 693), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), *Neovenator* (Hutt *et al.* 1996), *Deltadromeus* (SGM-Din 2), abelisaurids (MACN CH 894), and carcharodontosaurids (pers. obs., undescribed carcharodontosaurid from the Cretaceous of Patagonia), while it is narrow with subparallel margins in *Herrerasaurus* (Novas 1993), *Coelurus* (YPM 2010), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Avimimus* (ROM 46144), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/985, 100/986), ornithomimosaurids (AMNH 5201, ROM 851, 852), and tyrannosaurids (ROM 807).

This character is coded as ‘?’ in all taxa that do not have a well-developed pubic boot. However, the broadly triangular shape of the distal end of the articulated pubes in theropods that lack a true pubic boot, for example *Coelophysis* (UCMP V 82250), indicates that this morphology is the primitive character state in dinosaurs. This stands in contrast to Holtz’ (1994) assumption that the triangular shape was an allosaurid synapomorphy.

186. Pubic boot: more posteriorly than anteriorly expanded (0); more anteriorly than posteriorly expanded (1) and

187. Pubic boot: with distinct anterior expansion (0); only expanded posteriorly (1); only expanded posteriorly and posterior expansion more than half the length of the pubic shafts (2) (modified from Gauthier 1986; Holtz 1994; ordered)

In most theropod dinosaurs that have a well-developed pubic boot, this structure is expanded both anteriorly and posteriorly and the posterior expansion is longer than the anterior one. In a few theropods, including *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Deltadromeus* (SGM-Din 2), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (Barsbold and Maryanska 1990), and tyrannosaurids (ROM 807), the pubic boot is more anteriorly than posteriorly expanded (Text-fig. 39D–E). In several other taxa, including ‘*Szechuanosaurus*’ *zigongensis* (Gao 1993), *Compsognathus* (BSP A.S. I 563; Bidar *et al.* 1972), *Sinosauropteryx* (Chen *et al.* 1998), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin and Munich specimens; *Rahonavis*: UA 8656), and dromaeosaurids (IGM 100/985, 100/986), an anterior expansion is absent and the pubic boot is only expanded posteriorly (Text-fig. 39F). In *Compsognathus* and the unnamed compsognathine the posterior expansion is, furthermore, greatly elongated, and is more than half as long as the pubic shafts. As discussed by Hutchinson (2001a), these changes in pubic boot morphology were probably correlated with changes in pelvic myology.

Since character state 2 includes character state 1, character 187 is treated as ordered.

188. Obturator process on ischium: confluent with pubic peduncle (0); offset from pubic peduncle by a distinct notch (1) and
189. Obturator process: proximally placed (0); distally placed (1) (modified from Gauthier 1986)

Gauthier (1986, p. 25, character 47) argued that an obturator process was absent in archosaurs ancestrally and also in ornithischians, sauropodomorphs, and several theropods. However, Novas (1993) identified the anterior plate-like expansion of the ischium below the pubic peduncle as the obturator process in *Herrerasaurus*, and this view is followed here (Text-fig. 39A–B; see also Hutchinson 2001a). Thus, an obturator process is present in basal dinosauriforms, sauropodomorphs and all theropods, but it is confluent with the pubic peduncle of the ischium in the former taxa and several theropods. In ornithischians ancestrally, the expanded plate underneath the pubic peduncle of the ischium is reduced (Serenó 1991b), and the obturator process that is found in ornithomimosaurs is certainly a novelty.

In many theropods, including *Allosaurus* (DNM 116, MOR 693, USNM 4734), *Compsognathus* (BSP A.S. I 563), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), *Caudipteryx* (NGMC 97-4-A), *Neovenator* (Hutt *et al.* 1996), *Siamotyrannus* (Buffetaut *et al.* 1996), *Sinosauropteryx* (NGMC 65), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin and Eichstätt specimens), carcharodontosaurids (Stromer 1931), dromaeosaurids (IGM 100/985, YPM 5235), ornithomimosaurs (ROM 851, USNM 4736), oviraptorosaurs (ROM 43250), therizinosauroids (Barsbold and Maryanska 1990), troodontids (Russell 1969), and tyrannosaurids (Osborn 1916; Lambe 1917; Maleev 1974), the obturator process is offset from the pubic process of the ischium by a distinct notch (Text-fig. 39C–F). In some specimens where the process is well preserved (e.g. *Allosaurus*: DNM 116, Compsognathinae indet.: SMNK 2349 Pal), it has a narrow, tapering process towards the anterior end of the pubic peduncle of the ischium, which sometimes contacts this process so that the notch may be developed as a large fenestra within the obturator plate (e.g. SMNK 2349 Pal., left side).

The situation in baryonychids is somewhat uncertain. In *Baryonyx* (BMNH R 9951) and *Suchomimus* (MNN GDF 500), the plate-like expansion underneath the pubic peduncle of the ischium is reduced and an elongate, low flange, which appears to represent a muscle attachment, is present in the same position as the obturator process in, for example, *Allosaurus*. Although this condition might well have arisen from an *Allosaurus*-like morphology, the character is coded as uncertain in baryonychids.

In dinosauriforms ancestrally, and in many theropods, the obturator process is located on the proximal third of the ischial shaft. In several taxa (specimens and references as listed above), including *Caudipteryx*, *Unenlagia*, birds, dromaeosaurids, oviraptorosaurs, therizinosauroids, and troodontids, the process is situated at the mid-length of the shaft, or lower (Text-fig. 39E–F).

190. Ventral notch between obturator-process or -flange on ischium: absent (0); present (1) (modified from Sereno *et al.* 1996)

In basal dinosauriforms, saurischians, and some theropods the obturator process (as defined above) is confluent with the ischial shafts distally. In a number of theropod taxa (specimens and references as in character 187 unless otherwise stated), including *Coelophysis* (Colbert 1989), *Dilophosaurus* (UCMP V 4214), *Syntarsus* (QG 1), *Piatnitzkysaurus* (MACN CH 895), '*Szechuanosaurus*' *zigongensis* (Gao 1993), *Allosaurus*, *Ceratosaurus* (USNM 4735), sinraptorids, *Afrovenator*, abelisaurids (MACN CH 894), baryonychids (MNN GDF 500), and carcharodontosaurids, a small notch separates the process distally from the ischial shafts (Text-fig. 39B–C).

Serenó *et al.* (1996) used the triangular morphology of the obturator process in coelurosaurs as a synapomorphy for this group. However, this morphology is a result of the absence of the notch described above in these taxa. As discussed above, the notch represents a derived character within theropods, so its absence in coelurosaurs is most probably a reversal.

191. Ischium at least three-quarters the length of pubis (0); ischium two-thirds or less the length of the pubis (1) (Gauthier 1986)

As in archosaurs ancestrally, the pubis and ischium are subequal in length in basal dinosauriforms, basal ornithischians, sauropodomorphs, and many theropods, although the pubis might be slightly longer than

the ischium. In a number of theropods, including *Coelophysis* (Colbert 1989), *Liliensternus liliensterni* (MB R. 2175), *Syntarsus* (Raath 1990), *Sinosauropteryx* (NGMC 65), *Unenlagia* (MCF PVPH 78), birds (*Archaeopteryx*: Berlin and Munich specimens; *Rahonavis*: UA 8656), and dromaeosaurids (IGM 100/985, 100/986), the ischium is reduced in length compared with the pubis and is only two-thirds or less the length of the latter bone (Text-fig. 39B, F).

192. Posterior process on proximal part of ischium: absent or only developed as a small flange (0); well-developed (1)

In many theropods, a small flange is present on the posterior rim of the iliac process of the ischium (ischial tuberosity in Hutchinson 2001a). This flange probably served as a muscle insertion since a muscle scar is present in this position in *Ceratosaurus*, abelisaurids, ornithomimosaurids, and tyrannosaurids. However, this flange is poorly developed in most taxa and not obvious in the lateral view of the ischium. Only in *Unenlagia* (MCF PVPH 78) and basal birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens) is this flange developed as a triangular posterior process (Text-fig. 39F).

193. Distal end of ischium: slightly expanded (0); strongly expanded, forming ischial 'boot' (1); tapering (2) (modified from Smith and Galton 1990; Holtz 1994)

In ornithischians, sauropodomorphs, and many theropods the distal end of the ischium is slightly expanded, but the anteroposterior length of this expansion is usually not more than twice the anteroposterior length of the ischial shafts. In several theropods, including '*Szechuanosaurus*' *zigongensis* (Gao 1993), *Ceratosaurus* (Gilmore 1920), *Elaphrosaurus* (MB dd unnumbered), and abelisaurids (MACN CH 894), the distal end of the ischium is expanded into a well-developed ischial boot, the length of which exceeds twice the length of the ischial shafts. A similar expansion is found in some ornithomimosaurids (e.g. *Archaeornithomimus*: AMNH 6558), but not in all members of this clade (absent e.g. in *Dromiceiomimus*: AMNH 5201); therefore, the character is coded as uncertain in ornithomimosaurids.

In a variety of other theropod taxa, including *Ornitholestes* (AMNH 619), *Caudipteryx* (NGMC 97-4-A), birds (*Archaeopteryx*: Berlin, Eichstätt and Munich specimens), dromaeosaurids (YPM 5235), oviraptorosaurs (ROM 43250), troodontids (Russell 1969), and tyrannosaurids (Osborn 1916; Maleev 1974), the ischium tapers to a point distally (Text-fig. 39D), probably in connection with a shift of the m. ischiocaudalis to the pubis (Hutchinson 2001a).

### *Hindlimb*

194. Femoral head: confluent with greater trochanter (0); separated from greater trochanter by a distinct cleft (1) (Holtz 1994)

The presence of an inturned head of the femur and thus the distinction of the proximal end of the femur into a femoral head medially and a greater trochanter laterally is a dinosaurian synapomorphy (Gauthier 1986; Benton 1990; Novas 1996a). In sauropodomorphs and many theropods, the femoral head is not offset from the greater trochanter proximally so that the two structures are confluent and the proximal end is straight or slightly convex in anterior view. In ornithischians and several theropods, including *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (Marsh 1880), dromaeosaurids (IGM 100/986), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (IVPP V 11559; Russell and Dong 1993a), troodontids (MOR 553S), and tyrannosaurids (Osborn 1916; Maleev 1974), the greater trochanter is offset from the femoral head by an anteroposteriorly directed groove on the proximal end so that the proximal end is concave in anterior view.

195. Femoral head: directed anteromedially (0); directed strictly medially (1) (reversed from Holtz 1994)

As noted above, the presence of an inturned femoral head is a dinosaurian synapomorphy, although the proximal end of the femur is slightly expanded medially in basal dinosauriforms (Sereno and Arcucci

1994). In comparison with the orientation of the distal condyles (i.e. under the assumption that the condyles are strictly anteroposteriorly oriented), the inturned proximal end of the femur is directed strongly anteromedially in basal dinosauriforms, basal ornithischians, basal sauropodomorphs, and some theropods. The femoral head often forms an angle of approximately 45 degrees with the anteroposterior long axis of the bone.

In *Magnosaurus oxoniensis* (OUM J 13558), *Allosaurus* (DNM 116, MOR 693), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), *Caudipteryx* (NGMC 97-9-A), *Chilantaisaurus tashuikouensis* (IVPP V 2884), *Microvenator* (AMNH 3041), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), baryonychids (MNN GDF 500), carcharodontosaurids (Harris 1998), dromaeosaurids (IGM 100/986), ornithomimosaurids (AMNH 21800), oviraptorosaurs (Currie and Russell 1988; Barsbold *et al.* 1990), therizinosauroids (Russell and Dong 1993a), troodontids (MOR 553S), and tyrannosaurids (Osborn 1916; Maleev 1974) the femoral head is perpendicular to the anteroposterior axis of the bone and faces strictly medially.

Based on statements in Bonaparte (1991b), Holtz (1994, p. 1104) considered an anteromedially directed femoral head as a synapomorphy of neoceratosaurs [*Ceratosaurus* + (*Elaphrosaurus* + Abelisaurids)]. However, as noted above, the presence of an anteromedially directed femoral head in many basal theropods, and in non-theropodan outgroups, indicates that this is the plesiomorphic character state for dinosaurs (see also Hutchinson 2001b).

196. Greater trochanter: anteroposteriorly narrow and narrowing from medial to lateral (0); anteroposteriorly expanded, forming a trochanteric crest (1) (Hutchinson 2001b)

In dinosaurs ancestrally, the greater trochanter is narrow laterally and widens towards the femoral head medially. This condition is retained in basal dinosauriforms, sauropodomorphs, and many theropods (Text-fig. 42A–B, D). In ornithischians and a number of theropods, including *Caudipteryx* (NGMC 97-9-A), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (Russell and Dong 1993a), and troodontids (IVPP V 9612, MOR 553S), the greater trochanter forms an anteroposteriorly expanded trochanteric crest laterally that is wider anteroposteriorly than the femoral head (Text-fig. 42E).

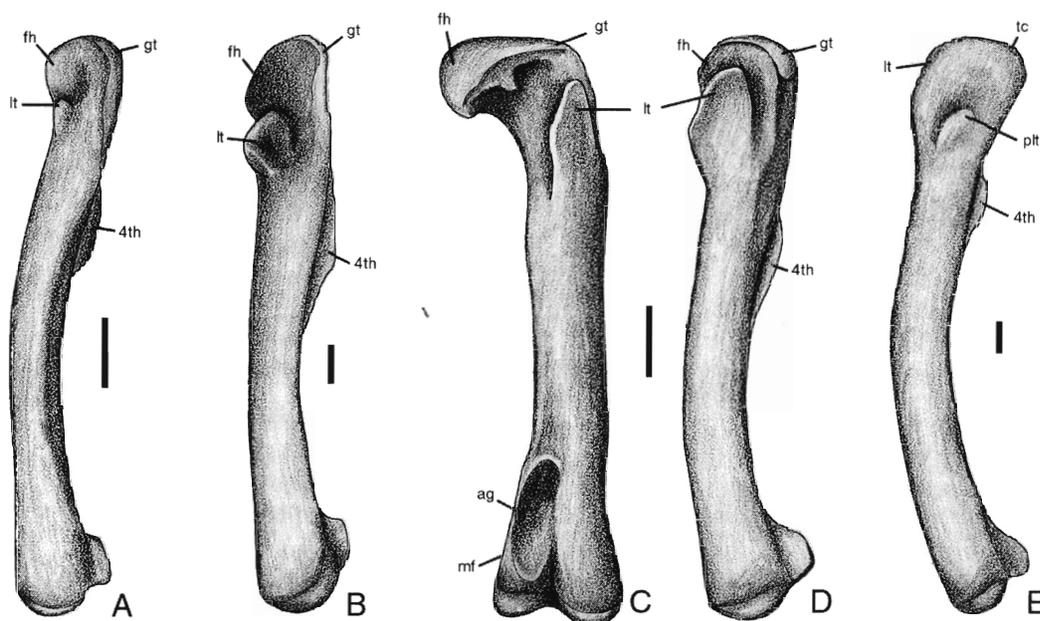
197. Oblique ligament groove on posterior surface of femoral head: absent or very shallow (0); deep, bound medially by a well-developed posterior lip (1)

The path of the ligamentum capitis femoris on the posterior side of the femoral head is not marked or only indicated by a shallow groove in basal dinosauriforms, ornithischians, sauropodomorphs, and *Herrerasaurus* (Novas 1996a). In all other theropods with the exception of *Avimimus* (ROM 46144) and abelisaurids (MACN CH 894), a well-developed ligament groove that runs obliquely from proximomedially to laterodistally, is present on the posterior side of the femoral head. Usually the groove is largely defined by a posteriorly expanded lip on the medial part of the femoral head.

198. Lesser trochanter: absent or poorly developed (0); spike-like or developed as trochanteric shelf (1); broadened ('wing-like') (2); fused with greater trochanter (3) and

199. Placement of lesser trochanter: at distal end of femoral head (0); more proximally placed, but below greater trochanter (1); as high or higher than greater trochanter (2) (modified from Gauthier 1986; ordered)

A lesser trochanter on the femur, the insertion area for the iliopsoas musculature in birds (McGowan 1979; Hutchinson 2001b), is absent in archosaurs ancestrally. In basal dinosauriforms, a short, poorly developed trochanteric shelf may be present (Novas 1996a), and in sauropodomorphs, a low, rounded, vertical ridge is often found on the lateral side of the anterior surface of the proximal femur (e.g. *Plateosaurus*: SMNS 13200). By contrast, ornithischians and all theropods have a prominent lesser



TEXT-FIG. 42. Left femora of theropod dinosaurs, illustrating several hindlimb characters. A, *Liliensternus liliiensterni*; lateral view; based on MB R. 2175. B, *Ceratosaurus* sp.; lateral view; based on UMNH VP 5278. C–D, *Allosaurus fragilis*; anterior and lateral view; redrawn from Madsen (1976). E, *Velociraptor mongoliensis*; lateral view; based on IGM 100/986. Abbreviations: ag, anterior groove; fh, femoral head; gt, greater trochanter; lt, lesser trochanter; mf, medial flange; plt, posterolateral trochanter; tc, trochanteric crest; 4th, fourth trochanter. Scale bars represent 50 mm (A–B), 100 mm (C–D), and 10 mm (E).

trochanter that has several different morphologies and positions relative to the femoral head and the greater trochanter in different taxa (Text-fig. 42).

In *Herrerasaurus* (Novas 1993, 1996a), *Coelophysis* (Rowe and Gauthier 1990), *Liliensternus liliiensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), and *Syntarsus* (QG 1, QG 691), the lesser trochanter is placed entirely below the femoral head and is developed as a lateral, almost horizontal trochanteric shelf that is flexed proximally anteriorly and ends in a pointed spike. The trochanteric shelf may be absent in some individuals, possibly due to sexual dimorphism (Raath 1990); in these cases, only a narrow, proximally pointed, almost vertical ridge is present (Text-fig. 42A).

In a variety of taxa, the lesser trochanter is strongly broadened anteroposteriorly ('wing-like' in Gauthier 1986, p. 25, character 49), and its proximal end may be placed directly below the femoral head (Text-fig. 42B), as in *Ceratosaurus* (UMNH VP 5278, USNM 4735), *Elaphrosaurus* (MB dd unnumbered), and abelisaurids (MACN CH 894), or more proximally at approximately the mid-height of the femoral head (Text-fig. 42C–D), as in *Magnosaurus oxoniensis* (OUM J 13558), *Piatnitzkysaurus* (Bonaparte 1986), *Allosaurus* (DNM 116, MOR 693), *Coelurus* (YPM 2010), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), *Caudipteryx* (NGMC 97-9-A), *Chilantaisaurus tashuikouensis* (IVPP V 2884), *Neovenator* (Hutt *et al.* 1996), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Deltadromeus* (SGM-Din 1), baryonychids (MNN GDF 500), and carcharodontosaurids (Stromer 1931; Harris 1998), or may even be level with, or higher than the greater trochanter, as in *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), ornithomimosaurs (AMNH 21800, 5201, 5385), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (IVPP V 11559), and tyrannosaurids (Osborn 1916; Maleev 1974).

Finally, the lesser trochanter is as high as the greater trochanter and fused with the latter (Text-fig. 42E) in *Bagaraatan* (Osmólska 1996), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids

(IGM 100/986), and troodontids (IVPP 9612). A small incision occasionally marks the border between the two trochanters.

Gauthier (1986, p. 9, definition of Ceratosauria, p. 25, character 49, p. 34, character 82) defined the morphology of the lesser trochanter (character 197 of the present analysis) as three binary characters in his analysis, but did not take the relative position of the trochanter into account. However, the great variation in the development of this structure makes a more detailed consideration of its morphology desirable (see also Hutchinson 2001b).

Since character state 2 includes character state 1 in character 199, the character is treated as ordered.

200. Posterolateral trochanter on proximal femur: absent or poorly developed (0); well developed (1) (Ostrom 1976b)

There is no pronounced muscle attachment on the posterolateral part of the proximal femur in basal dinosauriforms, ornithischians, and sauropodomorphs. A roughened area or a small eminence in this position is present in many theropods, including even basal taxa such as *Elaphrosaurus* (MB dd unnumbered), but it is usually poorly developed and has long escaped the attention of dinosaur palaeontologists (Ostrom 1976b). By contrast to this, the muscle attachment is developed as a prominent, cone-shaped tubercle that is usually pointed proximally (Text-fig. 42E) in basal birds (*Archaeopteryx*: Berlin specimen; *Rahonavis*: UA 8656), dromaeosaurids (Ostrom 1976b) and troodontids (IVPP V 9612, MOR 553S).

This muscle attachment was interpreted as the insertion of the m. ischio-trochantericus by Ostrom (1976b), and it is in approximately the same position as the insertion area for the avian homologue of this muscle, the m. ischiofemoralis (Romer 1923b), in *Apteryx* (McGowan 1979).

201. Fourth trochanter on the femur: forming a stout, well-developed, high ridge (0); reduced to a feeble, low ridge or absent (1) (Gauthier 1986)

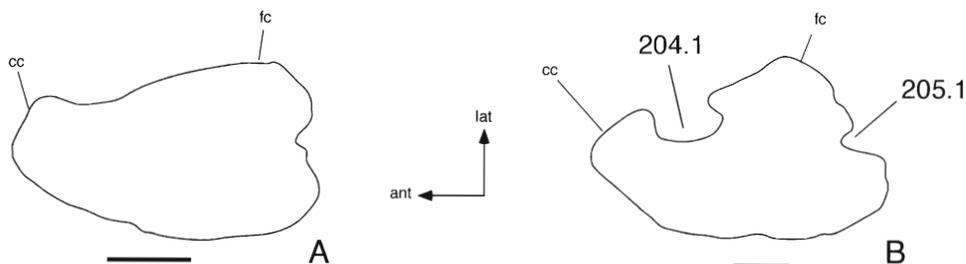
The fourth trochanter on the femur of dinosaurs is generally regarded as the insertion area for the m. caudofemoralis longus (e.g. Romer 1923a), which is the principal source for hindlimb propulsion in reptiles (Gatesy 1990). It is not surprising, therefore, that it is well developed in dinosaurs ancestrally, and it forms a large, blade-like structure on the posteromedial side of the femoral shaft in ornithischians and basal sauropodomorphs. In many theropods, it forms a stout, well-developed ridge that is positioned more proximally than the trochanter in ornithischians and sauropodomorphs. In several taxa, including *Ornitholestes* (AMNH 619), *Microvenator* (AMNH 3041), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), *Deltadromeus* (SGM-Din 1), *Unenlagia* (MCF PVPH 78), birds (*Rahonavis*: UA 8656), dromaeosaurids (Ostrom 1976b), ornithomimosaur (AMNH 21800, 5201, 5385), oviraptorosaurs (Barsbold *et al.* 1990), and troodontids (MOR 553S), the fourth trochanter is strongly reduced to a weakly developed crest or a slight depression, or it is entirely absent.

202. Broad groove on cranial surface of distal femur: absent or poorly developed (0); well developed and bound medially by an expanded medial lamella (1)

The anterior side of the distal end of the femur is transversely convex in basal dinosauriforms, ornithischians, and sauropodomorphs. In many theropods with the exception of *Eoraptor* (ROM 44686), *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), birds (*Rahonavis*: UA 8656), baryonychids (MNN GDF 500), and troodontids (MOR 553S), a shallow, broad longitudinal groove is present on the medial part of the anterior side of the distal end of the femur (Text-fig. 42c). This groove is usually bounded medially by an expanded lamella that slightly overhangs the medial side of the femur.

203. Distal end of femur: anteroposteriorly broad and distally flattened (0); less broad and well rounded (1)

In dinosaurs ancestrally, the distal end of the femur is anteroposteriorly broad and flat distally in lateral view; this condition is retained in basal ornithischians, basal sauropodomorphs, *Eoraptor*, *Herrerasaurus*,



TEXT-FIG. 43. Right theropod tibiae in proximal view, illustrating states for characters 204 and 205. A, *Dilophosaurus wetherilli*; based on UCMP V 4214. B, *Allosaurus fragilis*; based on AMNH 680. Abbreviations: ant, anterior; cc, crenial crest; fc, fibular condyle; lat, lateral. Scale bars represent 10 mm.

*Staurikosaurus*, *Coelophysis*, *Dilophosaurus*, and *Syntarsus*. In all other theropods, the distal condyli of the femur are well rounded in lateral view, and the distal end of this bone appears less broad (Text-fig. 42).

204. Fibular condyle on proximal end of tibia: confluent with crenial crest anteriorly in proximal view (0); strongly offset from crenial crest (1)

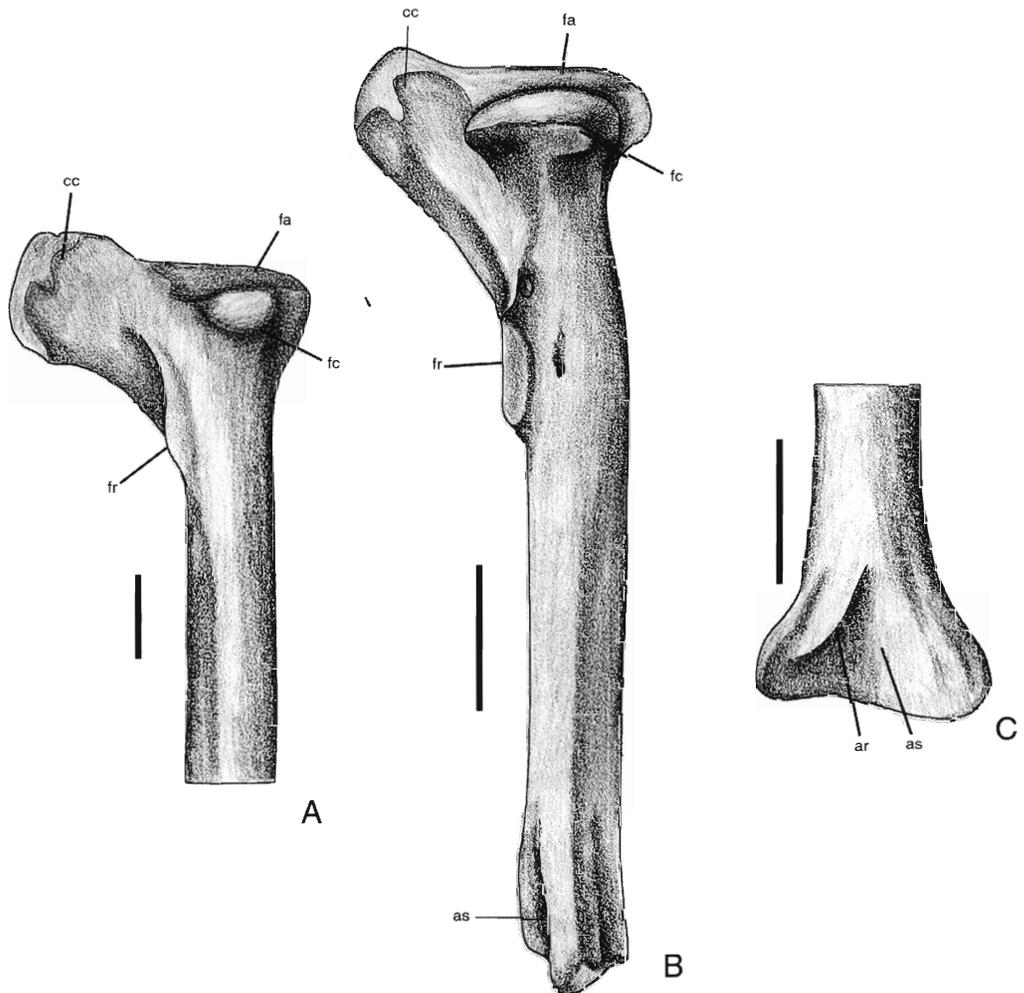
The fibular condyle of the tibia gradually tapers towards the crenial crest anteriorly in basal dinosauriforms, basal ornithischians, sauropodomorphs, *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Coelophysis* (UCMP V 82250), *Gojirasaurus* (MB 1985.G.1-3), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), *Segisaurus* (UCMP V 338), *Syntarsus* (QG 1), *Elaphrosaurus* (Janensch 1925), and abelisaurids (MACN CH 894), and is, thus, roughly triangular in proximal outline (Text-fig. 43A). In all other theropods the fibular condyle is strongly offset from the crenial crest by a well-developed incisura tibialis and is roughly rectangular in outline (Text-fig. 43B).

205. Posterior cleft between medial part of the proximal end of the tibia and fibular condyle: absent (0); present (1)

The fibular condyle of the tibia is confluent with the medial part of the proximal end of the tibia, or only separated from it by a shallow groove in basal dinosauriforms, ornithischians, sauropodomorphs, *Herrerasaurus* (Novas 1993), *Staurikosaurus* (Galton 1977), *Avimimus* (ROM 46144), and *Bagaraatan* (Osmólska 1996). In all other theropods, a deep cleft is present posteriorly between the fibular condyle and the medial part (Text-fig. 43).

206. Ridge on lateral side of tibia for connection with fibula: absent (0); present, extending from the proximal articular surface distally (1); present, clearly separated from proximal articular surface (2) (modified from Gauthier 1986)

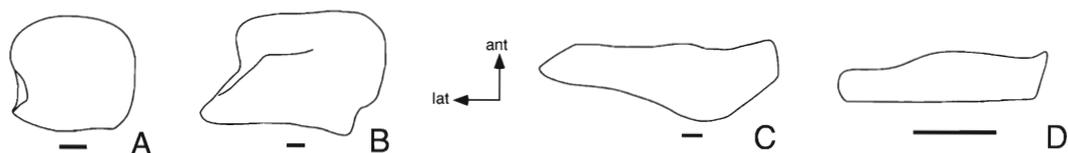
As noted by Gauthier (1986, p. 22, character 30), a lateral ridge or crest that is present in theropods for the attachment of the fibula is unknown in ornithischians, sauropodomorphs, *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus*. This ridge has two quite different morphologies in theropods (Text-fig. 44A–B). It is proximally placed, connected with the proximal end, and becomes gradually more pronounced distally (Text-fig. 44A) in *Gojirasaurus* (MB 1985.G.1-3), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), *Segisaurus* (UCMP V 338), *Syntarsus* (QG 1), *Ceratosaurus* (UMNH VP 5278, YPM 4681), *Elaphrosaurus* (MB dd unnumbered), and abelisaurids (MACN CH 894), whereas it is more distally placed, arises abruptly from the shaft of the tibia, and is not connected with the proximal end of the tibia in all other theropods (Text-fig. 44B).



TEXT-FIG. 44. Theropod tibiae, showing states for several hindlimb characters. A, *Majungatholus atopus*; proximal half of left tibia, lateral view; based on FMNH/UA 95263. B-C, *Allosaurus fragilis*; left tibia. B, lateral view. C, distal half in anterior view; redrawn from Madsen (1976). Abbreviations: ar, anterior ridge on the distal end of the tibia; as, facet for the ascending process of the astragalus; cc, cnemial crest; fa, articulation for femur; fc, fibular condyle; fr, lateral ridge for the attachment of fibula. Scale bars represent 50 mm (A) and 100 mm (B-C).

207. Bracing for ascending process of astragalus on anterior side of distal tibia: distinct 'step' running obliquely from mediolateral to lateroproximal (0); bluntly rounded vertical ridge on medial side (1); anterior side of tibia more or less flat (2)

The presence of a well-developed ascending process of the astragalus is a dinosaurian synapomorphy (Benton 1990), although a small ascending process is present in all dinosauriforms (e.g. Sereno and Arcucci 1993, 1994; Novas 1996a). The ascending process slots into a groove on the anterior side of the distal end of the tibia. This groove is bounded proximally by an oblique ridge that runs from the mediolateral corner of the tibia proximolaterally. This ridge is present in basal ornithischians, sauropodomorphs and many theropods (Text-fig. 44C). In *Chilantaisaurus tashukouensis* (IVPP V 2884) and



TEXT-FIG. 45. Theropod tibiae in distal view, illustrating different states of character 208. A, *Herrerasaurus ischigualastensis*; left tibia (reversed); redrawn from Novas (1993). B, *Dilophosaurus wetherilli*; right tibia; based on UCMP V 6468. C, *Piatnitzkysaurus floresii*; left tibia (reversed); based on MACN CH 895. D, *Rahonavis ostromi*; right tibia; based on UA 8656. Abbreviations: ant, anterior; lat, lateral. Scale bars represent 10 mm (A–C) and 5 mm (D).

baryonychids (MNN GDF 500) the ridge is absent, and only a bluntly rounded vertical ridge on the medial part of the anterior side of the tibia is present. In several other theropods, including *Coelurus* (YPM 2010), *Elaphrosaurus* (MB dd unnumbered), *Caudipteryx* (Ji *et al.* 1998), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, MOR 660), ornithomimosaurids (AMNH 6570, 21801, 5385), oviraptorosaurs (Currie and Russell 1988; Barsbold *et al.* 1990), troödontids (MOR 553S), and tyrannosaurids (AMNH 5227), the ridge is completely absent and the anterior side of the distal tibia is flat; only the medial rim might be slightly raised.

208. Distal articular surface of tibia: subrectangular in outline and only slightly wider transversely than anteroposteriorly (0); subrectangular with small lateral process (1); narrow triangular in outline and strongly mediolaterally expanded (2); rectangular and more than three times wider transversely than anteroposteriorly (3) (ordered)

The distal end of the tibia is subrectangular to round in outline (Text-fig. 45A) and only slightly wider transversely than anteroposteriorly in basal dinosauriforms, sauropodomorphs, *Herrerasaurus*, and *Staurikosaurus*.

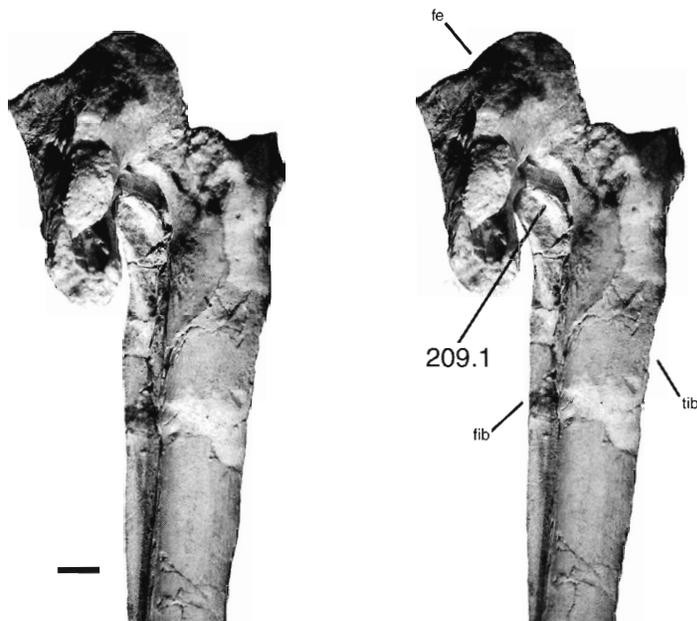
In *Coelophysus* (UCMP V 82250), *Gojirasaurus* (MB 1985.G.1-3), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 6468), and *Syntarsus* (QG 1, QG 69) the subrectangular shape is retained, but a small lateral process is present posterior to the facet for the ascending process of the astragalus (Text-fig. 45B).

In ornithischians and a variety of other theropods, including both species of *Magnosaurus* (OUM J 12143, 13558), *Piatnitzkysaurus* (MACN CH 895), *Poekilopleuron* (Eudes-Deslongchamps 1838), *Allosaurus* (AMNH 680, 5750, MOR 693), *Compsognathus* (BSP A.S. I 563), *Elaphrosaurus* (MB dd unnumbered), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), *Chilantaisaurus tashuikouensis* (IVPP V 2884), *Deltadromeus* (SGM-Din 2), abelisaurids (Martínez *et al.* 1987), baryonychids (MNN GDF 500), carcharodontosaurids (Stovall and Langston 1950), ornithomimosaurids (AMNH 6570, 21801, 5385), and tyrannosaurids (AMNH 5227), the distal end of the tibia is anteroposteriorly compressed and the lateral process is enlarged, so that the outline of the articular surface is broadly triangular (Text-fig. 45C).

In several theropods, including *Coelurus* (YPM 2010), *Avimimus* (ROM 46144), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, MOR 660), and troödontids (MOR 553S), the tibia is further compressed so that the outline is broadly rectangular, and at least three times wider transversely than anteroposteriorly (Text-fig. 45D).

In some theropods, the tibia exhibits intermediate stages between the character states described above, or its morphology cannot be evaluated definitely because of fusion with the astragalus. Thus, *Ceratosaurus* is coded as '1/2', and *Caudipteryx*, *Microvenator*, *Bagaraatan*, and oviraptorosaurs are coded as '2/3'.

Since higher character states include lower states, the character is treated as ordered.

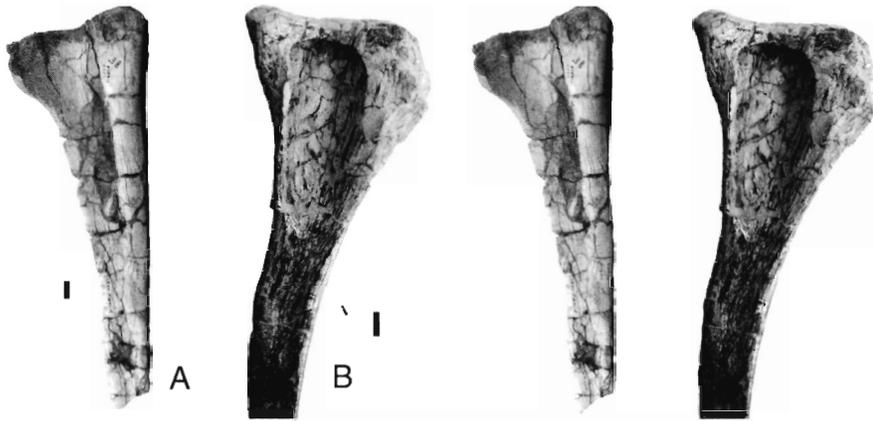


TEXT-FIG. 46. *Segisaurus halli*; UCMP V 338; stereophotographs of the left femur, tibia and fibula, illustrating state 1 of character 209. Abbreviations: fe, femur; fib, fibula; tib, tibia. Scale bar represents 10 mm.

209. Ridge on medial side of proximal end of fibula, that runs anterodistally from the posterproximal end: absent (0); present (1) (modified from Rowe and Gauthier 1990) and
210. Deep groove on medial side of proximal end of fibula: absent (0); present, but covering less than two-thirds of the width of the fibula (1); present and wide, covering more than two-thirds the width of the fibula (2) (modified from Sereno *et al.* 1996; ordered)

The medial side of the proximal end of the fibula is flat in ornithischians, sauropodomorphs, *Herrerasaurus*, *Staurikosaurus*, *Liliensternus liliensterni*, *Magnosaurus oxoniensis*, *Microvenator*, birds, and troodontids. In *Coelophysis* (UCMP V 82250), *Segisaurus* (UCMP V 338), and *Syntarsus* (QG 1) a broadly rounded ridge is present in this position and runs from the posterproximal edge of the medial side obliquely anterodistally (Text-fig. 46), which may be hollowed posteriorly. This character was defined as 'sulcus excavated into the base of the crista tibio-fibularis' in the diagnosis of the Ceratosauria by Rowe and Gauthier (1990, p. 154), but the sulcus might only be present in *Syntarsus kayentakatae* (Rowe 1989; Rowe and Gauthier 1990), since it was not found in the specimens studied in this analysis, so the presence of the ridge seems to be the more consistent character.

In many theropods a deep groove is present on the medial side of the proximal end of the fibula. This groove may be anteroposteriorly narrow, mainly restricted to the anterior half of the medial side of the fibula, and start some way below the proximal end (Text-fig. 47A), as in *Dilophosaurus* (UCMP V 4214), '*Szechuanosaurus*' *zigongensis* (Gao 1993), *Allosaurus* (AMNH 287, MOR 693), *Ceratosaurus* (UMNH VP 5278, YPM 4681), *Coelurus* (YPM 2010), *Ornitholestes* (AMNH 619), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal), and carcharodontosaurids (Stromer 1931), or it may cover almost the complete medial side proximally (Text-fig. 47B), as in *Deltadromeus* (SGM-Din 2), baryonychids (MNN GDF 500), dromaeosaurids (TMP 88.121.39), ornithomimosaurids (AMNH 5355, 5375), and tyrannosaurids (AMNH 6554, 5227).



TEXT-FIG. 47. Stereophotographs of theropod fibulae in medial view, illustrating different character states of character 210. A, *Dilophosaurus wetherilli*; left fibula; UCMP V 4214. B, *Struthiomimus altus*; right fibula; AMNH 5355. Scale bars represents 10 mm.

In *Elaphrosaurus* the total extent of the medial groove could not be observed since the specimen is mounted, and in *Afrovenator* only a very shallow groove is present. Therefore, these two taxa are coded as uncertain for character 210.

Since character state 2 includes character state 1 in character 210, the character is treated as ordered.

211. Insertion of m. iliofibularis on fibular shaft: not especially marked (0); present as a well-developed anterolateral tubercle (1) (modified from Mader and Bradley 1989; Holtz 1994)

The insertion of the tendon of the m. iliofibularis on the fibula is not especially marked in basal dinosauriforms, ornithischians, sauropodomorphs, or *Staurikosaurus*. In all other taxa the insertion is developed as a pronounced anterolateral, usually proximodistally elongate tubercle on the proximal half of the fibula (Text-fig. 48).

This character was considered to be a tyrannosaurid synapomorphy by Mader and Bradley (1989, p. 47, character 6). However, a well-developed tubercle for the insertion of the m. iliofibularis on the anterolateral side of the proximal fibula has a much wider distribution amongst theropods, although it is often especially pronounced in large taxa.

212. Fibular shaft: gradually narrowing from proximal end to mid-shaft (0); abruptly narrowing below the insertion of m. iliofibularis (1)

In basal dinosauriforms, ornithischians, sauropodomorphs, and many theropods, the fibula has a strongly anteroposteriorly expanded proximal end and gradually narrows towards the mid-shaft. In *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), birds (*Archaeopteryx*: Munich specimen), dromaeosaurids (MOR 660, TMP 88.121.39), oviraptorosaurs (IGM 100/9/72), and troodontids (MOR 553S), the fibula is considerably narrower just below the tubercle for the insertion of the m. iliofibularis than above it (Text-fig. 48).

213. Fibular facet on the astragalus: large and facing partially proximally (0); reduced and facing laterally or absent (1) (modified from Holtz 1994)

The presence of a well-developed fibular facet on the astragalus is the ancestral condition for dinosaurs, and this character state is retained in ornithischians, sauropodomorphs, and many theropods (Text-fig. 49A–D). In these animals, the fibular facet on the astragalus is developed as a large, anteroposteriorly and transversely concave facet lateral to the ascending process of the astragalus. The usually larger lateral side of the facet faces proximally, while the medial side faces laterally. In



TEXT-FIG. 48. *Saurornitholestes langstoni*; TMP 88.121.39; fibula, lateral view, showing state 1 for characters 211 and 212. Scale bar represents 10 mm.

*Caudipteryx* (Ji *et al.* 1998), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Deltadromeus* (SGM-Din 2), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, TMP 88.121.39, YPM 5226), ornithomimosaurids (AMNH 6570, 5385, ROM 851), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (IVPP V 11559), troödontids (MOR 553S), and tyrannosaurids (AMNH 6554, 5227), the fibular facet on the astragalus is strongly reduced and restricted to a small, laterally facing facet on the lateral side of the ascending process of the astragalus (Text-fig. 49E). In advanced birds, where the fibula is reduced distally, the facet is completely absent.

The reduction of the fibular facet of the astragalus is used here as a measure for the reduction of the distal end of the fibula (Holtz 1994, character 101) since it is easier to quantify than the relative width of the distal fibula shaft.

214. Ascending process of astragalus: arising out of the lateral part of the astragal body (0); arising out of the complete breadth of the astragal body (1) (modified from Welles and Long 1974)

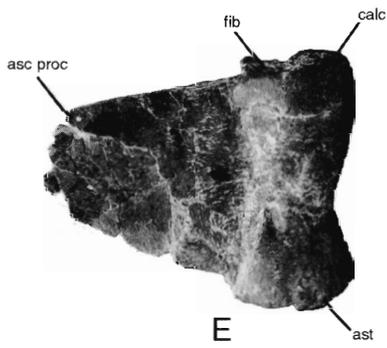
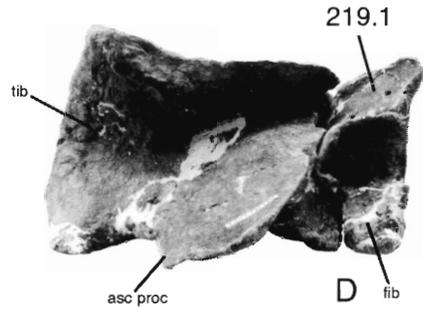
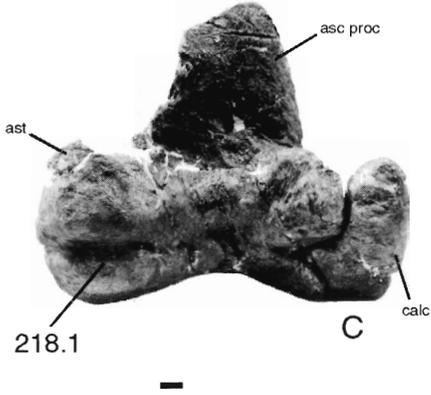
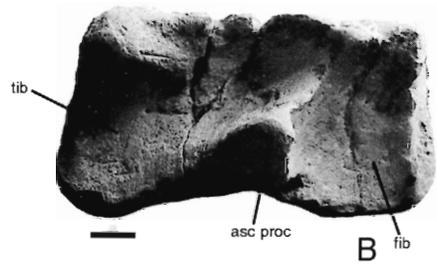
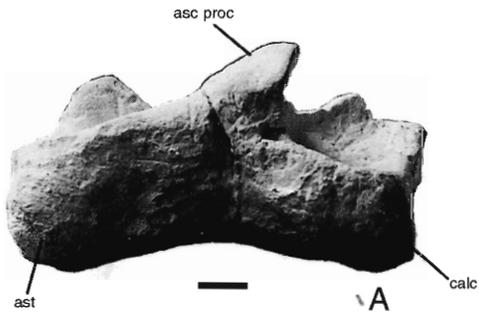
In dinosauriforms ancestrally, the ascending process of the astragalus is restricted to the lateral side of the astragal body ('ceratosauroid' and 'allosauroid' tarsus of Welles and Long 1974), medial to the fibular facet, and this condition is retained in many theropods (Text-fig. 49A–D). In a number of theropods, including *Caudipteryx* (Ji *et al.* 1998), *Microvenator* (AMNH 3041), *Sinosauropteryx* (Currie, pers. comm. 1999), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, TMP 88.121.39, YPM 5226), ornithomimosaurids (AMNH 6570, 5385, ROM 851), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (IVPP V 11559; Barsbold and Maryanska 1990), troödontids (MOR 553S), and tyrannosaurids (AMNH 6554, 5227), the basis of the ascending process is strongly broadened transversely and the process arises from the complete breadth of the astragal body (Text-fig. 49E; 'albertosauroid' and 'ornithomimid' tarsus of Welles and Long 1974).

215. Ascending process of astragalus: lower than astragal body (0); higher than the astragal body (1); more than twice the height of astragal body (2) (modified from Welles and Long 1974)

The ascending process of the astragalus is a stout, anteroposteriorly broad structure that is lower than the astragal body in dinosaurs ancestrally, and this condition is retained in several theropods (Text-fig. 49A–B; 'ceratosauroid' tarsus of Welles and Long 1974). In *Magnosaurus oxoniensis* (OUM J 13558), *Poekilopleuron* (Eudes-Deslongchamps 1838), *Allosaurus* (MOR 693), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), and baryonychids (MNN GDF unnumbered; undescribed specimen

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TEXT-FIG. 49. Theropod astragali and calcanei, illustrating several tarsal characters. A–B, *Liliensternus liliensterni*; MB R. 2175; left astragalo-calcaneum; anterior view and proximal view (reversed). C–D, *Allosaurus fragilis*; MOR 693; stereophotographs of left astragalo-calcaneum in anterior and proximal view. E, *Deinonychus antirrhopus*; YPM 5226; left astragalo-calcaneum; anterior view (stereophotographs). Abbreviations: asc proc, ascending process of the astragalus; ast, astragalus; calc, calcaneum; fib, facet for fibula; tib, facet for tibia. Scale bars represent 10 mm.



referred to *Suchomimus*) the ascending process is anteroposteriorly compressed and higher than the astragalar body (Text-fig. 49C–D; ‘allosauroid’ tarsus of Welles and Long 1974). In *Caudipteryx* (Ji *et al.* 1998), *Microvenator* (AMNH 3041), *Sinosauropteryx* (Currie, pers. comm. 1999), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, TMP 88.121.39, YPM 5226), ornithomimosaurids (AMNH 6570, 5385, ROM 851), oviraptorosaurs (Barsbold *et al.* 1990), therizinosauroids (IVPP V 11559; Barsbold and Maryanska 1990), troödontids (MOR 553S), and tyrannosaurids (AMNH 6554, 5227) the process is further compressed and plate-like, and it is at least twice as high as the astragalar body (Text-fig. 49E; ‘albertosauroid’ and ‘ornithomimoid’ tarsus of Welles and Long 1974).

Welles and Long (1974) defined the relative height of the ascending process of the astragalus by using the ratio of its size compared to the combined length of the tibia plus astragalus. A different measure, comparing the height of the ascending process with the height of the astragalar body, is used here in order that this character can be coded in taxa where the tibia may be unknown or incomplete.

216. Ascending process of astragalus: confluent or only slightly offset from astragalar body (0); offset from astragalar body by pronounced groove (1) (modified from Welles and Long 1974)

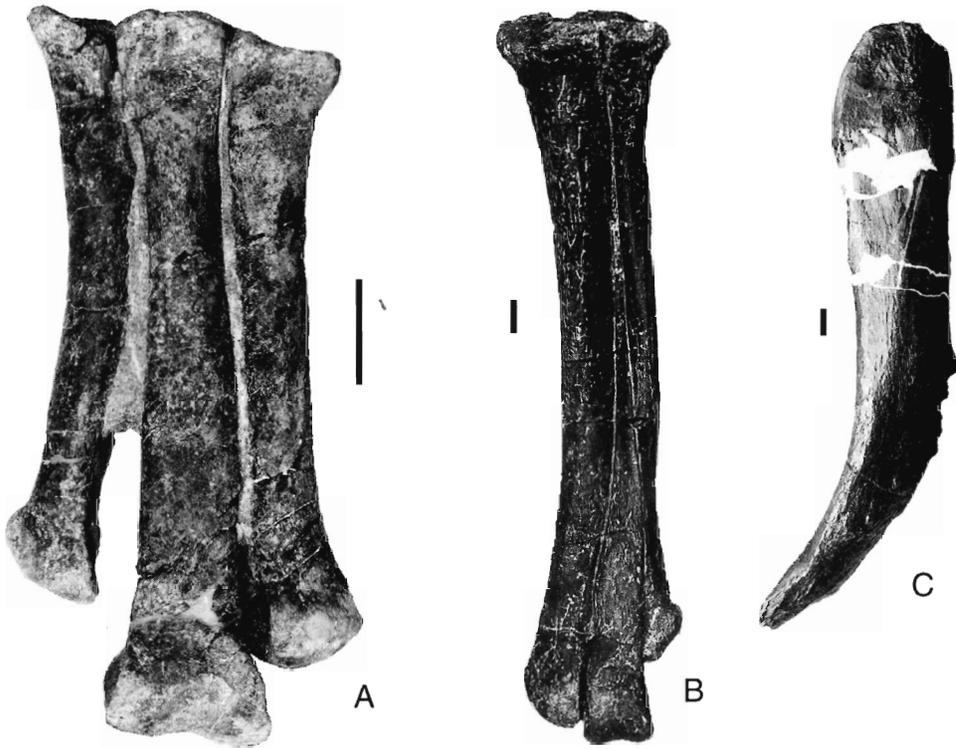
In basal dinosauriforms, ornithischians, sauropodomorphs, and many theropods the ascending process of the astragalus is confluent with the anterior rim of the astragalar condyles (Text-fig. 49A) or only slightly offset posteriorly from them (Text-fig. 49C). In a variety of theropods, including *Caudipteryx* (Ji *et al.* 1998), *Microvenator* (AMNH 3041), *Avimimus* (ROM 46144), *Bagaraatan* (Osmólska 1996), *Deltadromeus* (SGM-Din 2), birds (*Rahonavis*: UA 8656), dromaeosaurids (IGM 100/986, TMP 88.121.39, YPM 5226), ornithomimosaurids (AMNH 6570, 5385, ROM 851), oviraptorosaurs (Barsbold *et al.* 1990), troödontids (IVPP V 9612, MOR 553S), and tyrannosaurids (AMNH 6554, 5227), the ascending process of the astragalus has a pronounced groove at its base anteriorly (Text-fig. 49E). This groove is almost straight in tyrannosaurids (the ‘albertosauroid’ tarsus of Welles and Long 1974), but arched to various degrees in other theropods (the ‘ornithomimoid’ tarsus of Welles and Long 1974).

217. Astragalar condyles: almost entirely below tibia and face distally (0); significantly expanded proximally on anterior side of tibia and face anterodistally (1) (Serenó *et al.* 1996)

In dinosauriforms ancestrally, the astragalus covers the distal surface of the tibia and only the ascending process keys into a slot on the anterior part of the facet on the distal end of the tibia; the condyles for the articulation with the distal tarsals face almost entirely distally. This condition is retained in ornithischians, sauropodomorphs, *Herrerasaurus* (Novas 1993), *Coelophysis* (Welles and Long 1974), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), and *Syntarsus* (QG 1, 184, 782). In *Ceratosaurus* (UMNH VP 5278, YPM 4681), *Elaphrosaurus* (MB dd unnumbered), and abelisaurids (Martínez *et al.* 1987) the articular condyles of the astragalus are also located entirely below the tibia (Text-fig. 49A), but the ascending process of the astragalus seems to show an intermediate stage between the theropods listed above and all other theropods, in which the process overlaps the anterior side of the distal tibia rather than fitting into a distal slot. In all other theropods, the articular condyles of the astragalus are expanded proximally so that they face anterodistally and part of the astragalar body is situated anterior to the distal end of the tibia (Text-fig. 49C–E).

218. Horizontal groove across astragalar condyles anteriorly: absent (0); present (1) (Welles and Long 1974)

In several theropods, including *Magnosaurus oxoniensis* (OUM J 13558), *Allosaurus* (MOR 693), *Ceratosaurus* (UMNH VP 5278, YPM 4681), *Elaphrosaurus* (MB dd unnumbered), sinraptorids (Currie and Zhao 1993b), *Torvosaurus* (Britt 1991), *Afrovenator* (UC OBA 1), *Deltadromeus* (SGM-Din 2), and abelisaurids (Martínez *et al.* 1987), a broad, shallow groove is present on the astragalar body. This groove runs across the anterior face of the astragalar condyles (Text-fig. 49C). It is unknown in ornithischians, sauropodomorphs, and all other theropods.



TEXT-FIG. 50. Theropod metatarsals, illustrating several tarsal characters. A, *Allosaurus* sp.; DNM 116; left metatarsals II–IV, anterior view. B, *Troödon formosus*; MOR 748; right metatarsals II–IV, anterior view. C, *Albertosaurus sarcophagus*; ROM 807; left metatarsal V; lateral view, proximal is to the right. Scale bars represent 50 mm (A) and 10 mm (B–C).

219. Calcaneum: without facet for tibia (0); well-developed facet for tibia present (1) (Serenó *et al.* 1996)

In dinosauriforms ancestrally, the tibia articulates only with the astragalus (Text-fig. 49B), and this condition is retained in sauropodomorphs, *Herrerasaurus* (Novas 1993), *Coelophysis* (UCMP V 82250), *Liliensternus liliensterni* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), and *Syntarsus* (QG 1, 184, 782). In ornithischians and all other theropods the tibia also articulates with the calcaneum, and a well-developed facet for the tibia is present on the latter element (Text-fig. 49D).

220. Metatarsal III: subequal in width to Mt II and IV proximally (0); pinched between II and IV and not visible in anterior view proximally (arctometatarsalian condition of Holtz 1994b) (1)

In most dinosaurs, including the majority of theropods, metatarsal III is a stout element that is subequal in width to metatarsals II and IV proximally (Text-fig. 50A). In a variety of theropods, including *Caudipteryx* (NGMC 97-4-A, 97-9-A; contra Ji *et al.* 1998), *Avimimus* (ROM 46144), troödontids (IVPP V 9612, TMP 92.36.575), and tyrannosaurids (AMNH 6554, 5432, ROM 807), the metatarsus is strongly modified. In these taxa, metatarsal III has a broad distal end with a well-developed articulation for the digital phalanx 1, but it narrows rapidly proximally and becomes much narrower than metatarsals II and IV. At the proximal end of the metatarsus, metatarsals II and IV contact each other anteriorly and thus exclude metatarsal III from the anterior tarsal articulation in anterior view (Text-fig. 50B). This morphology has been termed the arctometatarsalian pes by Holtz (1994b).

In ornithomimosaur and oviraptorosaur the situation is somewhat uncertain. Representatives of the crown group ornithomimosaur, the ornithomimids, show a well-developed arctometatarsalian condition (e.g. AMNH 6565), but the metatarsus seems to have a more primitive morphology in more basal members of this clade, including *Garudimimus* (Barsbold 1981), and *Harpymimus* (Barsbold and Perle 1984). In oviraptorosaurs the arctometatarsalian condition is present in caenagnathids (ROM 781, TMP 82.16.6), but not in oviraptorids (IGM 100/9/72). However, in both basal ornithomimosaur and oviraptorids metatarsal III is considerably more slender proximally than either II or IV, and it cannot be determined whether this is the primitive character state for these clades, or a reversal from an ancestral arctometatarsalian morphology. Therefore, the character is coded as uncertain in these two groups.

221. Pedal digit IV: significantly shorter than III and subequal in length to II (0); significantly longer than II and only slightly shorter than III (1) (Gauthier 1986)

In theropods ancestrally, pedal digit III is the longest element of the pes, and the pes is more or less symmetrical so that digits II and IV are subequal in length (Gauthier 1986). This condition is retained in the majority of theropods. In the theropod clades Dromaeosauridae (IGM 100/985, 100/986) and Troodontidae (IVPP V 9612) digit IV is significantly longer than digit II and closer to III in length. In the basal bird *Archaeopteryx* pedal digit IV is also longer than digit II, but the difference is not as marked as in dromaeosaurids and troodontids (see Wellnhofer 1974, p. 205, table 1).

222. Metatarsal I: contacts the ankle joint (0); reduced, elongated splint-like, attached to Mt II and not reaching the ankle joint (1); broadly triangular and attached to the distal part of Mt II (2) (modified from Gauthier 1986)

In archosaurs ancestrally, metatarsal I is in contact with the ankle joint, and this condition is retained in basal dinosauriforms, ornithischians, sauropodomorphs, *Eoraptor* (ROM 44686), and *Herrerasaurus* (Novas 1993). In all other theropods metatarsal I is strongly reduced and attached to the medial side of metatarsal II. In advanced therizinosauroids metatarsal I contacts the ankle joint, but this is not the case in the basal therizinosaur *Beipiaosaurus* (IVPP V 11559); thus, the character is coded as uncertain in this group.

Within theropods, two different morphologies can be observed in metatarsal I. In *Coelophysis* (Colbert 1989), *Dilophosaurus* (UCMP V 4214), *Segisaurus* (UCMP V 338), and *Syntarsus* (QG 1), the element is elongate and splint-like, whereas it is further reduced, broadly triangular and more distally placed in all other theropods. The situation is unclear in *Sinosauropteryx* and *Avimimus*, although it can be said with some certainty that either character state 1 or 2 was present.

223. Metatarsal V: with rounded distal articular facet (0); strongly reduced and lacking distal articular facet (1); short, without articular surface, transversely flattened and bowed anteriorly distally (2) (modified from Gauthier 1986)

In archosaurs ancestrally, sauropodomorphs and *Herrerasaurus*, metatarsal V has a rounded distal articular facet and bears at least one phalanx. In the basal dinosauriform *Marasuchus* (Serenio and Arcucci 1994) and all theropods, metatarsal V is reduced to a distally tapering splint and does not bear any phalanges. The metatarsal may be very slender and rod-like, as in *Coelophysis* (Colbert 1989), *Segisaurus* (UCMP V 338), *Syntarsus* (QG 1), *Avimimus* (ROM 46144), birds (*Archaeopteryx*: Eichstätt specimen), dromaeosaurids (YPM 5217, 5263), oviraptorosaurs (IGM 100/9/72), and troodontids (IVPP V 9612), or strongly compressed transversely and considerably bowed anteriorly towards the distal end (Text-fig. 50c), as in *Dilophosaurus* (UCMP V 4214), *Allosaurus* (DNM 116, MOR 693), *Compsognathus* (BSP A.S. I 563), sinraptorids (Currie and Zhao 1993b), *Afrovenator* (UC OBA 1), *Deltadromeus* (SGM-Din 2), ornithomimosaur (ROM 852), and tyrannosaurids (AMNH 5423). The situation in *Sinosauropteryx* and therizinosauroids is somewhat uncertain, but character state 1 or 2 was present in these taxa.

224. Pedal digit II: not specialized if compared to other digits (0); highly specialized: shortened, hyperextensible, phalanx II-2 with pronounced ventral heel proximally, unguis enlarged, transversely flattened and strongly curved (1) (modified from Ostrom 1969b)

In ornithischians, sauropodomorphs, and the majority of theropods pedal digit II is used for locomotion and is thus not specialized when compared to other pedal digits. In dromaeosaurids (IGM 100/985, 100/986, MOR 660, YPM 5205) and troodontids (IVPP V 9612, MOR 553S), the second pedal digit is strongly modified and was not used in locomotion. The digit is shortened and the strongly ginglymoidal distal articular facets of phalanges II-1 and II-2 indicate that it was hyperextensible and held off the ground during locomotion. Phalanx II-2 has a pronounced ventral heel proximally and the unguis is enlarged and transversely flattened.

A very similar morphology is found in the second digit of the basal bird *Rahonavis* (UA 8656), but I could not confirm Paul's (1988a) claim that the second pedal digit was also hyperextensible in *Archaeopteryx*; all of the specialisations noted above are absent in this taxon. Thus, the character is coded as uncertain in birds.

### PHYLOGENETIC ANALYSIS

Detailed investigation of theropod specimens and the literature resulted in the construction of a data matrix of 57 taxa and 224 characters (see Appendix). The matrix includes three outgroup taxa and 56 saurischian ingroup taxa. Of the 224 characters, 87 (38.84%) are from the cranial skeleton, 43 (19.2%) from the axial skeleton, 34 (15.18%) from the pectoral girdle and forelimb, 59 (26.34%) from the pelvic girdle and hindlimb, and 1 character (0.45%) is an integumentary character.

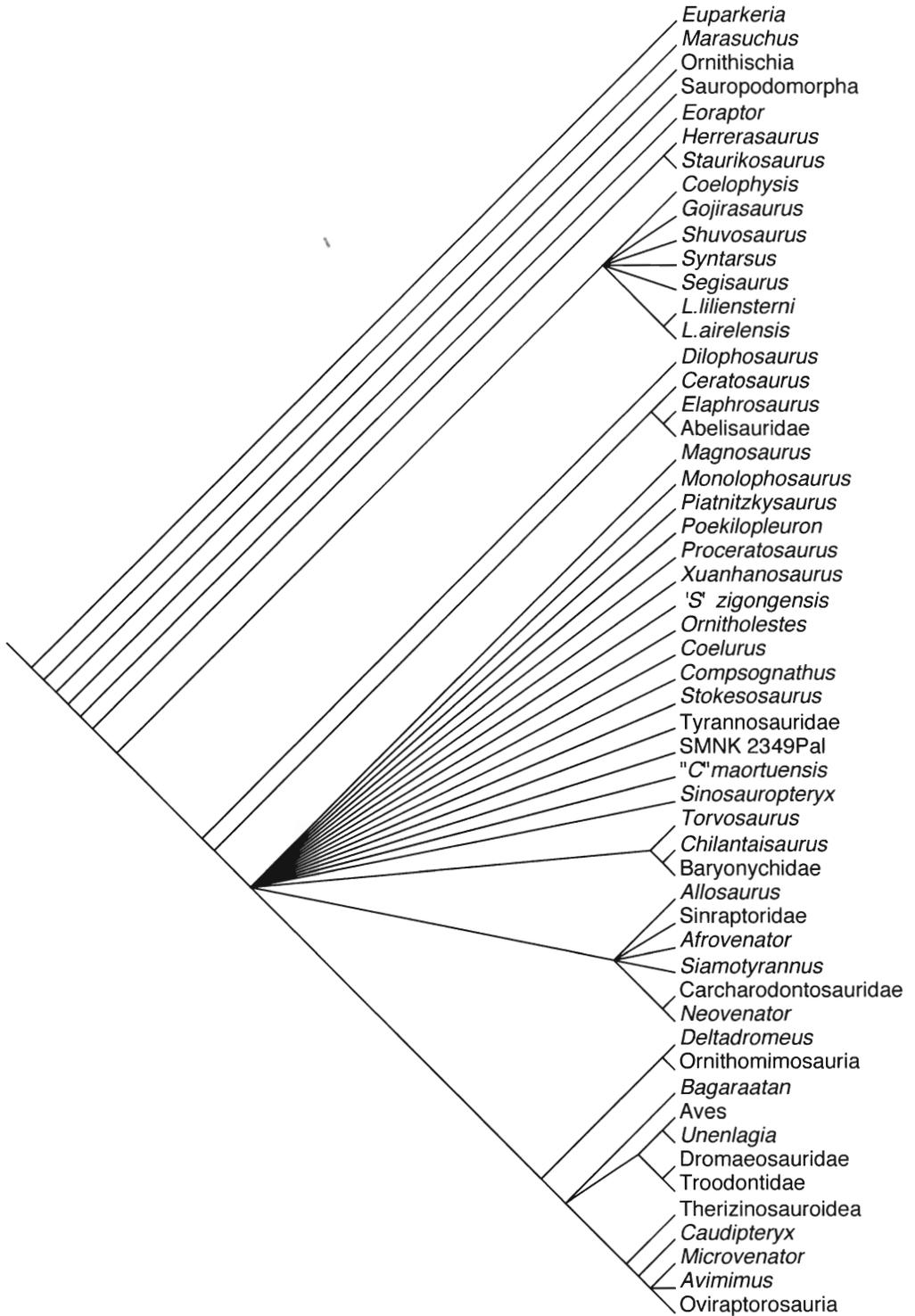
The application of safe taxonomic deletion criteria (Wilkinson 1995) resulted in the exclusion of several taxa that shared identical character codings with other OTUs for all codable characters, but are less well known. The deleted taxa are: *Procompsognathus* (identical with *Coelophysus* and *Syntarsus*); *Ligabueino* and *Velocisaurus* (identical with *Elaphrosaurus*)

If included in the analysis, these taxa would thus appear in the same position as other taxa with identical character codings. However, since all of these taxa are very poorly known, their inclusion in the analysis would result in a strong increase in the number of equally parsimonious trees.

The reduced data set of 54 taxa still contained a high amount of missing data: of the total 12096 data points in the matrix, 5795 (47.9%) were question marks. The remaining codings were 3735 (30.9%) character state '0', 2075 (17.2%) state '1', 359 (3%) state '2', and 30 (0.25%) state '3'. The remaining 102 (0.84%) data points were uncertainties, indicated by codings such as '0/1', '1/2'. The highest amount of missing data was found in *Stokesosaurus* (94.2%), *Gojirasaurus* (90.6%), *Chilantaisaurus tashuikouensis* (90.2%), *Poekilopleuron* (89.7%), *Liliensternus airelensis* (86.6%), and *Siamotyrannus* (86.2%). *Bagaraatan*, '*Chilantaisaurus*' *maortuensis*, *Deltadromeus*, *Neovenator*, *Proceratosaurus*, SMNK 2349 Pal, *Unenlagia*, and *Xuanhanosaurus* were also coded for less than 25 per cent of characters. Not surprisingly, higher category taxa were generally well represented, since character codings could be based on a variety of included taxa. However, the least amount of missing data (0.4%: a single character) was found in the genus *Allosaurus*, in which every detail of the skeletal anatomy is known. Further well-represented taxa were dromaeosaurids (1.3% missing data), ornithomimosaurs (1.8%), sauropodomorphs (3.1%), tyrannosaurids (3.6%), birds (5.4%), ornithischians (5.8%), and *Syntarsus* (5.8%). The relatively high amount of missing data in birds reflects the attempt to code characters mainly from the most basal members of this clade. The highest amounts of missing data in higher level taxa were found in carcharodontosaurids (36.2%), therizinosaurs (27.7%), and baryonychids (26.3%).

The matrix was analyzed using the heuristic search algorithm in PAUP 3.1.1 (Swofford 1992) and PAUP 4.0b2a (Swofford 1999). The heuristic search used the tree-bisection reconnection (TBR) branch swapping algorithm. Starting trees were obtained via stepwise addition, and the addition sequence was set to random, with 100 replicates.

The analysis hit a problem at 32700 equally parsimonious trees, when PAUP 3.1.1 was unable to store more trees (32766 trees in PAUP 4.0b2a). This tree number represents a software limitation of the versions



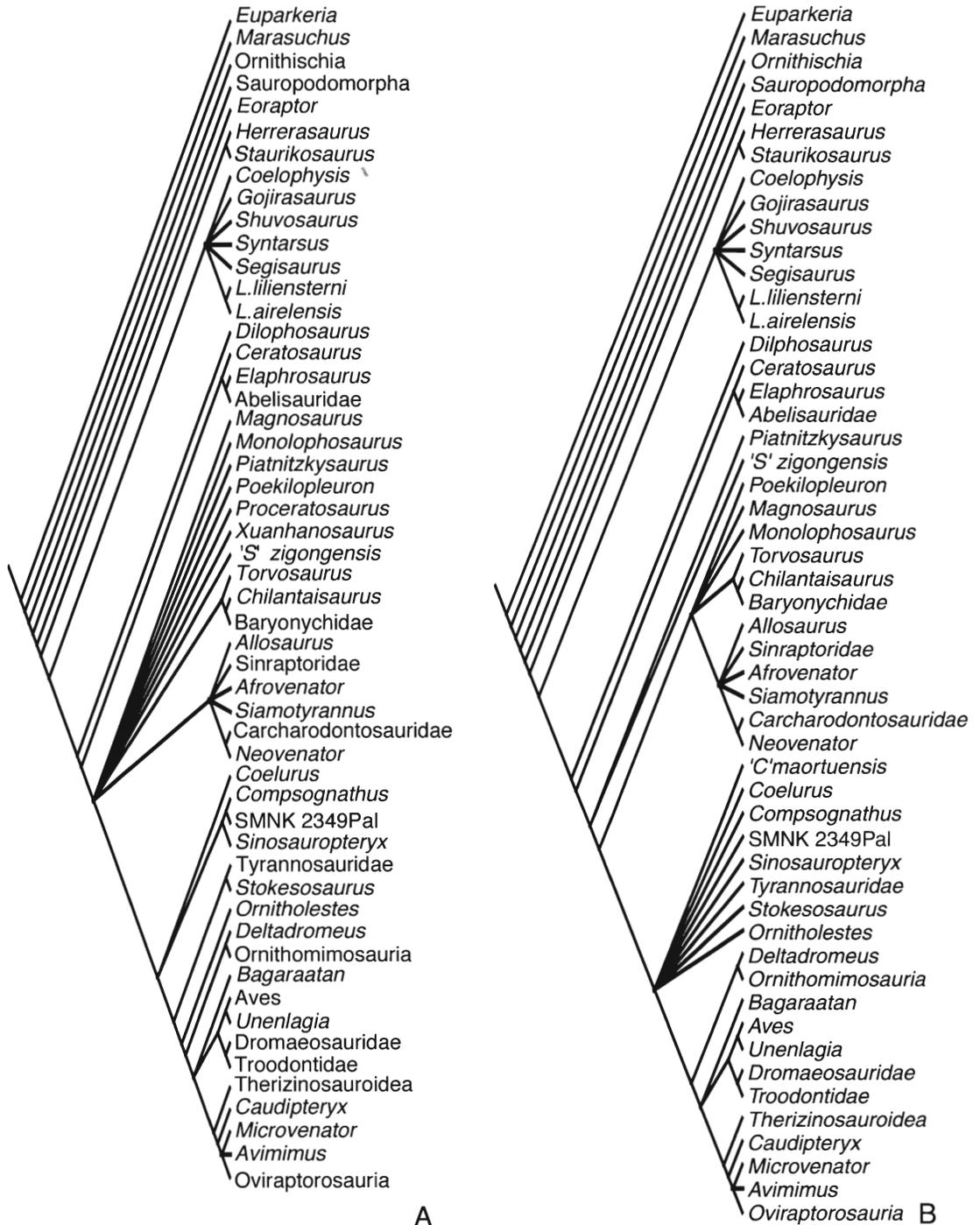
of the software used (Wilgenbusch, pers. comm. 2000). Thus, several analyses to the tree limit were run, and a strict consensus tree of all analyses is shown in Text-fig. 51. The trees had a length of 657 steps, a consistency index (CI) of 0.417, a retention index (RI) of 0.746, and a rescaled consistency index (RCI) of 0.311. One tree set of 32766 trees that resulted in the same strict consensus tree as the combined data from all analyses was subjected to a reduced consensus analysis, using STRICT 2.0 (Thorley and Wilkinson 1997). This reduced consensus analysis resulted in seven simple reduced consensus trees that showed a considerably higher degree of resolution than the strict consensus tree (Text-fig. 52). However, it must be noted that the reliability of these results is reduced by the possibility that the original tree file did not contain all shortest tree morphologies.

In order to solve the problem of tree limitation, several taxa were deleted from the matrix. Reanalysis of the data after deletion of all taxa with fewer than 20, 25, and 33 per cent coded characters resulted in strict consensus trees that were better resolved than the strict consensus tree of the complete data set, but did not contradict the latter nor its reduced consensus trees in any way. The only significant change in the analysis of the data set with all taxa with fewer than 33 per cent coded characters deleted was that the deletion of *Shuvosaurus* resulted in a loss of resolution at the base of the theropod cladogram. This aspect is discussed below.

Three poorly known taxa that were identified as problematic were finally deleted to reduce the number of equally parsimonious trees below the 32766 threshold, to be certain that all shortest trees were recovered: '*Chilantaisaurus*' *maortuensis*, *Siamotyrannus*, and *Xuanhanosaurus*. These taxa were mainly chosen because their deletion did not change the basic relationships between other theropod taxa (as expressed in the strict consensus and reduced consensus trees of the 32766 trees), but resulted in a considerable reduction of the number of equally parsimonious trees. Furthermore, *Xuanhanosaurus* only differs from '*Szechuanosaurus*' *zigongensis* in the distribution of missing data; all characters that are coded for both taxa are identical. *Xuanhanosaurus* certainly represents a basal tetanuran, but it is uncertain whether it lies at the base of Tetanurae, or is a basal carnosaur. Further considerations that led to the exclusion of *Siamotyrannus* were that the taxon is only known from poor material that has not been described in detail (Buffetaut *et al.* 1996). Since I have not seen the material, some uncertainty thus remain in the codings for this taxon. It is interesting to note, however, that the consensus tree for the complete data matrix suggests that this taxon does not represent a primitive tyrannosaur, as argued by Buffetaut *et al.* (1996), but an allosauroid. '*Chilantaisaurus*' *maortuensis* has a unique combination of basal tetanuran and more advanced coelurosaurian characters that makes a placement within the basal taxa of coelurosaurs difficult. Although this taxon certainly represents a basal coelurosaur (Text-fig. 52B), its inclusion in the analysis results in a loss of resolution at the base of this clade. As noted above, its exclusion from the data matrix did not change the interrelationships of other basal coelurosaurs as expressed by the reduced consensus tree of the complete data set.

The pruned data matrix of 51 taxa and 224 characters was reanalyzed using the same software and software settings as described above. The analysis resulted in 5544 equally parsimonious trees with a length of 652 steps. The trees have a CI of 0.42, an RCI of 0.314, and an RI of 0.748. The strict consensus tree of these trees exhibits remarkably good resolution (Text-fig. 53), and this was further improved by the application of reduced consensus methods.

Bootstrap support values for the pruned data matrix were calculated using the bootstrap search option in PAUP 4.0b2a with multiple replicates of a heuristic search with simple addition sequence. For temporal reasons, only 100 replicates could be carried out in the bootstrap analysis (processing time: 484 hours on an Apple Macintosh PowerBook G3 with 333 MHz and 128 MB RAM). Bootstrap support for many nodes is low (<50%), but some nodes are remarkably well supported by the current data (Text-fig. 53). The best supported nodes are Neotheropoda (96%), Ceratosauria (94%), Abelisauroida (92%), node 35 (92%), node 11 (90%), Maniraptora (89%), and Deinonychosauria (89%).



A decay analysis of the pruned data matrix was also constrained by the tree limitation, since an analysis that kept all trees that are one step longer than the shortest tree resulted in more than 32766 trees. Many nodes are only poorly supported, which reflects the high amount of missing data, but also homoplasy in the data set.

### TREE DESCRIPTION

To reduce the amount of polytomies in the phylogenetic hypothesis, the following tree description is based on a reduced consensus tree of 5544 trees derived from an analysis of a matrix of 51 taxa and 224 characters (Text-fig. 54). The original trees have a length of 652 steps, a consistency index of 0.42, a rescaled consistency index of 0.314, and a homoplasy index of 0.58. STRICT excluded three taxa from the trees (*Shuvosaurus*, *Segisaurus*, and *Poekilopleuron*), which increased the resolution of the consensus tree by four nodes. However, characters that are present in these animals and interpreted as synapomorphies of a certain clade, are mentioned in the tree description at the given nodes. The strict consensus tree of all 5544 trees (Text-fig. 53) shows that *Shuvosaurus* and *Segisaurus* fall within Coelophysoidea, whereas *Poekilopleuron* is a basal carnosaur.

The interrelationships between the outgroup taxa *Euparkeria*, *Marasuchus* and *Ornithischia* were not analyzed in this study, and characters that may have resolved the interrelationships of these taxa were not included in the matrix. Thus, the tree description begins at the node 'Saurischia'. The description includes synapomorphies and, under separate headings, further possible apomorphies under delayed and accelerated transformation (DELTRAN and ACCTRAN). Character states at the nodes are stated.

#### *Node 1. Saurischia* Seeley, 1887

*Included taxa.* Sauropodomorpha Huene, 1932; Theropoda Marsh, 1881a.

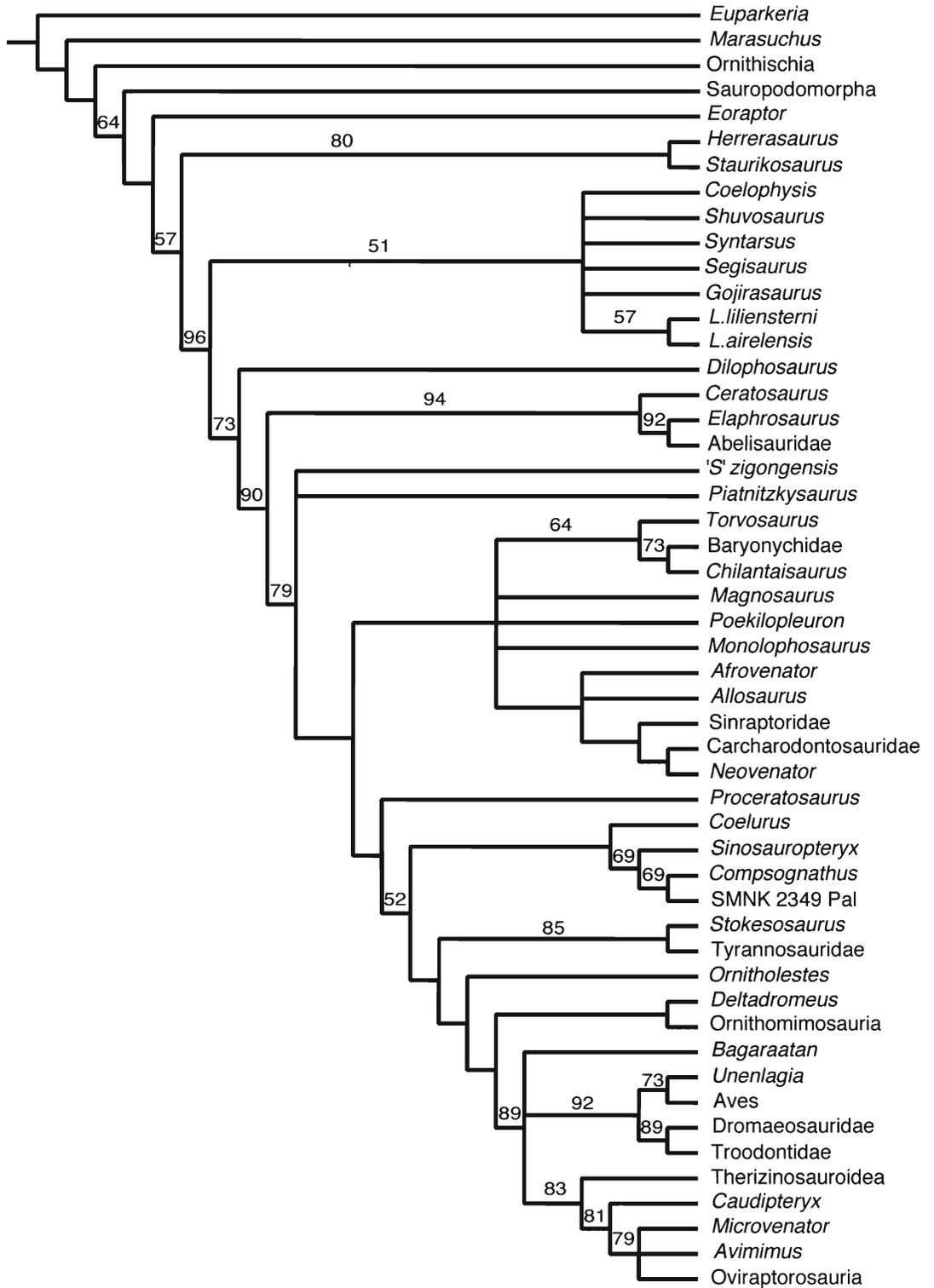
*Known temporal range.* Late Triassic (Carnian)–Recent.

*Synapomorphies.* Character 6 (0→1): reduction of the subnarial posterior process of the premaxillary. Reversed in *Herrerasaurus* and ornithomimosaur. Character 29 (0→1): dorsoventral elongation of the lacrimal. Reversed in *Herrerasaurus*. Character 49 (0→1): quadrate foramen almost completely enclosed in the quadrate. Convergently developed at node 21 and in *Ornitholestes*. Character 52 (0→1): paroccipital processes directed ventrolaterally. Character 78 (0→1): completely enclosed foramen (anterior mylohyoid foramen) present in the ventral part of the splenial. This character state might be reversed in ornithomimosaur and oviraptorosaurs. Character 103 (0→1): presence of a hyosphene-hypantrum articulation in the dorsal vertebrae. Reversed in crown-group birds (Chiappe *et al.* 1996) and a similar articulation is convergently present in some crurotarsans (e.g. Chatterjee 1985). Character 149 (0→1): distal condyles of Mc I strongly asymmetrical. Reversed in *Herrerasaurus*.

*Possible additional apomorphies under ACCTRAN.* Character 11 (0→1): ascending process of the maxilla offset from anterior rim of maxillary body, and anterior projection of maxillary body shorter than high. Since character 11 is an ordered character with three character states, and basal sauropodomorphs have state 2, and the basal theropod *Eoraptor* state 1, the interpretation of this character at the basis of the tree is equivocal. Under ACCTRAN, this character state is regarded as a saurischian synapomorphy that is reversed at node 3, while DELTRAN interprets it as a convergent development in sauropodomorphs and *Eoraptor*. Since the anterior projection of the maxillary body is only slightly developed in *Eoraptor*, and it is significantly different from the development of this structure in sauropodomorphs, a convergence is regarded as being more likely here. Character 61 (0→1): mid-cerebral vein exits the braincase through a separate foramen anterodorsal to the trigeminal foramen. The interpretation of this character is difficult because it cannot be determined in most basal theropods. A separate foramen is clearly present in the basal sauropodomorph

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TEXT-FIG. 52. Two selected reduced consensus trees from the analysis of the complete data set. A, after deletion of '*Chilantaisaurus*' *maortuensis*. B, after deletion of *Proceratosaurus* and *Xuanhanosaurus*.



*Plateosaurus* (GPIT Skelett 1) and all theropods examined with the possible exception of *Syntarsus* (QG 194) and the basal bird *Archaeopteryx* (Elzanowski and Wellnhofer 1996). Unfortunately, the course of the mid-cerebral vein could not be determined on the medial side of any of the *Syntarsus* braincases examined. Given this uncertainty in the interpretation of this character in basal theropods, the separation of the foramen for the mid-cerebral vein from the trigeminal foramen is tentatively regarded as a true saurischian synapomorphy, unless new braincases of other basal theropods might prove the opposite. The probable absence of a separate foramen in *Archaeopteryx* is interpreted as a reversal under both ACCTTRAN and DELTRAN. Character 92 (0→1): cervical epiphyses well developed. This character state was regarded as a theropodan synapomorphy by Gauthier (1986) and Sereno and Novas (1993), and this is also the interpretation supported under DELTRAN. However, cervical epiphyses are well developed in at least some basal sauropodomorphs (e.g. *Thecodontosaurus*: BMNH RU P 24; *Plateosaurus*: MB Skelett 25). Although they are only poorly developed in other specimens (e.g. *Plateosaurus*: GPIT Skelett 1), the presence of well-developed epiphyses is regarded as a saurischian synapomorphy here.

## Node 2. Theropoda Marsh, 1881a

*Included taxa.* *Eoraptor* Sereno, Forster, Rogers and Monetta, 1993; *Herrerasauridae* Benedetto, 1973; Neotheropoda Bakker, 1986.

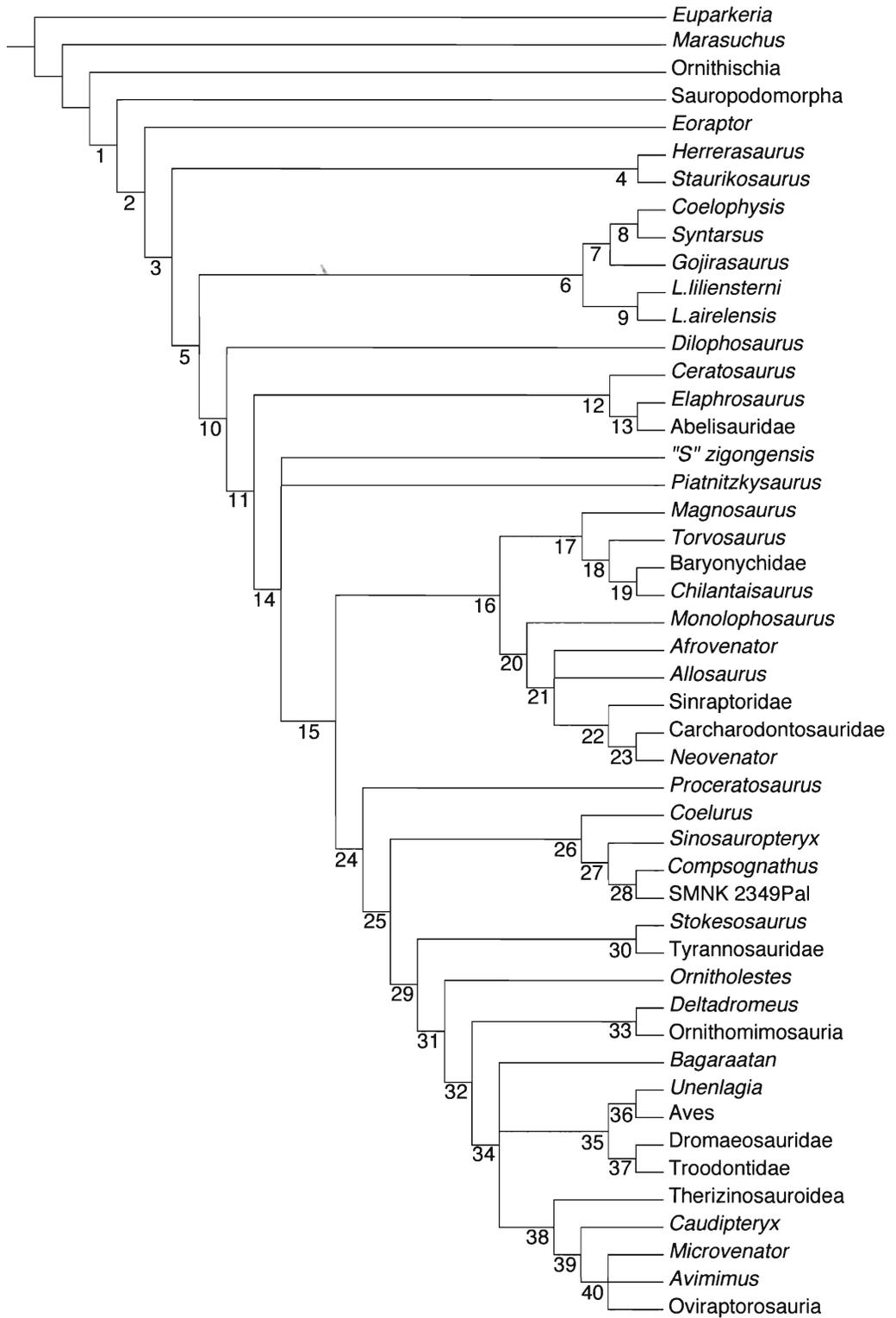
*Known temporal range.* Late Triassic (Carnian)–Recent.

*Synapomorphies.* Character 153 (0→1): fifth digit of the manus absent, and fourth digit reduced to the metacarpal and only one phalanx. Character 155 (0→1): presence of deep extensor pits on the dorsal surface of the distal end of the metacarpals. Character 159 (0→1): penultimate phalanx of the second digit of the manus longer than first phalanx.

*Possible additional apomorphies under ACCTTRAN.* Character 24 (0→1): jugal excluded from the rim of the antorbital fenestra. The jugal is excluded from the internal antorbital fenestra in *Eoraptor* and possibly *Syntarsus*, but the character is unknown in all other basal theropods, with the exception of *Herrerasaurus*, where the jugal participates in the rim of the fenestra. Since the latter character state is also found in the vast majority of theropods, it is rather questionable whether state 1 of character 24 really represents a synapomorphy of theropods. It seems more likely that this state was acquired independently in *Eoraptor*, oviraptorosaurs, *Ceratopsaurus*, *Allosaurus*, and possibly *Syntarsus*. Character 28 (0→1): lacrimal inverted L-shaped and broadly exposed on the skull roof. This character state is found in *Eoraptor* and all other theropods, with the exception of *Herrerasaurus*. Therefore, ACCTTRAN interprets it as a theropod synapomorphy that is reversed in *Herrerasaurus*, while DELTRAN regards it as a neotheropodan synapomorphy that is convergently present in *Eoraptor*. The question of which interpretation is correct, can only be solved by new material of other basal theropods. Character 45 (0→1): quadratojugal process of the squamosal at least slightly expanded. This character state is present in most theropods, including basal forms such as *Herrerasaurus*, but, unfortunately, it is unknown in *Eoraptor*. Whether it represents a synapomorphy of theropods (ACCTTRAN), or of the unnamed node 3 (DELTRAN), can only be shown by further material of the most basal theropod, *Eoraptor*. Character 87 (1→0): teeth without a basal constriction. This character state is based on the ACCTTRAN interpretation that a basal constriction in the teeth is a dinosaurian synapomorphy, since it is present in ornithischians and basal sauropodomorphs. However, since the teeth are highly modified for a herbivorous diet in these two groups, and the vast majority of archosaurs with the exception of some crocodiles and advanced coelurosaurs do not have a basal constriction, this interpretation seems unlikely. It is more convincing to assume that ornithischians and basal sauropodomorphs acquired the constriction independently (as suggested by DELTRAN), in connection with the convergent adaptation towards a herbivorous diet. Character 96 (0→1): presence of camerate internal pneumatic chambers in the cervical vertebrae. Camerate or camellate internal pneumatic chambers are present in many theropods, but our knowledge about their distribution is still patchy. Their presence in basal theropods is still unknown, but since they are known to be present in *Coelophysis* and basal tetanurans, ACCTTRAN assumes that they were present in theropods ancestrally. Although the final solution to this question can only come from studies of the internal

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TEXT-FIG. 53. Strict consensus tree resulting from the analysis of the pruned data matrix with 51 taxa. Numbers at the nodes indicate bootstrap support values in branches that have more than 50 per cent support. The consensus tree is based on 5544 trees of 652 steps (CI 0.42, RI 0.748, RCI 0.314).



architecture of the cervical vertebrae in the most basal theropods, *Eoraptor* and herrerasaurids, the absence of other pneumatic features in the cervicals of these taxa casts doubt on this interpretation. Character 122 (0→1): elongation of the distal caudal prezygapophyses. Unknown in *Eoraptor*. Character 128 (0→1): presence of a cranial process at the bases of the chevrons. Unknown in *Eoraptor* and herrerasaurids. Character 131 (0→1): presence of a furcula. Unknown in *Eoraptor* and herrerasaurids. The lack of a furcula in the otherwise fairly complete and articulated type skeleton of *Eoraptor* and in all known specimens of *Herrerasaurus* might indicate that the presence of a furcula is a neotheropodan synapomorphy, as suggested by DELTRAN, rather than a theropodan synapomorphy. However, unfused clavicles have not been identified in these specimens either; thus, the absence of a true furcula in these animals is based on negative evidence.

*Remarks.* As in Sereno (1998) and Padian *et al.* (1999), the name Theropoda is used here for a stem-based clade to retain the principal dichotomy of the Saurischia that has been accepted since Colbert's (1964) influential work on saurischian systematics.

### Node 3. unnamed node

*Included taxa.* Herrerasauridae Benedetto, 1973; Neotheropoda Bakker, 1986.

*Known temporal range.* Late Triassic (Carnian)–Recent.

*Synapomorphies.* Character 23 (0→2): sublacrimal part of jugal expanded. Character 109 (0→1): neural spine of posterior dorsals significantly higher than long. Reversed in several theropod clades, including coelophysids, *Elaphrosaurus*, coelurids, and *Avimimus*. It is convergently present in a variety of ornithischians and sauropods, and might thus be regarded as a rather weak synapomorphy. Character 158 (0→1): phalanx I-1 longer than Mc I. Character 160 (0→1): penultimate phalanx of the third digit of the manus longer than more proximal phalanges.

*Possible additional apomorphies under ACCTRAN.* Character 11 (1→0): ascending process of the maxillary confluent with the anterior rim of the maxillary body; see node 1 (Saurischia). Character 24 (1→2): jugal with anterior process that extends anteriorly below the antorbital fenestra. Whether this character state change really represents a change from state 1 to state 2, or from state 0 to 2 depends on whether one accepts the state change from 0 to 1 at node 1 (Saurischia) for this character (see discussion there). However, an anterior process is present in the jugal of the majority of theropods, including *Herrerasaurus*, and thus the acquisition of character state 2 of character 24 most probably represents a synapomorphy of this node. Character 184 (0→1): presence of an expanded pubic boot. A pubic boot is present in herrerasaurids and most other theropods, with the exception of coelophysoids and the *Torvosaurus*–baryonychid clade. Whether the presence of a pubic boot represents a synapomorphy at this node, or at node 10 (DELTRAN), cannot be judged at present. There are differences in the development of the pubic boot in herrerasaurids and later theropods, but it is unclear if these differences indicate convergence or just represent a synapomorphy of herrerasaurids. The absence of a pubic boot in *Torvosaurus* and baryonychids clearly represents a reversal. Character 198 (0→1): lesser trochanter spike-like or developed as trochanteric shelf. The lesser trochanter is poorly developed in prosauropods where it usually forms a low, rounded longitudinal ridge. In comparison with this morphology, the lesser trochanter in *Herrerasaurus* and *Staurikosaurus* is more pronounced, and a trochanteric shelf is present in some individuals. In this respect, these animals represent an intermediate stage between the morphology found in basal sauropodomorphs on the one hand, and in coelophysoids and *Dilophosaurus* on the other. Therefore, the question whether this character state represents a synapomorphy at this node, or at node 5 (Neotheropoda), depends on whether the character state in herrerasaurids is regarded as 0 or 1. Character 211 (0→1): insertion area of m. iliofibularis on the fibula developed as an anterolateral tubercle. As in character 198, the situation is unclear because the exact character

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TEXT-FIG. 54. Reduced consensus tree of the pruned data matrix after the deletion of *Shuvosaurus*, *Segisaurus*, and *Poekilopleuron*. Named nodes: 1, Saurischia; 4, Herrerasauridae; 5, Neotheropoda; 6, Coelophysoidea; 8, Coelophysidae; 9, *Liliensternus*; 12, Ceratosauria; 13, Abelisauroidae; 14, Tetanurae; 16, Carnosauria; 17, Spinosauroidae; 20, Allosauroidae; 24, Coelurosauria; 26, Coeluridae; 27, Compsognathinae; 30, Tyrannosauroidae; 34, Maniraptora; 37, Deinonychosauria.

state in herrerasaurids is unknown: *Herrerasaurus* shows a tubercle on the anterolateral side of the fibula (Novas 1993), but *Staurikosaurus* does not (Colbert 1970; Galton 1977). However, the tubercle seems to be less marked in *Herrerasaurus* than in later theropods, and thus this feature might have been missed in the descriptions and drawings of the less well-preserved *Staurikosaurus* fibula. However, no decision can be made here because I have not seen the original specimen of *Staurikosaurus*.

*Possible additional apomorphies under DELTRAN.* Character 45 (0→1): quadratojugal process of squamosal at least slightly expanded; see node 2 (Theropoda). Character 92 (0→1): cervical epiphyses well-developed; see node 1 (Saurischia). Character 122 (0→1): distal caudal prezygapophyses markedly elongated; see node 2 (Theropoda).

#### Node 4. Herrerasauridae Benedetto, 1973

*Included taxa.* *Herrerasaurus* Reig, 1963; *Staurikosaurus* Colbert, 1970.

*Known temporal range.* Late Triassic (Carnian).

*Synapomorphies.* Character 112 (1→0): posterior dorsal vertebral centra considerably shorter than high. Convergetly present in *Allosaurus*. Character 113 (1→0): two sacral vertebrae. This is regarded as a reversal of the dinosaurian synapomorphy: at least three sacral vertebrae. However, there are several problems associated with this interpretation. Ornithischians have five sacrals, and sauropodomorphs and *Eoraptor* three, but there is the possibility that the incorporation of further sacrals happened independently in these clades (see above). Thus, it seems possible that the addition of a third sacral vertebra is a neotheropodan synapomorphy that is convergetly present in ornithischians, sauropodomorphs, and *Eoraptor*, whereas herrerasaurids retained the ancestral condition. Character 116 (0→2): sacral ribs very massive and markedly expanded.

*Possible additional apomorphies under ACCTAN.* Character 6 (1→0): subnarial posterior process of the premaxilla wide, plate-like, and excludes the maxillary from the external nares. This is a reversal of a saurischian synapomorphy. Unknown in *Staurikosaurus*. Character 10 (0→1): maxillaries subparallel in dorsal view. Unknown in *Staurikosaurus*. Character 28 (1→0): lacrimal triangular in lateral view. Character 29 (1→0): lacrimal significantly shorter than the height of the orbit. Both these are reversals of saurischian synapomorphies and unknown in *Staurikosaurus*. Character 51 (0→1): mandibular joint positioned posterior to the quadrate head. Unknown in *Staurikosaurus*. Character 133 (0→1): no expansion at the distal end of the scapula. Unknown in *Staurikosaurus*. Character 149 (1→0): distal condyles of metacarpal I more or less symmetrical. Reversal of a saurischian synapomorphy. Unknown in *Staurikosaurus*. Character 150 (0→1): no expansion on the medial side of the proximal end of Mc II. Unknown in *Staurikosaurus* and convergetly present in *Liliensternus* and most coelurosaurs. Character 167 (0→1): opisthopubic pelvis. The pelvis is slightly opisthopubic in *Herrerasaurus*. In *Staurikosaurus* the exact orientation of this bone is unknown because of the incomplete preservation of the peduncles, but the morphology of the element indicates that it was probably retroverted as well. Character 185 (0→1): pubic boot narrow and with subparallel margins. This character state seems to be present in *Herrerasaurus* (Novas 1993), although this needs to be confirmed by my own observations of the actual specimen. Unknown in *Staurikosaurus*.

*Possible additional apomorphies under DELTRAN.* Character 184 (0→1): presence of a strongly expanded pubic boot; see node 3.

*Remarks.* The name Herrerasauridae is used for this clade here since it includes both taxa that were originally united in this family by Benedetto (1973).

#### Node 5. Neotheropoda Bakker, 1986

*Included taxa.* Coelophysoidea (Nopcsa, 1928); *Dilophosaurus* Welles, 1970; Ceratosauria Marsh, 1884; Tetanurae Gauthier, 1986.

*Known temporal range.* Late Triassic (Norian)–Recent.

*Synapomorphies.* Character 12 (0→1): maxillary antorbital fossa shallow and margins formed by low ridges only. This synapomorphy is reversed in abelisaurids, baryonychids, ornithomimosaur, and the therizinosaur-oviraptorosaur-clade. Character 57 (0→1): basisphenoid recess well developed. Reversed in troodontids and therizinosauroids; however, the basisphenoid is highly pneumatized in these taxa. Character 59 (0→1): presence of an anterior tympanic recess in the braincase. Character 65 (0→1): tetraradiate palatine. Character 88 (0→1): presence of pleurocoels in the cervical vertebrae. Character 106 (0→1): presence of pleurocoels in the anterior dorsal vertebrae. Reversed in *Elaphrosaurus* and *Avimimus*. Character 113 (1→2): more than three sacral vertebrae. This character state is convergently present in ornithischians and advanced sauropodomorphs. Character 120 (0→1): ventral groove present in anterior caudals. Reversed at node 13, and in *Magnosaurus*, baryonychids, and ornithomimosaur. Character 146 (0→1): presence of an enlarged distal carpal that overlaps the proximal ends of metacarpals I and II. Reversed in ornithomimosaur, in which the carpals are strongly reduced. Character 151 (0→1): shaft of Mc III considerably more slender than shaft of Mc II. Character 154 (0→1): third finger of the hand shorter than second finger. This character state is also present in sauropodomorphs, and was interpreted as a saurischian synapomorphy by Gauthier (1986). However, the inclusion of *Eoraptor* and herrerasaurids in the Theropoda in the present analysis leads to the interpretation that the presence of this state in sauropodomorphs represents a convergent development with that found in neotheropods. Character 166 (0→1): dolichoiliac ilium. Character 190 (0→1): presence of a notch between the obturator process of the ischium and the ischial shaft distally. Reversed in *Elaphrosaurus*, *Magnosaurus*, *Torvosaurus*, and coelurosaurs. Character 197 (0→1): presence of a deep ligament groove on the posterior surface of the femoral head that runs obliquely from the proximomedial part distolaterally and is bound medially by a well-developed posterior lip. Reversed in abelisaurids and *Avimimus*. Character 205 (0→1): presence of a cleft between the medial side of the proximal end of the tibia and the fibular condyle posteriorly. Reversed in *Bagaraatan* and *Avimimus*. Character 206 (0→1): presence of a ridge on the proximal end of the lateral side of the tibia for the attachment of the fibula. Character 208 (0→1): distal articular facet of tibia subrectangular in outline and with a small lateral process posteriorly. Character 222 (0→1): metatarsal I reduced, attached to Mt II and does not reach the ankle joint proximally. Reversed in the majority of therizinosauroids, but the morphology of the first metatarsal and the more typically neotheropodan situation in the oldest member of this clade (Xu *et al.* 1999) indicate that this is a secondary modification.

*Possible additional apomorphies under ACCTRAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares and angle between anterior margin and alveolar margin less than 70 degrees. Since this character state is present in coelophysids and *Dilophosaurus*, it is interpreted as a neotheropodan synapomorphy that is reversed at node 11 under ACCTRAN. However, the patchy distribution of this character state on the cladogram indicates that it is not very reliable for phylogenetic reconstructions. Character 6 (1→2): subnarial posterior process of premaxilla does not contact the nasals and maxilla participates in the rim of the external nares. A reduced subnarial process of the premaxilla is a saurischian synapomorphy (Gauthier 1986; see node 1). Whether the subnarial process of the premaxilla contacted the nasals or not is often difficult to determine because of the delicate nature of the tip of this process, which is rarely preserved. This at least partially accounts for the patchy distribution of character state 2 of this character, and makes it difficult to determine if state 2 represents a synapomorphy of neotheropodans. However, in most theropods, the maxillary participates in the rim of the external nares, even if it is flanked laterally by the reduced, rod-like process of the premaxilla. Character 8 (0→1): constriction between articulated premaxillaries and maxillaries present. A constriction between the premaxillaries and maxillaries is present in coelophysids and *Dilophosaurus*, and thus this character state is interpreted as a neotheropodan synapomorphy that is reversed at node 11 under ACCTRAN. DELTRAN interprets the presence of a constriction in these two taxa as convergence. Since the constriction seems to be correlated with the presence of a subnarial gap in *Syntarsus*, *Dilophosaurus*, and baryonychids (but not in oviraptorosaurs), the latter explanation seems to be more likely (see below). This is the first of a number of characters that are present in these two taxa. As discussed below, the phylogenetic position of *Dilophosaurus* depends on the inclusion or exclusion of *Shuvosaurus*, and if the latter taxon proves to be a non-theropodan archosaur, the interpretation of these characters might be different. Character 9 (0→1): subnarial gap present. Again, a subnarial gap is present in coelophysids and *Dilophosaurus*. However, the morphology of the subnarial gap differs in these two taxa: in coelophysids, the premaxillary has two short posterior processes that are separated by a short medial anterior process of the maxillary (*Syntarsus*: QG 193). The morphology of the subnarial gap in *Dilophosaurus* rather resembles the situation found in baryonychids: the premaxilla only has the usual subnarial

posterior process, and the medial anterior process of the maxilla is long, widened anteriorly and flexed downwards, so that it almost reaches the alveolar margin ventrally (UCMP V 6468). This structural difference indicates that the subnarial gap in coelophysids might not be homologous with the subnarial gap in *Dilophosaurus*. Unfortunately, good skull material for the basal coelophysoids included in the tree described here is not known, but further evidence for this interpretation is provided by *Shuvosaurus*. In this taxon, which is included in the Coelophyoidea according to the strict consensus tree of the more inclusive analysis, the premaxillary-maxillary articulation closely resembles that found in *Syntarsus*, but no subnarial gap is present. Character 22 (0→1): raised lateral margins of the nasals. As in the characters discussed above, this is a character state that is present in coelophysids and *Dilophosaurus*, and is, therefore, interpreted as a neotheropodan synapomorphy which is reversed at node 11 (ACCTRAN), or a convergence in these two taxa (DELTRAN). At the present state of knowledge, it is impossible to say which interpretation is correct. Character 46 (0→1): no contact between the squamosal and quadratojugal. This is another character state that is present in coelophysids and *Dilophosaurus*. Again, the explanation as a convergence is preferred in this analysis since the character state is not present in *Shuvosaurus*. The character state is also present convergently in abelisaurids, birds, and oviraptorosaurs. Character 83 (0→1): enlarged, fang-like teeth in the anterior part of the dentaries. This character state is present in coelophysoids and *Dilophosaurus*. In this case, however, *Shuvosaurus* cannot provide any additional evidence since its jaws are completely edentulous. Therefore, it is at present impossible to determine whether this character state represents a neotheropodan synapomorphy that is reversed at node 11 (ACCTRAN) or a convergent development in coelophysoids and *Dilophosaurus*. The occurrence of the same character state in *Magnosaurus* and baryonychids clearly represents a convergence. Character 112 (1→2): posterior dorsal vertebrae considerably longer than high. This character state is found in all coelophysoids included in the tree described here, and in *Dilophosaurus* and a number of other theropods, including *Elaphrosaurus*, *Magnosaurus*, SMNK 2349 Pal, ornithomimosaur, and *Avimimus*. The patchy distribution of this character state makes its reliability for phylogenetic reconstructions questionable, but in a revised form it might be useful for the diagnosis of coelophysids, which have extremely elongate posterior dorsals. Character 178 (0→1): articular facet of pubic peduncle of ilium subdivided with an anterior part that faces more anteriorly than ventrally. Again, this is a character state that is present in coelophysoids and *Dilophosaurus*. The anteriorly facing part of the pubic peduncle in *Dilophosaurus* is relatively considerably smaller than that in coelophysoids, but it cannot yet be determined if this indicates convergence or is only a stage in the reduction of this anterior facet that then leads to its loss at node 11. An anteriorly facing facet of the pubic peduncle is also present convergently in ornithomimosaur. Character 223 (0→1 or 0→2): metatarsal V reduced and without a distal articular facet. The absence of a distal articular facet on Mt V clearly represents a synapomorphy at this node, but it is uncertain if this character state change is from 0→1 or 0→2. Two morphologies of this reduced metatarsal V are found within neotheropodans: Mt V is represented by a rather slender, more or less straight rod of bone in coelophysids and maniraptorans (state 1), but it is transversely flattened and flexed anteriorly in its distal part in all other theropods (state 2). Since it seems likely that character state 2 is modified from state 1 (although the character was not treated as ordered in the analysis), a change from 0 to 1 seems to be highly likely at this node. Arguments in favour of this interpretation are that the metatarsal V is rather straight and rod-like in immediate neotheropodan outgroups, in which it still retains a distal articular facet and at least one phalanx. The morphology of Mt V in maniraptorans is a reversal from state 2 to state 1.

*Possible additional apomorphies under DELTRAN.* Character 28 (0→1): lacrimal dorsoventrally elongated, with an inverted L-shape in lateral view, and broadly exposed on the skull roof; see node 2 (Theropoda). Character 128 (0→1): presence of a cranial process at the bases of the chevrons; see node 2 (Theropoda). Character 198 (0→1): lesser trochanter of femur spike-like or developed as a trochanteric shelf; see node 3. Character 211 (0→1): presence of an anterolateral tubercle on the fibular shaft, for the insertion of the m. iliofibularis; see node 3.

*Remarks.* The name 'Neotheropoda' was first used by Bakker (1986, pp. 460–461) for a clade consisting of all theropods with the exception of podokesaurids (= coelophysids). However, the name only occurs in an illustration in Bakker's work, and no formal diagnosis for this clade was given. Sereno (1998) first provided a diagnosis for a clade called Neotheropoda, which, in contrast to Bakker's original concept, also included coelophysids. Although the original concept is very similar in taxonomic content to node 10 or 11 of the present analysis, the name is, therefore, used here for a more inclusive group, following Sereno (1998) and Padian *et al.* (1999).

#### *Node 6. Coelophyoidea (Nopcsa, 1928)*

*Included taxa.* *Liliensternus* Welles, 1984; *Gojirasaurus* Carpenter, 1997; Coelophysidae (Nopcsa, 1928).

*Known temporal range.* Late Triassic (Norian)–Early Jurassic (Sinemurian–Pliensbachian).

*Synapomorphies.* Character 15 (0→1): presence of a horizontal ridge on the maxillary, parallel to the tooth row. This character state is convergently present in *Eoraptor* and *Ornitholestes*. Character 23 (2→1): sublacrimal part of the jugal bluntly squared anteriorly. Character 67 (0→1): medial part of ectopterygoid expanded and with deep ventral fossa. This character state was interpreted as a theropodan synapomorphy by Gauthier (1986). The interpretation in this analysis depends on whether the character is treated as ordered or unordered. If the character is treated as ordered, state 1 is interpreted as a theropodan synapomorphy by ACCTRAN, whereas it is considered a coelophysoid synapomorphy if the character is treated as unordered, since the character state is unknown in *Dilophosaurus*, and state 0 is present in ceratosaurs. Since character states 1 and 2 are very similar, and just differ in the presence of a longitudinal groove invading the ectopterygoid from the medial depression in state 2, it seems reasonable to assume that state 2 is developed from state 1. Therefore, the character state should be regarded as a theropodan or neotheropodan synapomorphy rather than a coelophysoid synapomorphy. Character 176 (0→1): brevis fossa of ilium strongly expanded posteriorly. This character state is convergently present in ornithomimosaurs. Character 191 (0→1): ischium only two-thirds or less the length of the pubis. This character state is convergently present in *Sinosauropteryx*, at node 35, and in *Caudipteryx*.

*Possible additional apomorphies under ACCTRAN.* Character 4 (0→1): posterior end of the premaxillary body forked, with a dorsal and a ventral process. This character state is present in *Coelophysis* and *Syntarsus*, but it is unknown in *Liliensternus* and *Gojirasaurus*, and thus it is impossible to decide if this character state represents a coelophysoid synapomorphy (ACCTRAN) or a coelophysid synapomorphy (DELTRAN). A forked posterior end of the premaxillary body is also found in *Shuvosaurus* and *Compsognathus*. Whereas it clearly represents a convergence in *Compsognathus*, it is probably a coelophysoid or coelophysid synapomorphy in *Shuvosaurus*. Character 13 (0→1): anterior margin of antorbital fossa squared. Again, this character state is only known in coelophysids amongst coelophysoids. It is convergently present in *Eoraptor*. Character 24 (2→0): reduction of the anterior process of the jugal. This is a reversal of a possible synapomorphy at node 3; see discussion there. Character 36 (0→1): frontal elongated and triangular. Within coelophysoids, this character state is only known in *Syntarsus*. It is convergently present in ornithomimosaurs, birds, and troodontids. Character 56 (0→1): basisphenoid significantly elongated. This character state is only known in *Syntarsus* and *Shuvosaurus*. Character 61 (1→0): exit of the mid-cerebral vein included in the trigeminal foramen. This is a reversal of a possible saurischian synapomorphy and is unknown in all coelophysoids with the exception of *Syntarsus*; see node 1 (Saurischia). Character 84 (0→1): no serrations on the premaxillary teeth. Within coelophysoids, this character state is only known in *Coelophysis* and *Syntarsus*. However, the presence of serrations in the premaxillary teeth of a small, *Syntarsus*-like theropod represented by a fragment of the snout from South Africa (BP/II/5278) indicates that it is probably not a coelophysoid synapomorphy, but diagnoses a more exclusive clade, for example coelophysids, as suggested by DELTRAN. Character 184 (1→0): reduction of the pubic boot; see node 3.

*Possible additional apomorphies under DELTRAN.* Character 83 (0→1): presence of enlarged, fang-like teeth in the dentary; see node 5 (Neotheropoda). Character 112 (1→2): posterior dorsal vertebrae considerably longer than high; see node 5 (Neotheropoda). Character 178 (0→1): articular facet of pubic peduncle of ilium subdivided with an anterior part that faces more anteriorly than ventrally; see node 5 (Neotheropoda).

*Remarks.* The name Coelophysoidea is used here for a monophyletic clade that includes the Coelophysidae, reflecting a traditional superfamily-family hierarchy. Although no formal phylogenetic taxonomic definition is given here, the clade can be regarded as stem-based, as in Sereno (1998). The Coelophysoidea of the present analysis differ from the original concept of Holtz (1994) in the exclusion of *Dilophosaurus*.

*Node 7.* unnamed node

*Included taxa.* *Gojirasaurus* Carpenter, 1997; Coelophysidae (Nopcsa, 1928).

*Known temporal range.* Late Triassic (Norian)–Early Jurassic (Sinemurian–Pliensbachian).

*Synapomorphies.* Character 181 (0→1): presence of a pubic fenestra below the obturator foramen. This fenestra is also present in *Segisaurus*, which belongs to this clade, but is not included in the tree described here.

*Possible additional apomorphies under ACCTRAN.* Character 45 (1→0): quadratojugal process of the squamosal tapers ventrally. This is a reversal of a synapomorphy at node 2 (Theropoda; ACCTRAN) or 3 (DELTRAN). The character state is unknown in *Gojirasaurus*, so it cannot be determined whether it represents a synapomorphy at this node, or at node 8 (Coelophysidae). Character 116 (0→1): the sacral ribs form a more or less continuous sheet of bone in ventral or dorsal view. Unknown in *Gojirasaurus* and convergently present in ceratosaurs and birds. Character 209 (0→1): presence of an oblique ridge on the medial side of the proximal end of the fibula. Unknown in *Gojirasaurus*. This character state is also present in *Segisaurus*, which is further evidence that this taxon belongs in this clade.

#### Node 8. Coelophysidae (Nopcsa, 1928)

*Included taxa.* *Coelophysis* Cope, 1889; *Syntarsus* Raath, 1969.

*Known temporal range.* Late Triassic (Norian)–Early Jurassic (Sinemurian–Pliensbachian).

*Synapomorphies.* Character 109 (1→0): neural spines of posterior dorsals broadly rectangular and approximately as high as long. This is a reversal of a synapomorphy at node 3. Character 183 (0→1): pubic shafts anteriorly convex in lateral view. This character state is convergently present in *Ceratosaurus*, *Monolophosaurus*, *Coelurus*, and *Avimimus*.

*Possible additional apomorphies under DELTRAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body and angle between anterior margin and alveolar margin less than 70 degrees; see node 5 (Neotheropoda). Character 4 (0→1): posterior end of premaxillary body forked, with a dorsal and a ventral posterior process; see node 6 (Coelophysoidea). Character 6 (1→2): subnarial process of the premaxilla without contact with the nasals and maxillary forms part of the rim of the external nares; see node 5 (Neotheropoda). Character 9 (0→1): presence of a subnarial gap; see node 5 (Neotheropoda). Even if the presence of a subnarial gap in *Coelophysis* and *Syntarsus* is regarded as convergent with the situation in *Dilophosaurus*, it seems unlikely that this character state arose that late in coelophysoid evolution. In *Liliensternus liliensterni*, the premaxilla is unknown and thus the character is coded as '?'. However, the morphology of the anterior end of the maxillary suggests that a subnarial gap was present in this taxon (MB R. 2175; Welles 1984). Character 13 (0→1): anterior margin of the maxillary squared; see node 6 (Coelophysoidea). Character 22 (0→1): presence of pronounced, raised lateral rims of the nasals; see node 5 (Neotheropoda). Character 45 (1→0): quadratojugal process of the squamosal tapers ventrally; see node 7. Character 84 (0→1): no serrations on the premaxillary teeth; see node 6. Character 116 (0→1): the sacral ribs form a more or less continuous sheet of bone in ventral or dorsal view; see node 7. Character 209 (0→1): presence of an oblique ridge on the medial side of the proximal end of the fibula; see node 7. Character 223 (0→1): metatarsal V reduced to a slender rod of bone without a distal articular surface. The reduction of Mt V clearly represents a neotheropodan synapomorphy (node 5), but the exact character state change at the base of Neotheropoda is uncertain. Therefore, the character state change at this node would be 2→1, rather than 0→1. However, as discussed at node 5, the change from 0→1 is likely to occur at the base of neotheropods, and in this case no character state change of this character occurred in coelophysoids.

*Remarks.* Although the name Coelophysidae might be applied to any node within Coelophysoidea that includes *Coelophysis*, it is restricted to the genera *Coelophysis* and *Syntarsus* here, since all authors agree that these two taxa are closely related (Raath 1969; Paul 1988a, 1993; Colbert 1989; Rowe and Gauthier 1990; Holtz 1994; Sereno 1997), regardless of the interrelationships of other coelophysoids.

#### Node 9. *Liliensternus* Welles, 1984

*Included taxa.* *Liliensternus liliensterni* (Huene, 1934); *Liliensternus airelensis* Cuny and Galton, 1993.

*Known temporal range.* Late Triassic (Norian)–?Earliest Jurassic (Rhaetian–Hettangian).

*Synapomorphies*. Character 98 (0→1): presence of a broad ridge that extends from the posterior end of the diapophyses to the ventral rim of the posterior end of the vertebral centrum in the cervical vertebrae.

*Possible additional apomorphies under ACCTRAN*. Character 96 (1→0): no camerate internal spaces present in the cervical vertebrae. This is a reversal of a possible theropodan synapomorphy. Unknown in *Liliensternus airelensis*; see node 2 (Theropoda). Character 150 (0→1): metacarpal II without medial expansion proximally. Unknown in *Liliensternus airelensis*.

*Node 10*. unnamed node

*Included taxa*. *Dilophosaurus* Welles, 1970; Ceratosauria Marsh, 1884; Tetanurae Gauthier, 1986.

*Known temporal range*. Early Jurassic (?Sinemurian–Pliensbachian)–Recent.

*Synapomorphies*. Character 16 (0→1): presence of a promaxillary foramen in the maxillary. Reversed in *Torvosaurus* and possibly therizinosauroids. Character 34 (0→1): prefrontal excluded from the anterior rim of the orbit and displaced posteriorly and/or medially. Reversed in *Ornitholestes*. Character 70 (0→1): tooth row ends at the anterior rim of the orbit. Character 90 (0→1): pleurocoels in cervical vertebrae developed as foramina that invade the vertebral body. Character 92 (1→2): epipophyses of the axis are strongly pronounced and overhang the postzygapophyses. Reversed in *Monolophosaurus* and most advanced coelurosaurids. Character 101 (0→1): anterior articular facet of anterior cervical vertebrae significantly wider than high. Reversed in *Ceratosaurus*, *Allosaurus*, sinraptorids, *Coelurus*, tyrannosaurids, and *Avimimus*. Character 102 (1→2): epipophyses of the cervical vertebrae strongly pronounced and overhanging the postzygapophyses. Reversed in *Elaphrosaurus*, coelurids, and most advanced coelurosaurids. Character 182 (0→1): pubic apron with medial opening distally. Reversed in *Torvosaurus*. Character 210 (0→1): presence of a deep groove on the medial side of the proximal end of the fibula. Reversed in *Magnosaurus* and maniraptorans. Character 223 (1→2 or 0→2): Mt V flattened transversely and flexed anteriorly in its distal part. This character state certainly represents a synapomorphy at this node, but its transformation is interpreted differently by DELTRAN and ACCTRAN. However, as discussed at node 5 (Neotheropoda), it is most likely to be a change from state 1 to state 2.

*Possible additional apomorphies under ACCTRAN*. Character 31 (0→1): presence of a lacrimal fenestra. A lacrimal fenestra is present in ceratosaurids and all basal tetanurans for which this bone is known. The antorbital fossa clearly extends onto the lacrimal in *Dilophosaurus*, but unfortunately the lacrimal is too strongly modified in this taxon to decide whether this condition is derived from a lacrimal that had a lacrimal fenestra or not. Therefore, it is impossible to decide whether this character state represents a synapomorphy at this node (ACCTRAN), or at node 11 (DELTRAN). Character 32 (0→1): presence of a lacrimal horn. Again, the modification of the lacrimal in *Dilophosaurus* renders it impossible to determine if this character state is a putative synapomorphy at this node. However, it seems very probable that it represents a synapomorphy at this node, or at node 11, since a lacrimal horn is found in *Ceratosaurus*, the majority of carnosaurids, and some basal coelurosaurids, including tyrannosaurids. There are problems with explaining this character with DELTRAN since it is coded as unknown in abelisaurids, and as absent in *Sinosauropteryx*. However, the lacrimal is also strongly modified in abelisaurids, and the presence of a dorsal peg in the lacrimal that slots into the ventral side of the frontal in *Carnotaurus* (MACN CH 895) indicates that this condition is derived from a lacrimal that had a lacrimal horn. The absence of a lacrimal horn in the coelurid *Sinosauropteryx* can either be interpreted as a reversal that occurred in the evolution of coelurids, or a reversal that occurred at the base of coelurosaurids. In the latter case, the presence of a lacrimal horn in tyrannosaurids must be convergent with the situation found in more basal theropods. Another explanation might be that the occurrence of a lacrimal horn in theropods is size-related. Character 60 (0→1): cranial nerves X and XI exit the braincase through a foramen lateral to the exit of cranial nerve XII on the posterior face of the braincase. The cranial nerves X and XI exit the braincase posteriorly in *Dilophosaurus*, but laterally in the ceratosaur *Majungatholus*; the situation in other basal members of this clade is unknown. Whether this character state represents a synapomorphy at this node (ACCTRAN), or at node 14, or 15 (DELTRAN) cannot be determined with the present state of knowledge. More information from other ceratosaurids (e.g. a new *Ceratosaurus* skull from the Morrison Formation of Colorado) will help to resolve the problem. It should be noted that there is some uncertainty whether the cranial nerves X and XI exit the braincase laterally in *Majungatholus*.

(and thus other ceratosaurs); another possibility might be that, in this taxon, their exit is confluent with the exit for cranial nerve XII, which is unusually large. Character 74 (0→1): attachment of the m. depressor mandibulae on the retroarticular process of the mandible faces posterodorsally. The attachment area faces posterodorsally in *Dilophosaurus*, but not in ceratosaurs; it is unknown in the most basal tetanurans. Therefore, it cannot be determined whether this character state represents a synapomorphy at this node, or at node 14, or 15. Character 168 (0→1): presence of a ventral hook-like process on the anterior end of the iliac blade. This character state is unknown in *Dilophosaurus* and reversed in *Unenlagia* and birds.

*Possible additional apomorphies under DELTRAN.* Character 24 (0→2): jugal with anterior process that extends anteriorly below the antorbital fenestra; see node 3. Character 61 (0→1): mid-cerebral vein exits the braincase through a separate foramen anterodorsal to the trigeminal foramen; see node 1 (Saurischia). Character 184 (0→1): presence of a well-developed pubic boot; see node 3.

#### *Node 11.* unnamed node

*Included taxa.* Ceratosauria Marsh, 1884; Tetanurae Gauthier, 1986.

*Known temporal range.* Middle Jurassic (Aalenian–Bajocian)–Recent.

*Synapomorphies.* Character 11 (0→1): ascending process of the maxilla offset from the anterior end of the maxillary body. Reversed in '*Szechuanosaurus*' *zigongensis*, sinraptorids, and at node 25. Convergently present in sauropodomorphs, *Eoraptor* and *Ornitholestes*; see also node 1 (Saurischia). Character 54 (0→1): ventral margin of the medial basis of the paroccipital process situated at, or below the mid-height of the occipital condyle. Reversed in ornithomimosaurids. Character 73 (0→1): retroarticular process of the mandible broad and attachment of the m. depressor mandibulae developed as a posteriorly placed transverse groove. Reversed in *Avimimus* and oviraptorosaurs. Character 91 (0→1): presence of pleurocoels in the axis. Reversed in *Piatnitzkysaurus*, *Magnosaurus*, and *Afrovenator*. Character 198 (1→2): lesser trochanter broadened and wing-like. Character 202 (0→1): presence of a well-developed broad, but shallow groove that is bound medially by an expanded lamella on the anterior side of the distal end of the femur. Reversed in baryonychids and all maniraptorans with the exception of dromaeosaurids, and it is convergently present in *Syntarsus* and *Segisaurus*. The presence of this character state in the latter two coelophysoids might indicate that they represent a sister-group within Coelophysoidea. Character 203 (0→1): distal end of the femur well rounded. Character 208 (1→2): distal articular facet of tibia broadly triangular in outline. Character 219 (0→1): presence of a facet for the tibia on the calcaneum.

*Possible additional apomorphies under ACCTAN.* Character 2 (1→0): premaxillary body in front of the external nares shorter than body below the nares and angle between anterior margin of premaxillary and alveolar margin more than 75 degrees. Character 8 (1→0): no constriction between the articulated premaxillaries and maxillaries. Character 9 (1→0): absence of a subnarial gap. Character 22 (1→0): no pronounced, raised lateral rims of the nasals. Character 46 (1→0): ventral process of the squamosal contacts the quadratojugal. Character 83 (1→0): absence of enlarged, fang-like teeth in the dentary. Character 112 (2→1): posterior dorsal vertebrae approximately as long as high. Character 178 (1→0): articular facet of pubic peduncle of the ilium not subdivided and faces ventrally. All of the above characters are reversals of possible neotheropodan synapomorphies; see node 5. Character 49 (1→0): quadrate foramen developed as an opening between the quadrate and the quadratojugal. This is a reversal of a saurischian synapomorphy. The quadrate foramen is entirely lost in ceratosaurs and the condition is unknown in the most basal tetanurans; therefore, it cannot be determined whether this reversal represents a synapomorphy at this node or at node 14, or 15. Character 51 (0→1): mandibular joint positioned significantly posterior to quadrate head. This character state is present in ceratosaurs and carnosaurids, but it is unknown in the most basal tetanurans. Without information from the latter taxa, it is impossible to determine whether this character state represents a synapomorphy at this node that is reversed in coelurosaurs (ACCTAN), or a convergent development in ceratosaurs and carnosaurids (DELTRAN). The presence of character state 1 in *Herrerasaurus* clearly represents a convergence. Character 136 (0→1): anterior part of the coracoid with a hook-like ventral expansion. This character state is found in *Elaphrosaurus*, abelisaurids, and all tetanurans, but not in *Ceratopsid*. Since the distribution of this state in ceratosaurs is thus equivocal, it is impossible to determine whether it represents a synapomorphy at this node that is reversed in *Ceratopsid* (ACCTAN), or a

convergent development in abelisauroids and tetanurans (DELTRAN). Character 146 (1→2): presence of a large distal carpal that has the shape and morphology of a semilunate carpal in proximal view, but is rectangular rather than semilunate in palmar view. This morphology is present in the carnosaur *Allosaurus* and the coelurosaur *Coelurus*, and thus ACCTAN interprets it as a synapomorphy at this node. Unfortunately, no well-preserved hands are known for ceratosaurs and most basal tetanurans, including most carnosaur, making a decision concerning this character very difficult. However, a more basal morphology of the enlarged distal carpal is found in the carnosaur *Afrovenator* and in *Xuanhanosaurus*, which probably represents a basal tetanuran. This indicates that this special carpal morphology arose independently in *Allosaurus* and basal coelurosaurs. A very similar morphology to that found in *Coelurus* seems to be present in tyrannosaurids (Holtz, pers. comm. 1999), indicating that this character state probably represents a coelurosaurian synapomorphy. Character 156 (0→1): proximal outline of Mc III triangular with the apex dorsal. This character state is unknown in ceratosaurs. Character 158 (1→2): manual phalanx I-1 more than 1.5 times the length of Mc I. As noted above, no well-preserved manus is known for any ceratosaur, and the situation in '*Szechuanosaurus zigongensis*' is equivocal, since it represents a transitional state. Therefore, it is impossible to say whether this transition represents a synapomorphy at this node, or at node 14, or 15. Character 204 (0→1): fibular condyle of tibia well offset from cnemial crest. In this character, the distribution of state 1 is equivocal in ceratosaurs: whereas it is present in *Ceratopsaurus*, abelisauroids show state 0. Character 218 (0→1): presence of a horizontal groove across the astragalar condyles anteriorly. This character state is present in all ceratosaurs and carnosaur, but unfortunately it is unknown in the most basal tetanurans and basal coelurosaurs. Without further evidence for these taxa it is impossible to decide whether it represents a synapomorphy at this node that is then reversed in coelurosaur evolution (ACCTAN), or if it is a convergent development in ceratosaurs and carnosaur (DELTRAN). It is also present in *Deltadromeus*, which is interpreted as a convergence in the tree described here. However, the phylogenetic position of *Deltadromeus* is problematic because of the fragmentary nature of the type and only specimen. If *Deltadromeus* turns out to be a basal coelurosaur, as proposed by Sereno *et al.* (1996), the presence of a groove in this taxon would provide evidence for the interpretation suggested by ACCTAN. Character 222 (1→2): Mt I broadly triangular and attached to the distal half of Mt II. No Mt I is known in ceratosaurs, or in the most basal tetanurans.

*Possible additional apomorphies under DELTRAN.* Character 31 (0→1): presence of a lacrimal fenestra; see node 10. Character 168 (0→1): presence of a ventral hook-like process on the anterior end of the iliac blade; see node 10.

#### *Node 12. Ceratosauria* Marsh, 1884

*Included taxa.* *Ceratopsaurus* Marsh, 1884; Abelisauroidea (Bonaparte and Novas, 1985).

*Known temporal range.* Late Jurassic (Kimmeridgian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 1 (0→1): premaxillary body significantly higher than wide. Convergent present in tyrannosaurids and oviraptorosaurs. Character 7 (0→1): external nares face anterolaterally. Character 19 (0→1): presence of pneumatic foramina in the nasals. Convergent present in allosauroids and in oviraptorosaurs. Character 21 (0→1): nasals of subequal width throughout their length. This character state is probably correlated with the anterolateral facing nares of ceratosaurs. It is convergent present in carcharodontosaurids and advanced coelurosaurs (node 29), in which the nasals are, however, relatively much narrower than in ceratosaurs. Character 38 (0→1): infratemporal fenestra at least 1.5 times the size of the orbit. Convergent present in sinraptorids. Character 40 (0→1): jugal process of the postorbital with small anterior projection that probably indicates the lower delimitation of the eyeball. Convergent present at node 22 and in some advanced tyrannosaurids. Character 42 (0→1): posteriorly placed, knob-like projection of the parietals. Convergent present in baryonychids and at node 22. Character 43 (0→1): supratemporal fenestrae almost confluent posteriorly, but separated by a horizontal, anteriorly widening plate of bone formed by the parietals anteriorly. Character 49 (0→2 or 1→2): quadrate foramen absent. Whether this synapomorphy represents a change from state 0 to state 2 (ACCTAN) or 1 to 2 (DELTRAN) depends on the interpretation of the character state transformation at node 11 (see discussion there), and can only be solved when further material of basal ceratosaurs becomes known. Character 79 (1→0): posterior end of splenial straight. This character state is convergent present in most maniraptorans. Character 116 (0→1): sacral ribs form a continuous sheet of bone in dorsal or ventral view. This character state is convergent present in coelophysids and birds.

Character 124 (0→2): neural spines of mid-caudals rod-like and vertically orientated. Character 133 (0→1): distal end of scapula not expanded. This character state is convergently present in *Herrerasaurus*, sinraptorids, and advanced coelurosaurs. Character 143 (0→1): humerus straight in lateral view. This character state is convergently present at node 18, in tyrannosaurids, and at node 33. Character 193 (0→1): distal end of ischium expanded into an ischial boot. This character state is convergently present in '*Szechuanosaurus*' *zigongensis*, at node 22, and in most ornithomimosaurids.

*Possible additional apomorphies under ACCTRAN.* Character 18 (0→1): dorsal surface of the nasals rugose. The entire dorsal surface of the fused nasals has well-developed rugosities in abelisaurids, but only the nasal horn-core is rugose in *Ceratosaurus*. This indicates that some keratinous covering of this bone was present in both taxa, although less well developed in *Ceratosaurus* than in later ceratosaurs. Well-developed rugosities are convergently present on the nasals of *Monolophosaurus*, carcharodontosaurids, and tyrannosaurids. Character 60 (1→0): cranial nerves X and XI exit the braincase laterally through the jugular foramen; see node 10. Character 74 (1→0): attachment for the m. depressor mandibulae on the retroarticular process of the mandible faces dorsally; see node 10. Character 96 (1→2): presence of internal pneumatic cavities with camellate structure in the cervical vertebrae. This character state is only known in *Ceratosaurus*, so it cannot be determined whether it represents a synapomorphy at this node, or an autapomorphy of this taxon. It is convergently present in carcharodontosaurids and coelurosaurs, except in dromaeosaurids.

*Possible additional apomorphies under DELTRAN.* Character 6 (1→2): subnarial process of the premaxilla strongly reduced, lacking contact with the nasals, and maxilla forms part in the rim of the external nares. Although this character state is present in several clades of theropods (see also node 5), ceratosaurs exhibit the highest degree of reduction of this process, since it is virtually absent in members of this clade. Character 51 (0→1): mandibular joint placed significantly posterior to quadrate head; see node 11. Character 218 (0→1): presence of a horizontal groove across the astragalar condyles anteriorly; see node 11.

*Remarks.* The name Ceratosauria is used here for *Ceratosaurus* and its closest relatives, in reference to the original concept of the name as defined by Marsh (1884). Thus, although no formal phylogenetic definition is given here, the taxon is treated as stem-based, as in Padian *et al.* (1999). The clade Ceratosauria evident in most recent phylogenies is found to be paraphyletic in the present analysis. Thus, the clade is used here for a more exclusive group than in most recent analyses.

Sereno (1998) also presented a stem-based definition of the Ceratosauria that differed from that of Padian *et al.* (1999) in using *Coelophysus* as the reference taxon for this clade, instead of *Ceratosaurus*. However, if Sereno's definition were applied to the present cladogram, it would result in a Ceratosauria that does not include *Ceratosaurus*. Since this is in strong contrast to the original concept of this clade, as devised by Marsh (1884), Sereno's definition of Ceratosauria is rejected.

*Node 13.* Abelisauroida (Bonaparte and Novas, 1985)

*Included taxa.* *Elaphrosaurus* Janensch, 1920; Abelisauridae Bonaparte and Novas, 1985.

*Known temporal range.* Late Jurassic (Kimmeridgian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 97 (0→1): no ventral keel in anterior cervical vertebrae. This character state is convergently present in *Magnosaurus*, sinraptorids, and the majority of coelurosaurs. Character 113 (2→3): more than five sacral vertebrae. This character state is convergently present in advanced coelurosaurs (node 32). Character 120 (1→0): no ventral groove in the anterior caudal vertebrae. This is a reversal of a neotheropodan synapomorphy. Character 140 (0→1): proximal articular facet of humerus less than twice as broad anteroposteriorly than transversely. Character 142 (0→1): deltopectoral crest reduced. This character state is convergently present in tyrannosaurids and ornithomimosaurids.

*Possible additional apomorphies under ACCTRAN.* Character 12 (1→0): maxillary antorbital fossa deep, with sharply defined margins. This is a reversal of a neotheropodan synapomorphy. Since no cranial material is known for

*Elaphrosaurus*, it is impossible to determine if this and all following cranial characters represent synapomorphies of abelisauroids, or abelisaurids. Character 33 (0→1): presence of a posterior dorsal process of the lacrimal. Convergently present in advanced coelurosaurids (node 32), with the exception of therizinosauroids. Character 35 (0→1): lacrimal contacts frontal. Convergently present in most advanced coelurosaurids. Character 39 (0→1): lacrimal contacts postorbital. Convergently present in carcharodontosaurids and *Tyrannosaurus*. Character 46 (0→1): no contact between the squamosal and the quadratojugal. Convergently present in *Syntarsus*, *Dilophosaurus*, birds, and oviraptorosaurs; see also node 5 (Neotheropoda). Character 134 (0→1): acromion process of scapula not significantly expanded and dorsal margin of the proximal part of the scapula slopes gently downwards. The proximal ends of the scapulae in *Elaphrosaurus* are too poorly preserved to identify the character state in this taxon. This character state is convergently present at node 35 and in *Caudipteryx*. Character 145 (0→1): radius less than half the length of the humerus. Unknown in *Elaphrosaurus*, unless the radius referred to this taxon by Janensch (1929) really belongs to this genus. If this is the case, this character state represents an abelisaurid synapomorphy. A strongly shortened radius is convergently present in spinosauroids and tyrannosaurids. Character 204 (1→0): fibular condyle of tibia confluent with cnemial crest. This is a reversal of a possible synapomorphy at node 11; see that node. Character 207 (0→2): anterior side of distal end of tibia flat. Unknown in abelisaurids, and convergently present in coelurosaurids.

*Possible additional apomorphies under DELTRAN.* Character 136 (0→1): presence of a hook-like ventral process in the coracoid; see node 11.

*Remarks.* The name Abelisauroidea was originally proposed by Bonaparte (1991b) for the inclusion of the families Abelisauridae and Noasauridae. As noted above, the distinction between these two families is not accepted here, and both *Noasaurus* and abelisaurids (*sensu* Bonaparte 1991b) are included in a single family, Abelisauridae. The family Abelisauridae and its closest relative, *Elaphrosaurus*, are united in the Abelisauroidea here, in accordance with a traditional family-superfamily hierarchy.

#### *Node 14. Tetanurae Gauthier, 1986*

*Included taxa.* *Piatnitzkysaurus* Bonaparte, 1979; '*Szechuanosaurus*' *zigongensis* Gao, 1993; Carnosauria Huene, 1920; Coelurosauria Huene, 1914.

*Known temporal range.* Middle Jurassic (Aalenian–Bajocian)–Recent.

*Synapomorphies.* Character 17 (0→1): presence of a maxillary fenestra. Reversed at node 18, carcharodontosaurids, and therizinosauroids. Character 89 (0→1): one pair of pleurocoels in the cervical vertebrae. As discussed under 'characters', the present analysis supports the idea that the presence of two cervical pleurocoels represents the plesiomorphic character state within theropods, and the reduction of the posterior pleurocoel is a synapomorphy of tetanurans. Character 99 (0→1): prezygapophyses of anterior cervical vertebrae situated entirely lateral to the neural canal. Convergently present in abelisaurids. Character 108 (0→1): presence of a pronounced ventral keel in the anterior dorsal vertebrae. Reversed in *Magnosaurus* and ornithomimosaurids. It is also present in *Xuanhanosaurus*, a taxon that is not included in the tree described here, indicating that this genus belongs to the Tetanurae. Character 148 (0→1): metacarpal I closely appressed to basal half of Metacarpal II. Reversed in therizinosauroids. Character 199 (0→1): lesser trochanter proximally placed, but lower than greater trochanter. Character 206 (1→2): ridge for the attachment of the fibula on the lateral side of the tibia offset from the proximal end of the tibia.

*Possible additional apomorphies under ACCTRAN.* Character 6 (2→1): subnarial process of the premaxilla reduced and rod-like, but has a contact with the nasals. This is a reversal of a possible neotheropodan synapomorphy; see node 5. Character 10 (0→1): maxillaries subparallel in the articulated skull in ventral view. The character state for this and all the following cranial characters is unknown in *Piatnitzkysaurus* and '*Szechuanosaurus*' *zigongensis*. The derived state is also convergently present in *Herrerasaurus*. Character 25 (0→1): jugal antorbital fossa developed as a large, crescentic depression on the anterior end of the jugal. Character 58 (0→1): basiptyergoid processes significantly longer than wide at their bases. Character 67 (0→2): ectopterygoid with a deep ventral depression and a deep groove excavated into the ectopterygoid body from the medial side. As discussed at node 5, it seems very probable that this character state is derived from state 1, rather than from state 0. Character 70 (1→2): tooth row completely antorbital

and ends anterior to the vertical strut of the lacrimal. Character 75 (0→1): anterior part of the surangular dorsoventrally deep and more than half the height of the mandible at the level of the mandibular fenestra. Reversed in sinraptorids, *Avimimus*, and oviraptorosaurs. Character 77 (0→1): posterior end of dentary only slightly forked or straight. Character 93 (0→1): axial neural spine anteroposteriorly reduced and rod-like. This character state is present in *Piatnitzkysaurus*, baryonychids, allosauroids, tyrannosaurids, and deinonychosaurs, but not in several other tetanuran groups. More material of basal tetanurans and basal coelurosaurs is needed to determine if it represents a synapomorphy at this node which is then reversed in several clades (ACCTRAN), or a convergence in several groups of tetanurans (DELTRAN). However, the distribution of this character state in known basal tetanurans suggests that it probably represents a synapomorphy of this group. Character 130 (0→1): mid-caudal chevrons L-shaped. Unknown in *Piatnitzkysaurus* and '*Szechuanosaurus*' *zigongensis*. Reversed in *Compsognathus*. Character 215 (0→1): ascending process of the astragalus higher than the astragalar body. Unknown in *Piatnitzkysaurus* and '*Szechuanosaurus*' *zigongensis*. Character 217 (0→1): astragalar condyles expanded proximally on the anterior side of the distal end of the tibia and face anterodistally. Unknown in *Piatnitzkysaurus* and '*Szechuanosaurus*' *zigongensis*.

*Possible additional apomorphies under DELTRAN.* Character 96 (0→1): presence of internal pneumatic chambers with a camerate structure in the cervical vertebrae; see node 2 (Theropoda). Character 136 (0→1): coracoid with a tapering, hook-like ventral process anteriorly; see node 11. Character 156 (0→1): proximal outline of metacarpal III triangular, with the apex dorsal; see node 11. Character 204 (0→1): fibular condyle of tibia offset from cnemial crest; see node 11.

*Remarks.* The name Tetanurae was originally proposed for the sister group of the Ceratosauria in the basal theropod dichotomy advocated by Gauthier (1986). Although the Ceratosauria, as defined by Gauthier, are regarded as a paraphyletic group here, the name is used at this node since the present monophyletic clade includes basically the same taxa as Gauthier's Tetanurae.

#### *Node 15.* unnamed node

*Included taxa.* Carnosauria Huene, 1920; Coelurosauria Huene, 1914.

*Known temporal range.* Middle Jurassic (Aalenian–Bajocian)–Recent.

*Synapomorphies.* Character 111 (0→1): parapophyses of posterior dorsal vertebrae situated below the transverse processes. Reversed in *Magnosaurus*. Character 177 (0→1): pubic peduncle of ilium significantly longer anteroposteriorly than ischial peduncle, and ischial peduncle tapers distally and does not have a clearly defined articular facet. Reversed in *Sinraptor* and therizinosauroids, and convergently present in *Staurikosaurus*. Character 180 (0→1): obturator foramen in pubis open ventrally. Reversed in *Torvosaurus* and *Monolophosaurus*. Character 195 (0→1): femoral head directed medially.

*Possible additional apomorphies under ACCTRAN.* Character 153 (1→2): fourth digit of the hand absent. This character state was regarded as a tetanuran synapomorphy by Gauthier (1986). However, since digit IV is still present in the basal tetanuran '*Szechuanosaurus*' *zigongensis*, it might rather be a synapomorphy at this node. Unfortunately, well-preserved mani are only known for *Allosaurus* among the basal members of this clade. The presence of only three digits in the hand of this carnosaurian taxon and in all coelurosaurs, for which good manual material is known, indicates that the reduction of manual digit IV is a synapomorphy at this node. However, the presence of a metacarpal IV in *Sinraptor dongi* (Currie and Zhao 1993b) is problematical. Two explanations are possible: the presence of a fourth digit in *Sinraptor* is a reversal of the derived character state at this node (ACCTRAN), or digit IV was convergently lost in *Allosaurus* and coelurosaurs (DELTRAN). If the element in question was identified correctly by Currie and Zhao (1993b), I believe the latter explanation to be more likely. However, final resolution of this problem can only come from better manual material of carnososaurs and basal coelurosaurs. Character 190 (1→0): obturator process of the ischium confluent with ischial shaft distally. This is a reversal of a neotheropodan synapomorphy. The occurrence of a notch between the obturator process and the ischial shafts in basal tetanurans is problematic. It is present in most carnososaurs, with the exception of *Magnosaurus* and *Torvosaurus*, but absent in all coelurosaurs. Thus, ACCTRAN interprets the absence of a notch as a synapomorphy at this node, which is then reversed in allosauroids and baryonychids, whereas DELTRAN suggests that the notch is lost independently in *Magnosaurus*, *Torvosaurus*, and coelurosaurs. Given the distribution of this character state in carnososaurs, the latter explanation seems to be more likely.

*Possible additional apomorphies under DELTRAN.* Character 10 (0→1): maxillaries subparallel in the articulated skull in ventral view; see node 14. Character 25 (0→1): jugal antorbital fossa developed as a deep, crescentic depression; see node 14. Character 49 (1→0): quadrate foramen developed as a distinct opening between the quadrate and the quadratojugal. This is a reversal of a saurischian synapomorphy; see node 11. Character 58 (0→1): anteroposterior length of basiptyergoid processes significantly longer than the basal width of the processes; see node 14. Character 60 (0→1): cranial nerves X and XI exit the braincase posteriorly through a foramen lateral to the foramen for nerve XII; see node 10. Character 70 (1→2): tooth row completely antorbital and ends anterior to the vertical strut of the lacrimal; see node 14. Character 74 (0→1): attachment area for the m. depressor mandibulae in the mandible faces posterodorsally; see node 10. Character 75 (0→1): anterior part of the surangular more than half the height of the mandible at the level of the mandibular fenestra; see node 14. Character 77 (0→1): posterior end of dentary straight or only slightly concave; see node 14. Character 130 (0→1): mid-caudal chevrons L-shaped; see node 14. Character 131 (0→1): presence of a furcula. This character state is interpreted as a theropod synapomorphy by ACCTRAN (see node 2), but as a synapomorphy at this node by DELTRAN, since it is unknown in all basal theropods included in the tree described here. However, the presence of a furcula in the coelophysoid *Segisaurus* indicates that it represents a neotheropodan synapomorphy. Character 158 (1→2): phalanx I-1 more than 1.5 times the length of metacarpal I; see node 11. Character 215 (0→1): ascending process of astragalus higher than astragalar body; see node 14. Character 217 (0→1): astragalar condyles directed anterodistally; see node 14. Character 222 (1→2): metatarsal I broadly triangular and attached to distal half of Mt II; see node 11.

#### *Node 16. Carnosauria Huene, 1920*

*Included taxa.* Spinosauroida (Stromer, 1915); Allosauroida (Marsh, 1878).

*Known temporal range.* Middle Jurassic (Aalenian–Bajocian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 11 (1→2): ascending process of maxillary offset from anterior rim of maxillary body and anterior projection of maxillary body as long as high, or longer. Within carnosaurs, this character is reversed to state 1 in carcharodontosaurids, and to state 0 in sinraptorids. Sereno *et al.* (1996) regarded this character state as a spinosauroid synapomorphy; however, it is clearly present in the allosauroid taxa *Monolophosaurus*, *Afrotitan*, and *Allosaurus*. Character 95 (0→1): cervical vertebral centra strongly opisthocelous. This character state is convergently present in *Compsognathus*. Character 164 (0→1): metacarpal I very stout and approximately as broad as long. This character state is also present in *Poekilopleuron*, indicating that this genus is a carnosaur.

*Possible additional apomorphies under DELTRAN.* Character 32 (0→1): presence of a lacrimal horn; see node 10. Character 51 (0→1): mandibular joint significantly posterior to quadrate head; see node 11. Character 218 (0→1): presence of a horizontal groove across the astragalar condyles; see node 11.

*Remarks.* The name Carnosauria was first proposed by Huene (1920), and later widely used for the inclusion of all large theropod dinosaurs (e.g. Colbert 1964; Romer 1966; Steel 1970). In most theropod phylogenies published in pre-cladistic times, a basal dichotomy between carnosaurs and coelurosaurs was recognized. In this analysis, this dichotomy was found within tetanurans, and the taxonomic contents of both carnosaurs and coelurosaurs is very similar to that found by many authors for each of these clades in pre-cladistic times, although a few coelurosaur or carnosaur taxa are excluded from the Tetanurae. Thus, the names Carnosauria and Coelurosauria are used here for the two stem-based clades that form the major dichotomy within tetanurans.

The only major difference in this, and most other recent analyses (Novas 1992a; Holtz 1994; Sereno 1997, 1999) from most traditional, pre-cladistic concepts of coelurosaurs and carnosaurs is the inclusion of the tyrannosaurids in the former clade. However, early workers were uncertain about the systematic position of this family, and it was included in the coelurosaurs by some authors (e.g. Matthew and Brown 1922; Huene 1926a); hence, this difference does not seem to provide sufficient justification for abandoning these names.

Padian *et al.* (1999, p. 72) defined Carnosauria as all theropods more closely related to *Allosaurus* than to Neornithes, which is in accordance with the use of the name Carnosauria in this analysis.

*Node 17. Spinosauroida (Stromer, 1915)*

*Included taxa.* *Magnosaurus* Huene, 1932; *Torvosaurus* Galton and Jensen, 1979; *Chilantaisaurus tashuikouensis* Hu, 1964; Baryonychidae Charig and Milner, 1986.

*Known temporal range.* Middle Jurassic (Aalenian–Bajocian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares, and angle between anterior margin and alveolar margin less than 70 degrees; see node 5 (Neotheropoda). Character 41 (0→1): cross-section of the ventral process of the postorbital U-shaped. Convergently present in *Afrovenator*. Character 83 (0→1): presence of enlarged, fang-like teeth in the dentary. Convergently present in coelophysoids and in *Dilophosaurus*.

*Possible additional apomorphies under ACCTRAN.* Character 42 (0→1): presence of a posteriorly placed, knob-like process on the parietals. The character is unknown in all spinosauroids with the exception of baryonychids, in which state 1 is present; therefore, it cannot be determined at which node the character state transformation occurred within spinosauroid evolution. Convergently present in ceratosaurs and at node 22. Character 120 (1→0): no ventral groove in anterior caudals. This is a reversal of a neotheropodan synapomorphy. A ventral groove is absent in *Magnosaurus* and baryonychids, but present in *Torvosaurus*. Thus, it is impossible to determine whether the absence of the groove represents a spinosauroid synapomorphy that is reversed in *Torvosaurus* (ACCTRAN), or a convergence in *Magnosaurus* and baryonychids. Character 145 (0→1): radius less than half the length of the humerus. This character is unknown in *Magnosaurus*. It is convergently present in abelisaurids and tyrannosaurids. Character 161 (0→1): manual ungual I more than half the length of the radius. Unknown in *Magnosaurus* and convergently present in *Sinosauroptryx*.

*Remarks.* The name Spinosauroida was used by Sereno *et al.* (1996, 1998) and Sereno (1997) for the clade of basal tetanurans that comprised the genus *Torvosaurus* and the Spinosauridae (= Baryonychidae in the present analysis). Since both taxa are also contained in the present clade, the name Spinosauroida is used for it here. However, in contrast to the node-based definition of the Spinosauroida by Sereno (1998), here the clade is used like a stem-based taxon to include the more basal taxon *Magnosaurus*. Thus, a dichotomy of two taxa of formally superfamilial rank is recognized within Carnosauria.

*Node 18. unnamed node*

*Included taxa.* *Torvosaurus* Galton and Jensen, 1979; *Chilantaisaurus tashuikouensis* Hu, 1964; Baryonychidae Charig and Milner, 1986.

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 17 (1→0): maxillary fenestra absent. This is a reversal of a tetanuran synapomorphy. Character 143 (0→1): humerus straight in lateral view. Convergently present in ceratosaurs, tyrannosaurids, *Deltadromeus*, and ornithomimosaurids. Character 184 (1→0): pubic boot absent. This is a reversal of a synapomorphy at node 3 (ACCTRAN), or 10 (DELTRAN).

*Possible additional apomorphies under ACCTRAN.* Character 5 (1→0): three premaxillary teeth. Only three premaxillary teeth are present in *Torvosaurus*, but seven in baryonychids. The high number of teeth in the latter taxon makes it unlikely that the number of teeth was reduced at this node and increased again in baryonychids; the presence of only three premaxillary teeth in *Torvosaurus* probably represents an autapomorphy of this genus. Character 44 (0→1): postorbital part of the skull roof deflected ventrally. Unknown in *Torvosaurus* and *Chilantaisaurus tashuikouensis*, so it cannot be determined at which node this state might be apomorphic. Convergently present in many coelurosaurids. Character 51 (1→2): mandibular joint anterior to quadrate head. Unknown in *Torvosaurus* and *Chilantaisaurus tashuikouensis*, and convergently present in ornithomimosaurids and birds.

*Possible additional apomorphies under DELTRAN.* Character 145 (0→1): radius less than half the length of the humerus; see node 17. Character 161 (0→1): manual ungual I more than half the length of the radius; see node 17.

*Node 19.* unnamed node

*Included taxa.* *Chilantaisaurus tashukouensis* Hu, 1964; Baryonychidae Charig and Milner, 1986.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 207 (0→1): presence of a bluntly rounded vertical ridge on the antero-medial side of the distal end of the tibia.

*Possible additional apomorphies under ACCTRAN.* All of the following characters are unknown in *Chilantaisaurus*, so it cannot be determined whether they represent a synapomorphy at this node, or baryonychid synapomorphies. Character 5 (0→3): more than five premaxillary teeth. As noted above (node 18), it seems rather unlikely that the character state transition was from state 0 to 3; it was more likely to be from 1 to 3. Character state 3 is convergently present in the basal ornithomimosaur *Pelecanimimus*. Character 8 (0→1): presence of a constriction between the articulated premaxillaries and maxillaries. Character 9 (0→1): presence of a subnarial gap. Character 12 (1→0): maxillary antorbital fossa deep, with sharply defined margins. This is a reversal of a neotheropodan synapomorphy. Character 190 (0→1): presence of a notch between the obturator process and the ischial shafts distally; see node 15. Character 210 (1→2): deep groove on the medial side of the proximal end of the fibula. Convergently present in most coelurosaurs.

*Node 20.* Allosauroida (Marsh, 1878)

*Included taxa.* *Monolophosaurus* Zhao and Currie, 1993; *Afrovenator* Sereno, Wilson, Larsson, Dutheil and Sues, 1994; *Allosaurus* Marsh, 1877; Sinraptoridae Currie and Zhao, 1993b; *Neovenator* Hutt, Martill and Barker, 1996; Carcharodontosauridae Stromer, 1931.

*Known temporal range.* Middle Jurassic–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 19 (0→1): presence of a pneumatic foramen in the nasals. Convergently present in ceratosaurs and oviraptorosaurs. Character 20 (0→1): antorbital fossa extends onto the nasals. Character 26 (0→1): jugal pneumatised by a foramen in the posterior rim of the jugal antorbital fossa. Convergently present in tyrannosaurids. Character 52 (1→2): distal ends of the paroccipital processes situated entirely below the level of the foramen magnum.

*Possible additional apomorphies under ACCTRAN.* Character 22 (0→1): lateral rims of the nasals pronounced and raised. The lateral margins of the nasals are raised in *Allosaurus* and *Sinraptor*, but not in carcharodontosaurids; in *Monolophosaurus* the nasals are strongly modified. Therefore, it cannot be determined whether this character state represents an allosauroid synapomorphy, or a convergent development in *Allosaurus* and sinraptorids. Character 121 (0→1): anterior caudal vertebrae with a distinct ventral keel. Unknown in *Monolophosaurus* and *Afrovenator* and convergently present in *Torvosaurus* and *Ornitholestes*. Character 123 (0→1): anterior margin of neural spines of anterior mid-caudal vertebrae with distinct bend, dorsal part of anterior margin more strongly inclined posteriorly than ventral part. Unknown in *Monolophosaurus*. Character 125 (0→1): presence of an anterior spur in front of the neural spine in mid-caudals. Unknown in *Monolophosaurus*. Character 139 (1→0): femur more than 2.5 times the length of the humerus. Only known in *Allosaurus* among allosauroids, and convergently present in abelisaurids, *Sinosauropteryx*, and tyrannosaurids. Character 190 (0→1): ventral notch present between the obturator process and the ischial shafts; see node 15.

*Possible additional apomorphies under DELTRAN.* Character 93 (0→1): axial neural spines anteroposteriorly reduced and rod-like; see node 14 (Tetanurae).

*Remarks.* The Allosauroida was proposed by Currie and Zhao (1993b) to include the families Allosauridae and Sinraptoridae. Subsequently, Rauhut (1995) added the Carcharodontosauridae to this clade, and Sereno *et al.* (1996) included further basal taxa (*Cryolophosaurus*, *Monolophosaurus*) in the Allosauroida. Padian *et al.* (1999) defined the Allosauroida as a node-based taxon to include *Allosaurus*, *Sinraptor* and all descendants of their most recent common ancestor, whereas Sereno (1998) provided a

stem-based definition, Allosauroidae being all theropods closer to *Allosaurus* than to Neornithes. The latter definition is identical with the definition of Carnosauria by Padian *et al.* (1999). Thus, if these definitions were applied to the current cladogram, the taxonomic contents of Allosauroidae would differ widely, depending on the definition used. Therefore, Allosauroidae is here used at this node since it largely incorporates the taxa included in the Allosauroidae by Sereno *et al.* (1996). Furthermore, applying the name at this node reflects the dichotomy that divides carnosaurs into two monophyletic clades.

*Node 21.* unnamed node

*Included taxa.* *Afrovenator* Sereno, Wilson, Larsson, Dutheil and Sues, 1994; *Allosaurus* Marsh, 1877; Sinraptoridae Currie and Zhao, 1993b; *Neovenator* Hutt, Martill and Barker, 1996; Carcharodontosauridae Stromer, 1931.

*Known temporal range.* Late Jurassic (Kimmeridgian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 49 (0→1): quadrate foramen almost entirely enclosed in the quadrate. This character state represents a saurischian synapomorphy that is reversed at node 11 or 15, and occurs independently in this clade, and in *Ornitholestes*. Character 55 (0→1): basal tubera subdivided by a lateral longitudinal groove into a medial part that is entirely formed by the basioccipital, and a lateral part that is entirely formed by the basisphenoid. Character 188 (0→1): obturator process of ischium offset from pubic peduncle. Convergently present in coelurosaurs.

*Possible additional apomorphies under ACCTRAN.* Character 5 (1→2): five premaxillary teeth. *Allosaurus* and *Neovenator* have five premaxillary teeth, while sinraptorids have four; the number of premaxillary teeth in *Afrovenator* and carcharodontosaurids is unknown. Therefore, it cannot be determined whether five premaxillary teeth represent the ancestral state for this clade that is then reversed in sinraptorids, or if *Allosaurus* and *Neovenator* acquired this state independently.

*Possible additional apomorphies under DELTRAN.* Character 67 (0→2): ectopterygoid with a deep ventral depression and a deep groove excavated into the ectopterygoid body from the medial side; see node 14. Character 121 (0→1): anterior caudal vertebrae with a distinct ventral keel; see node 20. Character 123 (0→1): anterior margin of neural spines of anterior mid-caudal vertebrae with distinct bend, dorsal part of anterior margin more strongly inclined posteriorly than ventral part; see node 20. Character 125 (0→1): presence of an anterior spur in front of the neural spine in mid-caudals; see node 20.

*Node 22.* unnamed node

*Included taxa.* Sinraptoridae Currie and Zhao, 1993b; *Neovenator* Hutt, Martill, and Barker, 1996; Carcharodontosauridae Stromer, 1931.

*Known temporal range.* Late Jurassic–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 40 (0→1): ventral process of the postorbital with a small anterior spur that probably marks the ventral delimitation of the eyeball. Convergently present in ceratosaurs and in *Tyrannosaurus*. Character 42 (0→1): presence of a posteriorly placed, knob-like dorsal projection on the parietals. Convergently present in ceratosaurs and baryonychids. Character 193 (0→1): distal end of ischium with a significantly expanded boot. Convergently present in ceratosaurs, '*Szechuanosaurus*' *zigongensis*, and some ornithomimosaurids.

*Possible additional apomorphies under ACCTRAN.* Character 11 (2→1): ascending process of the maxillary offset from anterior end of the maxillary body, and anterior projection of the maxillary body shorter than high. This is a reversal of a carnosaur synapomorphy. Unfortunately, all the taxa included in this clade exhibit different character states for this character, so it is impossible to determine which state is plesiomorphic for this node at present. Character 75 (1→0): anterior end of surangular less than half the height of the mandible at the level of the mandibular fenestra.

This is a reversal of a synapomorphy at node 14 (Tetanurae) or 15. It is only known in sinraptorids, so it is impossible to determine whether it represents a synapomorphy of the present clade, or a synapomorphy of sinraptorids. Character 133 (0→1): distal end of scapula not expanded. Within this clade, this character state is only known in sinraptorids. It is convergently present in *Herrerasaurus*, ceratosaurs, and advanced coelurosaurs. Character 153 (2→1): four digits present in the manus. Unknown in *Neovenator* and carcharodontosaurids; see node 15.

#### Node 23. unnamed node

*Included taxa.* *Neovenator* Hutt, Martill, and Barker, 1996; Carcharodontosauridae Stromer, 1931.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Cenomanian).

*Synapomorphies.* Character 6 (1→2): subnarial process of the premaxillary reduced, without contact with the nasals, and maxillary expressed at the rim of the external nares; see node 5 (Neotheropoda). Character 106 (1→2): pleurocoels present in all dorsal vertebrae. Convergently present in *Torvosaurus* and several coelurosaurs.

*Possible additional apomorphies under ACCTRAN.* All of the following characters are currently unknown in *Neovenator*. Character 21 (0→1): nasals of subequal width throughout their length. Convergently present in ceratosaurs and advanced coelurosaurs (node 29). Character 22 (1→0): absence of pronounced lateral rims of the nasals; see node 20 (Allosauroidae). Character 39 (0→1): lacrimal contacts the postorbital. Convergently present in abelisaurids and *Tyrannosaurus*. Character 96 (1→2): presence of internal pneumatic chambers with camellate structure in the cervical vertebrae. Convergently present in *Ceratosaurus* and coelurosaurs. Character 115 (0→1): pleurocoels present in the sacral vertebrae. Convergently present in ornithomimosaurids and oviraptorosaurs.

#### Node 24. Coelurosauria Huene, 1914

*Included taxa.* *Proceratosaurus* Huene, 1926a; Coeluridae Marsh, 1881b; Tyrannosauroidae (Osborn, 1906); *Ornitholestes* Osborn, 1903; *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a; Maniraptora Gauthier, 1986.

*Known temporal range.* Middle Jurassic (Bathonian)–Recent.

*Synapomorphies.* Character 14 (0→1): maxillary antorbital fossa more than 40 per cent of the length of the external antorbital fenestra.

*Possible additional apomorphies under ACCTRAN.* Character 32 (1→0): lacrimal horn absent. Within basal coelurosaurs, the character state is only known in the coelurid *Sinosauroptryx*, which lacks a lacrimal horn, and in tyrannosaurids, that have a lacrimal horn, although this structure is less well developed in this clade than in *Ceratosaurus* and many carnosaurids. The question whether the lacrimal horn was lost in coelurosaurs ancestrally, and then independently acquired again in tyrannosaurids, or if it was independently lost in coelurids and more advanced coelurosaurs can only be determined with more complete skull material of basal coelurosaurs. Character 48 (0→1): quadrate pneumatised. This character is unknown in *Proceratosaurus* and coelurids. In more advanced coelurosaurs, the quadrate is pneumatised in tyrannosaurids and the majority of other taxa, but not in *Ornitholestes* and dromaeosaurids. Character 51 (1→0): mandibular joint straight below the quadrate head. This is a reversal of a possible synapomorphy at node 11; see that node. Character 53 (0→1): bases of the paroccipital processes pneumatised. Unknown in *Proceratosaurus* and coelurids. Character 67 (2→3): ectopterygoid body excavated by a foramen that invades the body from the medial side. Unknown in *Proceratosaurus* and coelurids. Character 68 (0→1): presence of a subsidiary palatal fenestra. Unknown in *Proceratosaurus* and coelurids. Character 93 (1→0): axial neural spine sheet-like. This is a reversal of a possible tetanuran synapomorphy. The distribution of character states 0 and 1 are ambiguous in basal coelurosaurs: while the coelurid *Compsognathus* has a sheet-like axial neural spine, it is anteroposteriorly reduced and rod-like in tyrannosaurids; the character is unknown in all other basal coelurosaurs. Thus, more basal coelurosaur material is needed to determine the character state transformations in this character. Character 96 (1→2): internal pneumatic chambers with camellate structure present in the cervical vertebrae. Unknown in *Proceratosaurus* and coelurids; convergently present in *Ceratosaurus* and carcharodontosaurids. Character 97 (0→1): ventral keel in anterior cervicals absent. Unknown in *Proceratosaurus* and ambiguous in

coelurids and tyrannosaurids. Character 100 (0→1): prezygapophyses in anterior cervical vertebrae flexed ventrally anteriorly. Unknown in *Proceratosaurus*. In the coelurid *Coelurus*, state 1 is present, while tyrannosaurids exhibit state 0 for this character. As in character 93, more basal coelurosaur material is needed for a better understanding of character state transformation in this character at the basis of Coelurosauria. Character 101 (1→0): anterior articular facets of anterior cervical vertebrae higher than wide, or approximately as high as wide. Within basal coelurosaurs, the character state is only known in *Coelurus* and tyrannosaurids, which both exhibit state 0, while more derived coelurosaurs have state 2 of this character. Again, character state transformation of this character in basal coelurosaurs is too poorly understood to determine at which node it might represent a synapomorphy. Character 124 (0→1): neural spines of mid-caudals subrectangular and sheet-like. Unknown in *Proceratosaurus*. Character 129 (0→1): distal chevrons skid-like. Unknown in *Proceratosaurus*. Character 132 (0→1): scapula slender and elongate. Unknown in *Proceratosaurus* and convergently present in *Allosaurus*. Character 155 (1→0): extensor pits on the distal ends of the metacarpals shallow or absent. This is a reversal of a theropod synapomorphy. Unknown in *Proceratosaurus* and coelurids. Character 160 (1→2): penultimate phalanx of the third digit of the hand longer than both proximal phalanges taken together. Unknown in *Proceratosaurus*, coelurids and tyrannosaurids, so it cannot be determined at which node the character state transformation occurred. Character 169 (0→1): preacetabular process of ilium subequal in length to postacetabular process. Unknown in *Proceratosaurus*. Character 171 (0→1): iliac blades inclined medially and contact the sacral neural spines. Unknown in *Proceratosaurus* and coelurids. Character 175 (0→1): pubic peduncle of ilium anteroposteriorly elongate and narrow transversely. Unknown in *Proceratosaurus*. Character 179 (0→1): anterior margin of pubic peduncle of ilium concave. Unknown in *Proceratosaurus* and reversed in maniraptorans. Character 185 (0→1): pubic boot narrow in ventral view, with subparallel lateral margins. Unknown in *Proceratosaurus* and reversed in *Deltadromeus*; this might be another indication that the latter genus could move to the base of Coelurosauria when more material becomes available (see character 218 at node 11). Character 188 (0→1): obturator process offset from pubic peduncle of the ischium. Unknown in *Proceratosaurus* and convergently present at node 21. Character 207 (0→2): anterior side of distal end of tibia flat. Unknown in *Proceratosaurus* and convergently present in *Elaphrosaurus*. Character 213 (0→1): fibular facet on astragalus reduced and faces entirely laterally. Unknown in *Proceratosaurus* and coelurids. Character 214 (0→1): ascending process of astragalus arises from the entire breadth of the astragalus body. Unknown in *Proceratosaurus*. Character 215 (1→2): ascending process of astragalus more than twice the height of the astragalus body. Unknown in *Proceratosaurus*. Character 216 (0→1): ascending process of the astragalus offset from the astragalus body by a pronounced oval groove. Unknown in *Proceratosaurus* and coelurids. Character 218 (1→0): no horizontal groove across the astragalus condyles present. This is a reversal of a possible synapomorphy at node 11. Unknown in *Proceratosaurus* and coelurids.

*Remarks.* The name Coelurosauria was created by Huene (1914), who regarded the coelurosaurs as the basal group of saurischians from which the Pachypodosauria originated. Later, the name was widely used for all small theropod dinosaurs (e.g. Romer 1956, 1966; Colbert 1964; Steel 1970). The name Coelurosauria is applied here to this clade for the reasons given at node 16 (Carnosauria).

#### Node 25. unnamed node

*Included taxa.* Coeluridae Marsh, 1881b; Tyrannosauroida (Osborn, 1906); *Ornitholestes* Osborn, 1903; *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a; Maniraptora Gauthier, 1986.

*Known temporal range.* Late Jurassic (Kimmeridgian)–Recent.

*Synapomorphies.* Character 11 (1→0): ascending process of maxillary confluent with the anterior rim of the maxillary body. This is a reversal of a synapomorphy at node 11. Character 84 (0→1): no serrations on the premaxillary teeth. Most coelurosaurs lack serrations on the premaxillary teeth, and the presence of serrations on these teeth in most tyrannosaurs and in deinonychosaurs most probably represents a reversal of this synapomorphy. In tyrannosaurs, the absence of serrations on the premaxillary teeth in one of the most basal taxa of this clade, *Aublysodon* (Molnar and Carpenter 1989; see also Holtz 2001), strengthens this hypothesis.

*Possible additional apomorphies under ACCTRAN.* Character 23 (2→0): sublacrimal part of jugal tapers anteriorly. This is a reversal of a synapomorphy at node 3. Although no well-preserved jugal is known in coelurids, the fragments

of this element in *Compsognathus* show that the anterior end of this bone was not expanded, unlike the situation seen in most other theropods, with the exception of coelophysoids and advanced coelurosaurs (node 32). However, members of the next crownward clade on the coelurosaurs branch, the tyrannosaurids, have an expanded anterior end of the jugal. Therefore, it is not clear what kind of character state transformations occurred in basal coelurosaur evolution and whether this reversal represents a synapomorphy of the present clade, or at node 31 or 32. Character 47 (0→1): quadratojugal with a short, broad posterior process that wraps around the lateroventral edge of the quadrate. Unknown in coelurids.

*Possible additional apomorphies under DELTRAN.* Character 124 (0→1): neural spines of mid-caudals subrectangular and sheet-like; see node 24. Character 129 (0→1): distal chevrons skid-like; see node 24. Character 132 (0→1): scapula slender and elongate; see node 24. Character 153 (1→2): fourth digit of the manus absent; see node 15. Character 169 (0→1): preacetabular process of ilium subequal in length to postacetabular process; see node 24. Character 175 (0→1): pubic peduncle of ilium anteroposteriorly elongate and narrow transversely; see node 24. Character 179 (0→1): anterior margin of pubic peduncle of ilium concave; see node 24. Character 185 (0→1): pubic boot narrow in ventral view, with subparallel lateral margins; see node 24. Character 188 (0→1): obturator process offset from pubic peduncle of the ischium; see node 24. Character 190 (1→0): absence of a ventral notch between the obturator process and the ischial shafts. This is a reversal of a neotheropodan synapomorphy. Several authors have used 'obturator process triangular' as a coelurosaur synapomorphy. However, the triangular shape of the process in this group is caused by the absence of the ventral notch, as can be seen in the asymmetric pelvis of SMNK 2349 Pal; see also node 15. Character 207 (0→2): anterior side of distal end of tibia flat; see node 24. Character 214 (0→1): ascending process of astragalus arises from the entire breadth of the astragalar body; see node 24. Character 215 (1→2): ascending process of astragalus more than twice the height of the astragalar body; see node 24.

#### *Node 26. Coeluridae Marsh, 1881b*

*Included taxa.* *Coelurus* Marsh, 1879; *Compsognathinae* (Marsh, 1882).

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Early Cretaceous (Aptian–Albian).

*Synapomorphies.* Character 102 (2→1): epiphyses in cervical vertebrae well-developed, but do not overhang the postzygapophyses. This is a reversal of a synapomorphy at node 10. Character 109 (1→0): neural spines of posterior dorsals low and approximately as long as high. This is a reversal of a synapomorphy at node 3.

*Possible additional apomorphies under ACCTRAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares and angle between anterior margin and alveolar margin less than 70 degrees. Unknown in *Coelurus*; see also node 5 (Neotheropoda). Character 4 (0→1): posterior end of the premaxillary body forked. Within coelurids, this character state is only known in *Compsognathus*, so it is impossible to decide at which node the character state transformation occurred. Convergent present in coelophysids. Character 6 (1→2): subnarial process of the premaxillary reduced, without contact with nasal, and maxillary forms a part of the rim of the external nares. As discussed at node 5 (Neotheropoda), the distribution of this character state in theropods is problematical. Within coelurids, it is only known in *Compsognathus*.

*Remarks.* The Coeluridae was proposed by Marsh (1881b) to include the genus *Coelurus*, and subsequently the name was often used as a 'waste bin' taxon for small coelurosaurian theropods that could not be assigned to one of the more distinct families of coelurosaurs. The present analysis retrieved a monophyletic clade that includes *Coelurus* and some other small coelurosaurs, and thus the name Coeluridae is used for this clade here.

#### *Node 27. Compsognathinae (Marsh, 1882)*

*Included taxa.* *Sinosauropteryx* Ji and Ji, 1996; *Compsognathus* Wagner, 1861; an unnamed compsognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal).

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Early Cretaceous (Aptian–Albian).

*Synapomorphies.* Character 110 (0→1): neural spines of posterior dorsal vertebrae fan-shaped. Convergently present in *Elaphrosaurus*. Character 187 (0→1): pubic boot without anterior expansion. Convergently present in '*Szechuanosaurus*' *zigongensis* and at node 35. In *Coelurus*, the anterior process of the pubic boot is already greatly reduced, which might be another indication of a close relationship between the latter taxon and compsoognathines.

*Possible additional apomorphies under ACCTTRAN.* Character 97 (1→0): presence of a ventral keel on the anterior cervical vertebrae. This is a reversal of a possible coelurosaur synapomorphy. Within compsoognathines, the character state is only known in *Compsognathus*; see also node 24 (Coelurosauria). Character 201 (0→1): fourth trochanter of femur reduced. Within compsoognathines, this character state is only known for the unnamed taxon from the Lower Cretaceous of Brazil.

*Possible additional apomorphies under DELTRAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares and angle between anterior margin and alveolar margin less than 70 degrees; see node 26.

*Remarks.* Marsh (1882) proposed the name Compsognathidae for the genus *Compsognathus*. The family was later variously used and often synonymized with the Coeluridae (e.g. Steel 1970). Recently, Chen *et al.* (1998) argued for a monophyletic Compsognathidae to include the genera *Sinosauropteryx* and *Compsognathus*. Since this close relationship is confirmed in the present analysis, the name is applied at this node. However, it is used as a subfamily name to indicate that this clade forms a subset of the Coeluridae, which is formally a family-rank taxon.

#### Node 28. unnamed node

*Included taxa.* *Compsognathus* Wagner, 1861; an unnamed compsoognathine from the Lower Cretaceous of Brazil (SMNK 2349 Pal).

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Early Cretaceous (Aptian–Albian).

*Synapomorphies.* Character 187 (1→2): pubic boot only posteriorly expanded and more than half the length of the pubic shafts.

*Possible additional apomorphies under ACCTTRAN.* All of the following characters are unknown in SMNK 2349 Pal, so it is uncertain if they represent synapomorphies of this clade, or autapomorphies of *Compsognathus*. Character 5 (1→0): three premaxillary teeth. Character 95 (0→1): cervical vertebrae strongly opisthocoelous. Character 124 (1→0): neural spines of the mid-caudal vertebrae rod-like and posteriorly inclined. This is a reversal of a coelurosaur synapomorphy. Character 130 (1→0): mid-caudal chevrons rod-like. This is a reversal of a synapomorphy at node 14 or 15.

#### Node 29. unnamed node

*Included taxa.* Tyrannosauroida (Osborn, 1906); *Ornitholestes* Osborn, 1903; *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a; Maniraptora Gauthier, 1986.

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Recent.

*Synapomorphies.* Character 21 (0→1): nasals of subequal width throughout their length. Convergently present in ceratosaurs and carcharodontosaurids. In contrast to ceratosaurs, the nasals are furthermore very slender in coelurosaurs. Character 43 (0→2): supratemporal fenestrae confluent over the parietals and parietals form a sagittal crest. Reversed in ornithomimosaurids and therizinosauroids. Character 117 (0→1): fewer than 41 caudal vertebrae. Character 118 (0→1): fewer than 16 caudal vertebrae with transverse

processes. Reversed in *Microvenator* and oviraptorosaurs. Character 150 (0→1): medial side of metacarpal II straight, without expansion proximally. Character 180 (1→2): obturator foramen in pubis completely absent. This character state is convergently present in *Elaphrosaurus*. Character 193 (0→2): ischial shaft tapers distally. Reversed in ornithomimosaurids, in which the ischium is expanded distally in many taxa. Character 194 (0→1): femoral head separated from the greater trochanter of the femur by a cleft. Convergently present in ornithischians. Character 199 (1→2): lesser trochanter as high or higher than greater trochanter. Convergently present in ornithischians. It is reversed in *Caudipteryx* and *Deltadromeus*, which might be another indication that the latter taxon could move to the basis of coelurosaurs when more material becomes available.

*Possible additional apomorphies under ACCTRAN.* Character 35 (0→1): lacrimal contacts frontal. The lacrimal is in contact with the frontal in a variety of coelurosaurs, including tyrannosaurids, birds, dromaeosaurids, troodontids, and oviraptorosaurs, but not in ornithomimosaurids and therizinosaurids. Given this distribution, it is impossible to determine whether the character state represents a synapomorphy at this node that is reversed in ornithomimosaurids and therizinosaurids (ACCTRAN), or a convergent development in the other clade. The character state is convergently present in abelisaurids. Character 152 (0→1): proximal articular end of Mc III not significantly expanded. The character state is unknown in tyrannosaurids and its distribution in the remaining coelurosaurs is ambiguous, although it is present in the majority of the taxa included in this clade. It seems probable, therefore, that the character state represents a synapomorphy at the present node, or at node 31, but the final solution to this problem can only come from more material of basal members of this clade. Character 186 (0→1): pubic boot more expanded anteriorly than posteriorly. The pubic boot is more expanded anteriorly in tyrannosaurids, *Deltadromeus*, and the therizinosaur-oviraptorosaur clade, but not in ornithomimosaurids and the bird-deinonychosaur clade. However, since the morphology of the pubic boot is different in tyrannosaurs on the one hand and therizinosaurids and oviraptorosaurs on the other hand, it seems more likely that the character state arose independently in the three clades that show state 1.

*Possible additional apomorphies under DELTRAN.* Character 47 (0→1): quadratojugal with short, broad posterior process that wraps around the lateroventral edge of the quadrate; see node 25. Character 53 (0→1): bases of the paroccipital processes pneumatized; see node 24 (Coelurosauria). Character 67 (0→3): ectopterygoid body excavated by a foramen that invades the body from the medial side ventrally; see node 24 (Coelurosauria). Character 68 (0→1): presence of a subsidiary palatal fenestra; see node 24 (Coelurosauria). Character 96 (1→2): internal pneumatic chambers with camellate structure present in the cervical vertebrae; see node 24 (Coelurosauria). Character 155 (1→0): extensor pits on the distal ends of the metacarpals shallow or absent; see node 24 (Coelurosauria). Character 171 (0→1): iliac blades inclined medially and in contact with the sacral neural spines; see node 24 (Coelurosauria). Character 213 (0→1): fibular facet on the astragalus reduced and faces laterally; see node 24 (Coelurosauria). Character 216 (0→1): ascending process of the astragalus offset from astragalus body by an oval groove; see node 24 (Coelurosauria).

### Node 30. Tyrannosauroida (Osborn, 1906)

*Included taxa.* *Stokesosaurus* Madsen, 1974; Tyrannosauridae Osborn, 1906.

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 172 (0→1): presence of a well-developed, sharply defined vertical ridge on the iliac blade above the acetabulum. Character 173 (0→1): anterior rim of iliac blade concave dorsally.

*Possible additional apomorphies under ACCTRAN.* All of the following characters are unknown in *Stokesosaurus*, so it cannot be determined if they represent synapomorphies of this clade, or of tyrannosaurids. Character 1 (0→1): premaxillary body significantly higher than wide. If the premaxilla referred to *Stokesosaurus* by Madsen (1974) does belong to this taxon, the character state is also found in this taxon. Convergently present in ceratosaurs and oviraptorosaurs. Character 18 (0→1): dorsal surface of the nasals rugose. Convergently present in ceratosaurs, *Monolophosaurus* and carcharodontosaurids. Character 23 (0→2): sublacrimar part of the jugal expanded. This is a reversal of a possible synapomorphy at node 25. Character 26 (0→1): jugal pneumatized by a foramen in the posterior rim of the jugal antorbital fossa. Convergently present in allosauroids. Character 32 (0→1): presence of a lacrimal horn; see node 24 (Coelurosauria). Character 93 (0→1): axial neural spine anteroposteriorly reduced and rod-like; see

node 24 (Coelurosauria). Character 100 (1→0): prezygapophyses of anterior cervical vertebrae straight. This is a reversal of a possible coelurosaur synapomorphy. Character 106 (1→2): pleurocoels present in posterior dorsals. Convergently present in *Torvosaurus*, at node 23, and in *Unenlagia*, *Microvenator*, and oviraptorosaurs. Character 139 (1→0): femur more than 2.5 times the length of the femur. Convergently present in abelisaurids, *Allosaurus*, and *Sinosauropteryx*. Character 142 (0→1): deltopectoral crest of humerus strongly reduced. Convergently present in abelisauroids and ornithomimosaurids. Character 143 (0→1): humerus straight in lateral view. Convergently present in ceratosaurs and at nodes 18 and 33. Character 145 (0→1): radius less than half the length of the humerus. Convergently present in abelisaurids and spinosauroids. Character 210 (1→2): presence of a deep groove on the medial side of the proximal end of the fibula that covers more than two-thirds of the width of the bone. Convergently present in baryonychids, at node 33, and in dromaeosaurids. Character 220 (0→1): arctometatarsalian pes. Convergently present in most ornithomimosaurids, troodontids, and at node 39.

*Remarks.* The name Tyrannosauroidae is used here to label a monophyletic clade that includes the family Tyrannosauridae and its immediate outgroup, reflecting a traditional family-superfamily hierarchy.

#### Node 31. unnamed node

*Included taxa.* *Ornitholestes* Osborn, 1903; *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a; Maniraptora Gauthier, 1986.

*Known temporal range.* Late Jurassic (Kimmeridgian–Tithonian)–Recent.

*Synapomorphies.* Character 45 (1→0): quadratojugal process of the squamosal tapers ventrally. This is a reversal of a synapomorphy at node 2 (Theropoda) or 3. Character 101 (1→2 or 0→2): anterior articular facets of cervical vertebrae wider than high and higher laterally than medially (kidney-shaped). Reversed in *Microvenator* and *Avimimus*. Whether the character transition at this node is from state 0 to state 2, or state 1 to 2 depends on the character state in basal coelurosaurids (see node 24). More material of basal coelurosaurids is needed to decide this issue. Character 114 (0→1): sacral vertebral centra flattened ventrally. Convergently present in *Syntarsus* and *Elaphrosaurus*. Character 201 (0→1): fourth trochanter of femur reduced. Convergently present in SMNK 2349 Pal and reversed in *Avimimus* and at least one specimen of *Velociraptor* (Norell and Makovicky 1997).

*Possible additional apomorphies under ACCTRAN.* Character 30 (0→1): nasolacrimal duct does not pierce the body of the lacrimal, but runs lateral to it. This character is unknown in many members of this clade. Character state 1 is present in ornithomimosaurids, birds, and troodontids, while state 0 is present in dromaeosaurids and therizinosaurs. More information on lacrimal morphology in advanced coelurosaurids is needed for a better understanding of character state transformations in this character. Character 36 (0→1): frontal elongated and triangular. Again, this character is unknown in several members of this clade, and its distribution in advanced coelurosaurids is poorly understood. Character 37 (0→1): medial delimitation of the eyeballs on the ventral side of the frontals expanded ventrally and forms a pronounced rim. Unknown in *Ornitholestes*. Character 63 (0→1): endocranium enlarged. Unknown in *Ornitholestes*. Character 64 (0→1): forebrain enlarged and triangular in dorsal view. Unknown in *Ornitholestes*. Character 80 (0→1): coronoid strongly reduced or absent. Unknown in *Ornitholestes* and reversed in dromaeosaurids. Character 92 (2→1): epiphyses of axis well developed, but not overhanging the postzygapophyses. This is a reversal of a synapomorphy at node 10. Unknown in *Ornitholestes*. Character 94 (0→1): axial neural spine not excavated by a deep groove posteriorly. Unknown in *Ornitholestes*. This character state is also present in '*Chilantaisaurus*' *maortuensis*, which is not included in the tree described here, indicating that this taxon is a member of the present clade. Character 107 (0→1): hypapophyses in anterior dorsals strongly pronounced. This character state was regarded as a maniraptoran synapomorphy by Gauthier (1986). However, it is present in *Ornitholestes*, which falls outside Maniraptora in the present analysis. Since hypapophyses are absent in ornithomimosaurids and *Microvenator*, it is uncertain whether it represents a synapomorphy at this node that is reversed in these two taxa, or if it represents convergent developments in the other members of this clade. Character 133 (0→1): scapular blade not expanded distally. Unknown in *Ornitholestes* and state 1 is convergently present in *Herrerasaurus*, ceratosaurs, and sinraptorids. Character 144 (0→1): olecranon process of ulna reduced. Unknown in *Ornitholestes*. Character 147 (0→1): metacarpus slender and elongated. As in several of the characters discussed above, the distribution of character states 0 and 1 is equivocal in this clade, so it remains uncertain if the character state represents

a synapomorphy at this node. Character 174 (0→1): dorsal margin of the posterior end of the ilium slopes downwards. This character state is present in *Ornitholestes*, but not in ornithomimosaurids. Therefore, it is uncertain if it represents a synapomorphy at this node that is reversed in ornithomimosaurids, or a convergence in *Ornitholestes* and maniraptorans.

*Possible additional apomorphies under DELTRAN.* Character 97 (0→1): no ventral keel on the anterior cervical vertebrae; see node 24 (Coelurosauria). Character 100 (0→1): prezygapophyses of anterior cervical vertebrae flexed ventrally; see node 24 (Coelurosauria). Character 160 (1→2): penultimate phalanx of the third digit of the hand longer than both proximal phalanges taken together; see node 24 (Coelurosauria).

#### Node 32. unnamed node

*Included taxa.* *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a; Maniraptora Gauthier, 1986.

*Known temporal range.* Late Jurassic (Tithonian)–Recent.

*Synapomorphies.* Character 25 (1→0): jugal antorbital fossa absent or developed as a slight depression. This is a reversal of a synapomorphy at node 14 or 15. Character 31 (1→0): lacrimal fenestra absent. This is a reversal of a synapomorphy at node 10 or 11. Character 33 (0→1): presence of a posterior dorsal process of the lacrimal. Reversed in therizinosaurs and convergently present in abelisaurids. Character 87 (0→1): presence of a constriction between the tooth crown and the root. Reversed in dromaeosaurids and convergently present in ornithischians and basal sauropodomorphs. Character 102 (2→1): epipophyses in anterior cervical vertebrae present, but do not overhang the postzygapophyses. This is a reversal of a synapomorphy at node 10. Character 113 (2→3): more than five sacral vertebrae. Reversed in *Caudipteryx*, *Archaeopteryx* and some dromaeosaurids, and convergently present in abelisaurids.

*Possible additional apomorphies under ACCTTRAN.* Character 3 (0→1): presence of a broad palatal shelf on the medial side of the premaxillaries. This character state is present in ornithomimosaurids and the members of the therizinosaur–oviraptorosaur clade, but not in deinonychosaurs. Derived birds also have a broad palatal shelf on the premaxilla, but the situation is unknown in *Archaeopteryx*, in which the tip of the snout seems to be rather narrow. Although the presence of this shelf in advanced birds thus indicates that the character state represents a synapomorphy at this node that is reversed in deinonychosaurs, some uncertainty remains. Character 12 (1→0): maxillary antorbital fossa deep and with sharply defined margins. This is a reversal of a neotheropodan synapomorphy. Again, character state 0 is present in ornithomimosaurids and the therizinosaur–oviraptorosaur clade, but not in the bird–deinonychosaur clade. This distribution does not allow a final decision whether the character state transformation represents a synapomorphy at this node that is reversed in the bird–dinosaur clade (ACCTTRAN), or a convergence in ornithomimosaurids and the therizinosaur–oviraptorosaur clade (DELTRAN). However, the latter explanation seems to be more likely in this case, because of the great similarity of the morphology of the antorbital fossa of deinonychosaurs to that in most theropods. Character 44 (0→1): postorbital part of the skull roof deflected ventrally. The distribution of this character state within the present clade is equivocal, and more material of basal members of this clade is necessary to determine whether it represents a synapomorphy at this node, or convergent developments in ornithomimosaurids, the bird–deinonychosaur clade, and *Avimimus*. Character 115 (0→1): presence of pleurocoels in the sacral vertebrae. Pleurocoels are present in the sacral vertebrae of ornithomimosaurids and oviraptorosaurs, and some dromaeosaurids. However, differences in the position and development of these pleurocoels suggest that they were acquired independently in all those clades, so it seems unlikely that this character state represents a synapomorphy of the present clade.

*Possible additional apomorphies under DELTRAN.* Character 23 (2→0): sublacrimal part of the jugal tapers anteriorly; see node 25. Character 37 (0→1): medial delimitation of the eyeballs on the ventral side of the frontals expanded ventrally and forms a pronounced rim; see node 31. Character 48 (0→1): quadrate pneumatized; see node 24 (Coelurosauria). Character 63 (0→1): enlarged endocranium; see node 31. Character 64 (0→1): forebrain enlarged and triangular in dorsal view; see node 31. Character 80 (0→1): coronoid strongly reduced or absent; see node 31. Character 92 (2→1): epipophyses on axis present, but do not overhang the postzygapophyses; see node 31. Character 94 (0→1): axial neural spine not excavated by a deep groove posteriorly; see node 31. Character 133 (0→1): distal end of the scapula not expanded; see node 31. Character 144 (0→1): olecranon process of ulna reduced; see node 31.

*Node 33. unnamed node*

*Included taxa.* *Deltadromeus* Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio and Wilson, 1996; Ornithomimosauria Barsbold, 1976a.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 143 (0→1): humerus straight in lateral view. This character state is convergently present in ceratosaurs, advanced spinosauroids, and tyrannosaurids. Character 210 (1→2): presence of a deep groove on the medial side of the proximal end of the fibula that covers more than two-thirds the width of the bone.

*Possible additional apomorphies under ACCTTRAN.* All of the following characters are unknown in *Deltadromeus*. Character 5 (1→3): more than five premaxillary teeth. This character state is only known in the basal ornithomimosaur *Pelecanimimus*, so it cannot be determined whether it represents a synapomorphy of this clade, of ornithomimosaur, or an autapomorphy of this genus. It is convergently present in baryonychids. Character 6 (1→0): subnarial posterior process of the premaxilla wide, plate-like, broadly contacts the nasals and excludes the maxilla from the external nares. This is a reversal of a saurischian synapomorphy. Character 35 (1→0): lacrimal without contact with the frontal. This is a reversal of a possible synapomorphy at node 29; see that node. Character 43 (2→0): supratemporal fenestrae separated by a horizontal plate of bone formed by the parietals. This is a reversal of a synapomorphy at node 29. Character 51 (0→2): mandibular joint situated significantly anterior to the quadrate head. Character 54 (1→0): the ventral rim of the bases of the paroccipital processes is situated above the occipital condyle. This is a reversal of a synapomorphy at node 11. Character 62 (0→1): parasphenoid expanded, cone-shaped and pneumatized. Convergently present in troodontids. Character 76 (0→1): anterior part of dentary flexed medially. Convergently present in troodontids and the therizinosaur–oviraptorosaur clade. Character 78 (1→0): no foramen in the splenial. This is a reversal of a saurischian synapomorphy. Character 85 (0→1): no serrations on maxillary and dentary teeth. This character state is only known for the basal ornithomimosaur *Pelecanimimus*. Character 107 (1→0): anterior cervical hypapophyses reduced. This is a reversal of a possible synapomorphy at node 31. Character 108 (1→0): ventral keel in anterior dorsals reduced. This is a reversal of a tetanuran synapomorphy. Character 112 (1→2): posterior dorsal vertebrae significantly elongated. Character 120 (1→0): no ventral groove in the anterior caudal vertebrae. This is a reversal of a neotheropodan synapomorphy. Character 146 (2→0): carpals reduced. This is a reversal of a neotheropodan synapomorphy. Character 147 (1→0): metacarpus relatively short and broad. This is a reversal of a possible synapomorphy at node 31. Character 152 (1→0): proximal articular end of Mc III expanded. This is a reversal of a possible synapomorphy at node 29. Character 174 (1→0): dorsal rim of posterior end of ilium slopes downwards. This is a reversal of a possible synapomorphy at node 31. Character 176 (0→1): brevis fossa on ilium markedly expanded posteriorly. Convergently present in coelophysoids. Character 178 (0→1): articular facet of pubic peduncle of ilium subdivided, with an anterior facet that faces anteroventrally. Convergently present in coelophysoids and *Dilophosaurus*. Character 193 (2→1): distal end of ischium expanded. This is a reversal of a synapomorphy at node 29.

*Node 34. Maniraptora Gauthier, 1986*

*Included taxa.* *Bagaraatan* Osmólska, 1996; *Unenlagia* Novas and Puerta, 1997; Aves Linnaeus, 1758; Deinonychosauria Colbert and Russell, 1969; Therizinosauroida (Maleev, 1954); *Caudipteryx* Ji, Currie, Norell and Ji, 1998; *Microvenator* Ostrom, 1970; *Avimimus* Kurzanov, 1981; Oviraptorosauria Barsbold, 1976a.

*Known temporal range.* Late Jurassic (Tithonian)–Recent.

*Synapomorphies.* Character 6 (1→2): subnarial posterior process of premaxilla without contact with the nasals and maxilla participates in the rim of the external nares; see node 5 (Neotheropoda). Character 117 (1→2): less than 35 caudal vertebrae. Character 137 (0→1): coracoid longer than high. Character 141 (0→1): internal tuberosity on humerus rectangular. Character 146 (1→3 or 2→3): presence of a true semilunate carpal. It seems very likely that the character state transformation at this node is from state 2 to 3, since the morphology of the carpal of state 2 is very similar to that of a true semilunate carpal. Furthermore, state 2 is present in the basal coelurosaur *Coelurus*. Character 162 (0→1): presence of a dorsal ‘lip’ on the proximal articular facets of the manual unguals. Character 165 (0→1): presence of contour feathers. Character 179 (1→0): anterior margin of pubic peduncle straight or convex. This is a

reversal of a synapomorphy at node 24 or 25. Character 189 (0→1): obturator process of ischium distally placed. Character 196 (0→1): presence of a trochanteric crest on the proximal end of the femur. Convergently present in ornithischians. Character 202 (1→0): groove on the anterior side of the distal end of the femur absent. This is a reversal of a synapomorphy at node 11. A groove is present in dromaeosaurids, but this is interpreted as a convergence in the present analysis. Character 208 (2→3): distal end of tibia broadly rectangular and more than three times wider than long. Character 210 (1→0): groove on the medial side of the proximal end of the fibula absent. This is a reversal of synapomorphy at node 10. A groove is present in dromaeosaurids, but this is interpreted as a convergence in the present analysis. Character 212 (0→1): fibular shaft narrows abruptly below the insertion area of the m. iliofibularis. Character 223 (2→1): metatarsal V strongly reduced and rod-like. This is a reversal of a synapomorphy at node 10.

*Possible additional apomorphies under ACCTAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares and angle between anterior margin and alveolar margin less than 70 degrees. This character state is present in birds and the therizinosaur–oviraptorosaur clade, but not in deinonychosaurs. Thus, it is uncertain if it represents a synapomorphy at this node that is reversed in deinonychosaurs, or if it is a convergence in birds and the therizinosaur–oviraptorosaur clade; see also node 5 (Neotheropoda). Character 79 (1→0): posterior end of splenial straight. This character state has the same distribution as the character state discussed above, and is thus equally equivalent. Character 198 (2→3): lesser trochanter fused with greater trochanter. This character state is present in the bird–deinonychosaur clade and *Bagaraatan*, but not in the therizinosaur–oviraptorosaur clade. Thus, it seems to be a synapomorphy of the former clade, rather than a maniraptoran synapomorphy, and the presence of this character state in *Bagaraatan* might indicate that this genus belongs to the bird–deinonychosaur clade. Character 205 (1→0): posterior cleft between medial part of the proximal end of the tibia and fibular condyle absent. This is a reversal of a neotheropodan synapomorphy. A cleft is absent in *Bagaraatan* and *Avimimus*, but not in the bird–deinonychosaur clade; the character state is unknown in all other members of the therizinosaur–oviraptorosaur clade. The interpretation of this character depends on the phylogenetic position of *Bagaraatan* and the character state in therizinosaurs and oviraptorosaurs, so more material, or further studies of known material are needed.

*Possible additional apomorphies under DELTRAN.* Character 107 (0→1): well-developed hypapophyses present in the anterior dorsal vertebrae; see node 31. Character 174 (0→1): dorsal margin of the posterior end of the ilium slopes downwards; see node 31.

*Remarks.* Gauthier (1986) named the Maniraptora to identify a monophyletic taxon within coelurosaurs. Since the taxonomic contents of the present clade are in general accordance with Gauthier's Maniraptora, the name is applied at this node. This is also in accordance with the phylogenetic definition of the Maniraptora given by Sereno (1998).

*Node 35.* unnamed node

*Included taxa.* *Unenlagia* Novas and Puerta, 1997; Aves Linnaeus, 1758; Deinonychosauria Colbert and Russell, 1969.

*Known temporal range.* Late Jurassic (Tithonian)–Recent.

*Synapomorphies.* Character 104 (0→1): hyposphene wide, formed by the ventrally flexed medial parts of the postzygapophyses, which are only connected by a thin horizontal lamella of bone. Character 118 (1→2): ten or fewer caudal vertebrae with transverse processes. Character 119 (0→1): fewer than 11 caudal vertebrae with well-developed neural spines. Character 127 (0→1): anterior caudal vertebrae box-like and anterior articular facet of the vertebrae rectangular in outline. Character 134 (0→1): acromion process of scapula low and dorsal margin of the proximal end of the scapula slopes gently downwards. Character 135 (0→1): glenoid facet on scapula faces ventrolaterally. Character 138 (0→1): coracoid subrectangular in outline. Convergently present in oviraptorosaurs. Character 157 (0→1): shaft of metacarpal III bowed laterally. Character 163 (0→1): flexor tubercle of manual unguals more than half the height of the articular facet. Character 169 (1→2): preacetabular process of ilium longer than

postacetabular process. Character 187 (0→1): pubic boot only expanded posteriorly. Convergently present in *Szechuanosaurus zigongensis* and compsognathines. Character 191 (0→1): ischium two-thirds or less the length of the pubis. Convergently present in coelophysoids and *Sinosauropteryx*.

*Possible additional apomorphies under ACCTRAN.* Character 3 (1→0): broad palatal shelf of the premaxillary absent. This is a reversal of a possible synapomorphy at node 32; see that node. Character 12 (0→1): maxillary antorbital fossa shallow and margins formed by low ridges; see node 32. Character 115 (1→0): no pleurocoels in the sacral vertebrae. This is a reversal of a possible synapomorphy at node 32; see that node. Character 167 (0→1): pelvis opisthopubic. The pelvis is opisthopubic in *Unenlagia*, birds, and dromaeosaurids, but not in troodontids. Given this distribution of character state 1, it is uncertain whether this character state represents a synapomorphy at this node that is reversed in troodontids, or if the retroversion of the pubis occurred independently in the bird–*Unenlagia* clade and dromaeosaurids. Character state 1 is convergently present in therizinosauroids and ornithischians. Character 186 (1→0): pubic boot more posteriorly than anteriorly expanded. This is a reversal of a possible synapomorphy at node 29; see that node. Character 200 (0→1): posterolateral trochanter present on the femur. This character state is present in deinonychosaurs and basal birds (*Archaeopteryx*, *Rahonavis*), but not in *Unenlagia*. Although the distribution of this character state is thus equivocal, it seems likely that it represents a synapomorphy at this node that is reversed in *Unenlagia*, as suggested by ACCTRAN. Character 205 (0→1): presence of a cleft posteriorly between the medial part of the proximal end of the tibia and the fibular condyle. This is a reversal of a possible maniraptoran synapomorphy (which represents a reversal itself); see node 34. Character 224 (0→1): second digit of the pes bears an enlarged unguis and is highly specialized. The second digit of the pes is highly specialized in dromaeosaurids and troodontids; in basal birds, the character state is equivocal. The earliest bird, *Archaeopteryx*, does not show any of the specialisations seen in deinonychosaurs, while the second digit in *Rahonavis* is very similar in morphology to that of dromaeosaurids. However, slight differences in the morphology of phalanx II-2 in *Rahonavis* might indicate convergence. The final solution of this problem can only come from more complete or better preserved pedal material of basal birds.

*Possible additional apomorphies under DELTRAN.* Character 35 (0→1): lacrimal contacts frontal; see node 29. Character 44 (0→1): postorbital part of the skull roof deflected ventrally; see node 32. Character 147 (0→1): metacarpus slender and elongated; see node 31. Character 152 (0→1): proximal articular end of metacarpal III not expanded; see node 29. Character 198 (2→3): lesser trochanter fused with greater trochanter; see node 34 (Maniraptora).

#### Node 36. unnamed node

*Included taxa.* *Unenlagia* Novas and Puerta, 1997; Aves Linnaeus, 1758.

*Known temporal range.* Late Jurassic (Tithonian)–Recent.

*Synapomorphies.* Character 168 (1→0): no ventral hook on the anterior end of the preacetabular process of the ilium. This is a reversal of a synapomorphy at node 10 or 11. Character 192 (0→1): presence of a pronounced posterior process on the proximal part of the ischium.

*Possible additional apomorphies under ACCTRAN.* All of the following characters are unknown in *Unenlagia* and it is, therefore, uncertain whether they represent synapomorphies at this node, or synapomorphies of birds. Character 27 (0→1): jugal very slender and rod-like. Convergently present in *Avimimus* and oviraptorosaurs. Character 46 (0→1): no contact between the squamosal and the quadratojugal. Convergently present in *Syntarsus*, *Dilophosaurus*, abelisaurids, and oviraptorosaurs. Character 50 (0→1): dorsal end of the quadrate double-headed. Convergently present in oviraptorosaurs. Character 51 (0→2): mandibular joint anterior to quadrate head. Convergently present in baryonychids and ornithomimosaurids. Character 61 (1→0): mid cerebral vein exits the braincase through the trigeminal foramen. This is a reversal of a synapomorphy at node 1 (Saurischia) or 10. Character 65 (1→2): jugal process of palatine strongly reduced or absent. Character 85 (0→1): serrations on maxillary and dentary teeth absent. Convergently present in the basal ornithomimosaur *Pelecanimimus*. Character 106 (1→2): pleurocoels present in all dorsal vertebrae. The character state is uncertain in birds. It might represent a synapomorphy at node 35, since pleurocoels are present in all dorsal vertebrae in the North American dromaeosaurids *Deinonychus* and *Sauromitholestes*. Thus, the absence of pleurocoels in the posterior dorsals in the Asian dromaeosaurid *Velociraptor* and troodontids might represent a reversal. Character 139 (1→2): humerus longer than femur.

*Possible additional apomorphies under DELTRAN.* Character 167 (0→1): pelvis opisthopubic; see node 35.

*Node 37. Deinonychosauria* Colbert and Russell, 1969

*Included taxa.* Dromaeosauridae (Matthew and Brown, 1922); Troödontidae Gilmore, 1924b.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 78 (1→2): splenial foramen open anteroventrally. Convergently present in *Monolophosaurus*. Character 84 (1→0): premaxillary teeth with serrated carinae. This is a reversal of a synapomorphy at node 25; see that node. Character 92 (1→2): axial epiphyses overhang the postzygapophyses. This is a reversal of a synapomorphy at node 31 or 32, which in itself is a reversal of a synapomorphy at node 10. Character 93 (0→1): axial neural spine reduced and rod-like. Convergently present in *Piatnitzkysaurus*, most carnosaurids, and tyrannosaurids. Character 102 (1→2): epiphyses of cervical vertebrae strongly pronounced and overhang the postzygapophyses. This is a reversal of a synapomorphy at node 32, which in itself is a reversal of a synapomorphy at node 10. Character 221 (0→1): pedal digit IV significantly longer than II and only slightly shorter than digit III.

*Possible additional apomorphies under ACCTRAN.* Character 2 (1→0): premaxillary body in front of the external nares shorter than body below the nares, and angle between anterior margin of premaxillary and alveolar margin more than 75 degrees. This is a reversal of a possible maniraptoran synapomorphy; see nodes 34 and 5. Character 79 (0→1): posterior end of splenial forked. Unknown in troödontids. Character 80 (1→0): coronoid well developed. This is a reversal of a synapomorphy at node 31 or 32. Unknown in troödontids.

*Possible additional apomorphies under DELTRAN.* Character 200 (0→1): presence of a posterolateral trochanter on the femur; see node 35. Character 224 (0→1): pedal digit II bears an enlarged ungual and is highly specialized; see node 35.

*Remarks.* The Deinonychosauria was proposed by Colbert and Russell (1969) for the inclusion of the family Dromaeosauridae. Colbert and Russell (1969) only included the genera *Dromaeosaurus*, *Deinonychus* and *Velociraptor* in the Dromaeosauridae, but in the same year, Ostrom (1969b) argued that *Saurornithoides* and *Stenonychosaurus* (= *Troödon*) should also be included in this family, because of the very similar specialization of the second pedal digit in these animals. Thus, the name became widely used for a taxon that comprised both dromaeosaurids and taxa that are now considered to be troödontids. Since monophyly of this taxonomic concept of deinonychosaurs is supported in the present analysis, the name is applied at this node.

*Node 38. unnamed node*

*Included taxa.* Therizinosauroida (Maleev, 1954); *Caudipteryx* Ji, Currie, Norell and Ji, 1998; *Microvenator* Ostrom, 1970; *Avimimus* Kurzanov, 1981; Oviraptorosauria Barsbold, 1976a.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 58 (1→2): basiptyergoid processes very short and narrow. Character 65 (1→0): palatine not tetradiate. This is a reversal of a neotheropodan synapomorphy. However, although the palate is not tetradiate in therizinosauroids and oviraptorosaurs, it is uncertain if this reversal represents a synapomorphy of this clade, since the morphology of the palatine in therizinosauroids and oviraptorosaurs is significantly different from each other. Character 66 (0→1): ectopterygoid situated lateral to the palatine. Character 76 (0→1): anterior part of dentary flexed medially. Convergently present in ornithischians, ornithomimosaurids, and troödontids. Character 89 (1→0): two pairs of pleurocoels in the cervical vertebrae. This is a reversal of a tetanuran synapomorphy. Character 122 (1→0): prezygapophyses of distal caudal vertebrae not elongated. This is a reversal of a synapomorphy at node 2 or 3. Character 126 (0→1): distal caudal vertebral centra not significantly elongated in relation to their height. Character 170 (0→1): preacetabular process of ilium significantly higher than postacetabular process.

*Possible additional apomorphies under ACCTRAN.* Character 30 (1→0): nasolacrimal duct pierces the body of the lacrimal. This is a reversal of a possible synapomorphy at node 32; see that node. Character 36 (1→0): frontal not elongated triangular. This is a reversal of a possible synapomorphy at node 31; see that node. Character 44 (1→0): postorbital part of the skull roof as high as the orbital region. This is a reversal of a possible synapomorphy at node 32; see that node. Character 67 (3→0): ectopterygoid slender and without ventral depression or pneumatic foramen. This is a reversal of a coelurosaurian synapomorphy. Within members of this clade, this character state is only known for oviraptorosaurs, so it cannot be determined where the character state transformation occurred. However, while therizinosaurs seem to have a rather conventional theropod palate, the whole palate is highly modified in oviraptorosaurs. This indicates that the character state transformation might rather have occurred at a later node. Character 68 (1→0): no subsidiary palatal fenestra. This character state is also a reversal of a coelurosaurian synapomorphy and only known in oviraptorosaurs, so the situation is as for character 67. Character 81 (0→1): premaxillary teeth absent. Premaxillary teeth are absent in therizinosaurs and oviraptorosaurs. However, the presence of premaxillary teeth in *Caudipteryx* indicates that the loss of these teeth in the two former clades occurred independently. Character 101 (2→1): anterior articular facet of anterior cervical vertebrae wider than high, but not kidney-shaped. This is a reversal of a synapomorphy at node 31. The reversal is present in *Microvenator* and *Avimimus*, but not in oviraptorosaurs; the character states in other members of this clade is unknown. More information on the distribution of character states of this character within the present group is needed to interpret the sequence of character state transformations within this clade. Character 160 (2→1): penultimate phalanx of the third manual digit longer than proximal phalanges, but not as long as both proximal phalanges taken together. This is a reversal of a synapomorphy at node 24 (Coelurosauria) or 31. Within members of this clade, the character state is only known for oviraptorosaurs, so it cannot be determined at which node the reversal occurred. Character 197 (1→0): no oblique ligament groove present on the posterior side of the femoral head. This is a reversal of a neotheropodan synapomorphy. Within members of this clade, the character state has only been observed in *Avimimus*. Character 199 (3→2): lesser trochanter not fused with greater trochanter. This is a reversal of a possible maniraptoran synapomorphy; see node 34.

*Possible additional apomorphies under DELTRAN.* Character 2 (0→1): premaxillary body in front of the external nares longer than body below the external nares and angle between anterior margin and alveolar margin less than 70 degrees; see nodes 34 (Maniraptora) and 5 (Neotheropoda). Character 3 (0→1): broad palatal shelf present in the premaxilla; see node 32. Character 12 (1→0): maxillary antorbital fossa deep, with sharply defined margins; see node 32. Character 79 (1→0): posterior end of dentary strongly forked; see node 34 (Maniraptora). Character 186 (0→1): pubic boot expanded more anteriorly than posteriorly; see node 29.

#### Node 39. unnamed node

*Included taxa.* *Caudipteryx* Ji, Currie, Norell and Ji, 1998; *Microvenator* Ostrom, 1970; *Avimimus* Kurzanov, 1981; Oviraptorosauria Barsbold, 1976a.

*Known temporal range.* Early Cretaceous (Barremian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 71 (0→1): preorbital region of the skull significantly shortened. Character 77 (1→0): posterior end of dentary strongly forked. This is a reversal of a tetanuran synapomorphy. However, the character state is even more marked in the members of this clade than in all basal theropods that show this state, with the exception of *Herrerasaurus*. Character 82 (0→1): maxillary and dentary teeth absent. Character 220 (0→1): arctometatarsalian pes. Convergently present in tyrannosaurids, many ornithomimosaurids, and troodontids.

*Possible additional apomorphies under ACCTRAN.* Character 8 (0→1): presence of a constriction between the articulated premaxillaries and maxillaries. Within the members of this clade, the character state is only known in oviraptorosaurs. Character state 1 is convergently present in *Syntarsus*, *Dilophosaurus*, and baryonychids. Character 19 (0→1): nasal pneumatised. Only known in oviraptorosaurs. This character state is convergently present in ceratosaurs and allosauroids, but the mode of pneumatisation is different in these clades. Character 24 (2→1): jugal excluded from the antorbital fenestra. Only known in oviraptorosaurs. Character 31 (0→1): lacrimal pneumatised. Only known in oviraptorosaurs. The lacrimal is also pneumatised in a variety of more basal theropods, but the mode of pneumatisation is different in these animals. Character 72 (0→1): presence of a pronounced coronoid eminence on the surangular. Unknown in *Caudipteryx* and *Microvenator*. Character 73 (1→0): retroarticular process of the mandible narrow. This is a reversal of a synapomorphy at node 11. Unknown in *Caudipteryx* and *Microvenator*. Character 75

(1→0): anterior part of the surangular less than half the height of the mandible at the level of the mandibular fenestra. This is a reversal of a tetanuran synapomorphy. The character state is unknown in *Caudipteryx* and *Microvenator*, but the morphology of the dentary in these two taxa indicates that the anterior portion of the surangular was rather low. Character 78 (1→0): splenial foramen absent. This is a reversal of a saurischian synapomorphy. The character state is only known in oviraptorosaurs. Character 105 (0→1): dorsal vertebral centra wider than high. Unknown in *Caudipteryx* and *Avimimus*. Character 183 (0→2): pubic shafts anteriorly concave in lateral view. This character is unknown in *Caudipteryx*; in *Avimimus*, the pubic shafts are convex anteriorly. Although the latter character state most probably represents an autapomorphy of *Avimimus*, the node at which the character state transformation occurred is uncertain.

*Possible additional apomorphies under DELTRAN.* Character 152 (0→1): proximal articular end of metacarpal III not expanded; see node 29.

*Node 40.* unnamed node

*Included taxa.* *Microvenator* Ostrom, 1970; *Avimimus* Kurzanov, 1981; Oviraptorosauria Barsbold, 1976a.

*Known temporal range.* Early Cretaceous (Aptian–Albian)–Late Cretaceous (Maastrichtian).

*Synapomorphies.* Character 27 (0→1): jugal very slender. Convergently present in birds. Character 118 (1→0): transverse processes present in more than 15 caudals. This is a reversal of a synapomorphy at node 29.

*Possible additional apomorphies under ACCTAN.* Character 6 (2→1): subnasal process of the premaxilla slender, but with contact to the nasals. This is a reversal of a maniraptoran synapomorphy. The character state is only known in oviraptorosaurs, so it is uncertain whether it represents a synapomorphy at the present node, or of the latter clade. Character 46 (0→1): no contact between the squamosal and the quadratojugal. Only known in oviraptorosaurs. State 1 is convergently present in *Syntarsus*, *Dilophosaurus*, abelisaurids, and birds. Character 50 (0→1): dorsal end of the quadrate double-headed. Only known in oviraptorosaurs and convergently present in birds. Character 106 (1→2): pleurocoels present in all dorsal vertebrae. Pleurocoels are present in all dorsals in *Microvenator* and oviraptorosaurs, but not in *Avimimus*, in which not even the anterior dorsals have pleurocoels. The apneumatic nature of the anterior dorsals clearly represents an autapomorphy of the latter taxon, but a resolution of the polytomy at this node is needed for a detailed interpretation of the character state changes of this character.

*Possible additional apomorphies under DELTRAN.* Character 72 (0→1): presence of a pronounced coronoid eminence on the surangular; see node 39. Character 73 (1→0): retroarticular of the mandible narrow; see node 39. Character 75 (1→0): anterior part of the surangular less than half the height of the mandible at the level of the mandibular fenestra; see node 39. Character 81 (0→1): premaxillary teeth absent; see node 38. Character 105 (0→1): dorsal vertebral centra wider than high; see node 39. Character 183 (0→2): pubic shafts concave anteriorly in lateral view; see node 39.

## DISCUSSION

The present analysis differs from other phylogenetic hypotheses of theropod relationships (e.g. Gauthier 1986; Holtz 1994; Sereno 1997, 1999) in several respects, mainly the paraphyly of the Ceratosauria *sensu* Gauthier (1986) and the recognition of a monophyletic Carnosauria (Text-figs 53–55). Since the objective of this paper is a better understanding of the phylogenetic relationships and evolution of basal theropods, the following discussion will mainly focus on aspects of theropod interrelationships at the base of the tree. All clade names used in this chapter refer to the clades described above unless otherwise indicated.

### *Theropod interrelationships*

*The phylogenetic position of Eoraptor and herrerasaurids.* Ever since the first discovery of *Herrerasaurus* (Reig 1963), the systematic position of this taxon and the subsequently discovered *Staurikosaurus* (Colbert

1970) and, to a lesser extent, *Eoraptor* (Serenó *et al.* 1993) has been a subject of debate. Variousy regarded as sister taxa in a monophyletic Herrerasauridae (Benedetto 1973; Novas 1989, 1992*b*), or as more distantly related basal dinosaurs (Colbert 1970; Galton 1977; Brinkman and Sues 1987; Benton 1990; Sues 1990), *Herrerasaurus* and *Staurikosaurus* have been considered to be outgroups to the Ornithischia-Saurischia dichotomy (Gauthier 1986; Novas 1989; 1992*b*; Benton 1990), as Saurischia *incertae sedis* (Benedetto 1973; Galton 1977), as sauropodomorphs (Colbert 1970; Cooper 1981), or as basal theropods (Bonaparte 1978; Galton 1985*a*). The latter view was supported in a series of papers on new specimens of *Herrerasaurus* from the Carnian of the Ischigualasto Formation of Argentina published by Sereno and Novas (1992, 1993; Novas 1993; Sereno 1993). *Eoraptor*, based on an almost complete skull and skeleton, was regarded as the most basal theropod by Sereno *et al.* (1993). However, herrerasaurid monophyly and the inclusion of herrerasaurids and *Eoraptor* in the Theropoda are not generally accepted (Holtz 1995*a*; Holtz and Padian 1995).

The present analysis supports both the monophyly of the Herrerasauridae as defined by Benedetto (1973), and the inclusion of this family in the Theropoda, as one of the most basal taxa of this clade, as advocated by Sereno and Novas (1992, 1993; Novas 1993; Sereno 1993). The position of *Eoraptor* as the most basal theropod currently known is also supported. In the present analysis, placement of herrerasaurids outside theropods requires five more steps, outside Saurischia eight additional steps, and the phylogenetic hypothesis advocated by Benton (1990), with a paraphyletic Herrerasauridae outside Saurischia, results in a tree that is 12 steps longer than the shortest tree found. In the case of *Eoraptor*, only three additional steps are needed for a placement outside Theropoda, and five more steps for a placement outside Saurischia. These lower numbers for *Eoraptor* might be partially related to the higher amount of missing data in this taxon.

However, despite the rather high values for herrerasaurids, some uncertainty about the phylogenetic relationships of this taxon, and of *Eoraptor* remains. In particular, the placement of herrerasaurids within Theropoda requires many reversals of saurischian synapomorphies, or convergent developments in sauropodomorphs and neotheropods. The morphology of the subnarial process of the premaxilla, the lacrimal, and the short second digit of the hand, for example, are all plesiomorphic in herrerasaurids compared to the condition found in sauropodomorphs and neotheropods. In *Eoraptor* the presence of palatal teeth is noteworthy, since palatal teeth are unknown in any other dinosaur. If the placement of *Eoraptor* as the most basal theropod is accepted, their presence in this taxon represents a very peculiar reversal, unless one assumes that they were lost independently in crurotarsans, ornithischians, sauropodomorphs, and later theropods. Furthermore, most of the synapomorphies that link *Eoraptor* and herrerasaurids to neotheropods are skull and manus characters, such as the deep extensor pits on the metacarpals or the elongate penultimate phalanges, that might be directly related to the predatory habits of these animals. Unfortunately, well-preserved skulls or hands are not known for any of the immediate dinosaurian outgroup taxa *Lagerpeton*, *Marasuchus*, and *Pseudolagosuchus* (Romer 1971, 1972; Bonaparte 1975; Arcucci 1986, 1987; Sereno and Arcucci 1993, 1994), so, in the present analysis, the plesiomorphic condition for these characters is determined by the only distantly related *Euparkeria* and the herbivorous Ornithischia and Sauropodomorpha. The possibility that these characters represent synapomorphies of the originally predatory dinosauriforms that were independently lost in the herbivorous groups cannot, therefore, be completely ruled out. Better cranial and manual material of basal dinosauriforms is needed to solve this problem.

Thus, although the placement of *Eoraptor* and herrerasaurids within Theropoda is supported in the present analysis, the phylogenetic position of these taxa might change in the light of new discoveries.

*Paraphyly of the Ceratosauria sensu Gauthier (1986).* As noted in the introduction, the vast majority of recent analyses of theropod phylogeny resulted in the recognition of a monophyletic clade at the base of Neotheropoda that represents a sister-group to tetanurans (Gauthier 1986; Rowe 1989; Rowe and Gauthier 1990; Novas 1992*a*; Pérez-Moreno *et al.* 1993; Holtz 1994, 2000; Sereno 1997, 1999). This clade, termed Ceratosauria by Gauthier (1986), usually included coelophysids, *Dilophosaurus*, *Ceratosaurus* and abelisaurids, plus several poorly known taxa such as *Segisaurus* or *Sarcosaurus*. Although the characters used to diagnose the Ceratosauria were essentially those listed by Rowe and Gauthier (1990) in all

analyses, only a few authors have questioned the monophyly of this group (Cuny and Galton 1993; Rauhut 1998; Carrano and Sampson 1999).

The present analysis does not support the monophyly of the Ceratosauria *sensu* Gauthier (1986). In contrast to the usual arrangement of coelophysids, *Dilophosaurus*, *Ceratosaurus*, and abelisaurids in a monophyletic clade, *Dilophosaurus* and a *Ceratosaurus*-abelisaurid clade were supported as successively closer outgroups to tetanurans (Text-fig. 54).

Rowe and Gauthier (1990) listed ten characters in their diagnosis of the Ceratosauria:

1. Transverse processes of dorsal vertebrae strongly backturned and triangular when viewed from above.

This character is difficult to assess, since the transverse processes are more or less triangular in dorsal view in the majority of saurischians. In *Plateosaurus* (GPIT Skelett I, MB Skelett XXV), *Sinraptor* (Currie and Zhao 1993b), and *Gallimimus* (Osmólska *et al.* 1972), for example, the transverse processes are not significantly different from the situation seen in *Ceratosaurus*, or abelisaurids. Furthermore, the degree to which the transverse processes are backturned differs with the position of the vertebra within the vertebral column, and may show considerable individual variation. Even in the holotype of *Syntarsus rhodesiensis* (QG 1), the dorsal transverse processes are not as strongly backturned as in the *Syntarsus* vertebra figured by Rowe and Gauthier (1990, fig. 5.3D). Thus, the character must be regarded as being of questionable validity.

2. Two pairs of pleurocoels in the cervical vertebrae.

All taxa traditionally included in the Ceratosauria, and the non-ceratosaurian therizinosauroids and oviraptorosaurs have two pairs of pleurocoels in the cervical vertebrae. However, since the absence of any pleurocoels is the plesiomorphic condition for saurischians, it is difficult to decide whether one or two pairs of pleurocoels represents the primitive state in theropods. On the basis of embryological data derived from birds, Britt (1993, cited in Makovicky 1995) argued that the presence of two pairs of pleurocoels represents the plesiomorphic condition within theropods, and this view is supported in the present analysis.

3. Pubic plate perforated by a large circular fenestra lying below the obturator foramen.

This character is also included in the present analysis (Character 181). A pubic fenestra, as defined above, is present in *Syntarsus rhodesiensis* (Raath 1969), *Gojirasaurus* (MB 1985.G.1-3), *Segisaurus* (UCMP V 338), and probably *Coelophysis* (Rowe and Gauthier 1990; Paul 1993), but not in *Ceratosaurus* (Gilmore 1920); the situation in *Dilophosaurus* is unclear, since no proximal pubis is completely preserved in this taxon. Rowe and Gauthier (1990, fig. 5.7.A) homologized a notch in the ventral rim of the ischial peduncle of the pubis in *Ceratosaurus* with the pubic fenestra of other proposed ceratosaurids. However, as noted in the character description, this homology is highly questionable, and not supported by character congruence in the present analysis. Furthermore, a pubic fenestra is absent in the coelophysoid *Liliensternus* (MB R. 2175), the abelisauroid *Elaphrosaurus* (MB dd unnumbered), and abelisaurids (MACN CH 894). Thus the distribution of this character within proposed ceratosaurian taxa is patchy, and it cannot be regarded as a synapomorphy of a monophyletic Ceratosauria *sensu* Gauthier (1986).

4. Sacral transverse processes, sacral ribs, neural arches, and spines completely fused to each other and sacral ribs fused to the ilium in adults.

This is a fusion character and therefore ontogenetically variable. The sacra are not completely fused to each other and the sacral ribs in *Dilophosaurus* and *Liliensternus*, and the sacral ribs are not fused with the ilium in abelisaurids and some specimens of *Syntarsus rhodesiensis* (e.g. QG 691), but one could argue, of course, that this reflects the juvenile to subadult status of the specimens concerned. Complete fusion, as described above, is only found in *Coelophysis* (Colbert 1989), the type specimen of *Ceratosaurus* (Gilmore 1920), the type of *Syntarsus* (Raath 1969, 1990), the type specimen of *Elaphrosaurus* (Janensch 1925), and birds. However, partial fusion of the vertebrae and their neural arches and of the sacral ribs to the vertebrae is variously present in many theropods. Thus, this character is very difficult to assess, and its status as a possible ceratosaurian synapomorphy is questionable.

5. Pubis, ischium, and ilium fused together in adults.

As for the previous character, this is a fusion character and ontogenetically variable. Thus, the pelvic bones are fused in the holotype of *Syntarsus rhodesiensis* (QG 1), but not in a slightly smaller individual (QG 691; see Raath 1990, fig. 7.5). Within putative ceratosaurian taxa the pelvic bones are unfused in *Dilophosaurus*, *Liliensternus*, *Gojirasaurus*, and abelisaurids. In the type specimens of *Ceratosaurus* and *Elaphrosaurus* the pelvis are only partially fused, but the mode of fusion is different in both taxa. Notably in *Elaphrosaurus* the incomplete fusion cannot be attributed to the ontogenetic state of the individual since several other osteological features (fusion of cervical ribs to their centra and excessive bony growth in the last dorsal and first caudal vertebrae) indicate that the type is a rather old individual. Thus, the validity of this character as a ceratosaurian synapomorphy is also highly questionable.

6. Trochanteric shelf present on lesser trochanter in robust individuals.

This character is also used here in a slightly modified form (Character 198). So far, within proposed ceratosaurs trochanteric shelves have only been described or figured in the genera *Ceratosaurus* (Gilmore 1920), *Syntarsus* (Raath 1969, 1990; Rowe 1989) and *Sarcosaurus* (Andrews 1921). Since this character seems to be sexually dimorphic (Raath 1990), its presence cannot be determined in taxa known only from gracile individuals. Therefore, it might be present in all 'ceratosaurs', but the evidence is circumstantial. Furthermore, the presence of a trochanteric shelf has been reported for the primitive theropod *Herrerasaurus* (Novas 1993), and a similar structure is found in some Dinosauriformes (Novas 1996a). Therefore, the validity of this character as a ceratosaurian synapomorphy is highly questionable; the presence of a well-developed trochanteric shelf might rather represent a theropodan or neotheropodan synapomorphy, as indicated in the present analysis.

7. A sulcus excavated into the base of the crista tibiofibularis.

This is another problematic character. It is used in a modified form in the present analysis (Characters 209 and 210). Rowe and Gauthier (1990, fig. 5.9F-H) only illustrated this character for a fibula of *Syntarsus kayentakatae*. In this specimen, the medial side of the proximal end of the fibula shows an oblique ridge, running from the proximoanterior end of the bone distoposteriorly, that is excavated by a deep trough (the fibular sulcus of Rowe and Gauthier) from the anterior side. This exact morphology was not observed in any of the specimens studied for this analysis. The ridge is present in the type of *Segisaurus* (UCMP V 338) and a specimen referred to *Coelophysis* (UCMP V 82250), but the sulcus is absent in these specimens. In *Liliensternus* (MB R. 2175) both the ridge and the sulcus are absent, and in *Dilophosaurus* (UCMP V 4214) only a narrow longitudinal groove is present, similar to the situation found in several tetanurans. In *Ceratosaurus* (UMNH VP 5278) the ridge is rudimentary and only represented by a slightly overhanging anterior edge, and the sulcus is largely open medially and closely resembles the situation found in many tetanurans (e.g. *Allosaurus* MOR 693). In *Elaphrosaurus* (MB dd unnumbered) the ridge is completely absent and the development of the medial groove is very similar to that found in baryonychids and many coelurosaurs. Within abelisaurids the proximal end of the fibula is only known in *Xenotarsosaurus* and *Genusaurus*. In the latter taxon the development of the medial groove seems to be very similar to that found in *Ceratosaurus* (Accarie *et al.* 1995). The situation in *Xenotarsosaurus* is somewhat unclear since the fibula is preserved in articulation with the tibia (Martínez *et al.* 1986), but it seems to be similar.

Thus, this character is more complex and variable than previously recognized. More research into the morphology and function of the character is needed, but at present it cannot be regarded as a probable ceratosaurian synapomorphy.

8. Astragalus and calcaneum fused to each other and to the tibia in late ontogeny.

This is another fusion character that is ontogenetically variable. Within proposed ceratosaurs the astragalus, calcaneum and tibia are known to be fused in large specimens of *Syntarsus* (Raath 1969, 1990; Rowe 1989), some specimens of *Coelophysis* (Colbert 1989), *Ceratosaurus* (Gilmore 1920), and abelisaurids (Martínez *et al.* 1986). The astragalus and calcaneum are fused to each other, but not to the tibia in *Liliensternus* and *Elaphrosaurus*, and the elements are completely unfused in *Dilophosaurus*.

Whereas the lack of fusion in *Liliensternus* and *Dilophosaurus* may be attributed to the presumably subadult status of the specimens, *Elaphrosaurus* is represented by what is clearly an adult, and presumably rather old individual, as noted above. Fusion of the proximal tarsals and of these elements with the tibia is also found in several non-ceratosaurian theropods, including troödontids (Osmólska 1987), some dromaeosaurids (*Velociraptor*: IGM 100/986), and birds. Furthermore, fusion of the proximal tarsals with the tibia may be individually rather than ontogenetically variable in *Coelophysis* since Colbert (1989, p. 107) noted that some large specimens of this taxon lacked fusion while it was present in other, smaller specimens.

In summary, the distribution of this character in proposed ceratosaurian and non-ceratosaurian taxa is problematical, and its status as a ceratosaurian synapomorphy is questionable.

9. Ascending process of astragalus directed vertically, subparallel with tibial shaft, and largely overlapped rostrally by the fibula.

The ascending process of the astragalus is more or less vertical and subparallel with the tibial shaft in the vast majority of theropods, so this part of the character cannot be used for the diagnosis of a subclade within Theropoda. The process is overlapped by the fibula in articulated specimens of *Syntarsus* (Text-fig. 55A; Raath 1969; Rowe 1989), but not in other specimens that were examined for this analysis. In *Liliensternus* (MB R. 2175), *Dilophosaurus* (UCMP V 4214), and *Ceratosaurus* (UMNH VP 5278), the distal end of the fibula is situated lateral to the ascending process of the astragalus and abuts the latter medially (Text-fig. 55B). The same seems to be the case in abelisaurids (Martínez *et al.* 1986). Thus, this character can hardly be regarded as a ceratosaurian synapomorphy, but it might represent an apomorphic character of coelophysids, or of the genus *Syntarsus*.

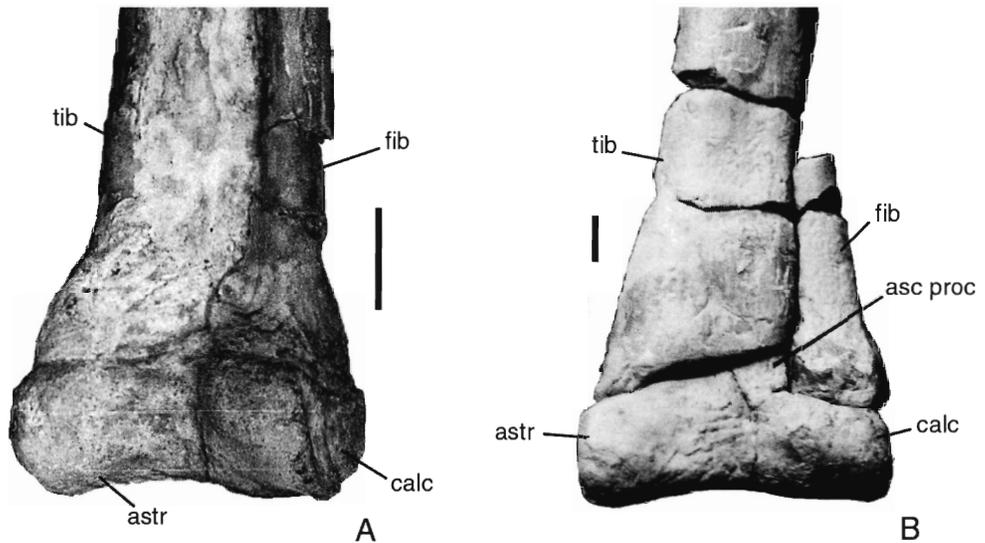
10. Distal tarsals II and III fused to their respective metatarsals by late ontogeny.

This is yet another fusion character that depends on the ontogenetic status of the specimens examined. The distal tarsals fuse with the metatarsals, and metatarsals II and III are fused to each other in large specimens of *Syntarsus* (Raath 1969, 1990; Rowe 1989) and some specimens of *Coelophysis* (Colbert 1990), although fusion does not seem to be related to size, and thus presumably age, in the latter taxon (Colbert 1990). The distal tarsals and metatarsals are separate in known specimens of *Liliensternus*, *Dilophosaurus*, and *Elaphrosaurus*. In the holotype of *Ceratosaurus* the metatarsals of the foot are fused (Gilmore 1920), but the mode of fusion is different from that seen in *Syntarsus*. Whereas the metatarsals are fused proximally in the latter taxon, fusion occurs along the medial portions of the bones in *Ceratosaurus*; the proximal ends are separated. Furthermore, the distal tarsals are not fused to the metatarsals in *Ceratosaurus* (Gilmore 1920, p. 110). Moreover, the fused metatarsals of the type of *Ceratosaurus* might represent a pathology, as indicated by the presence of unfused metatarsal fragments in another specimen of this genus (UMNH VP 5278). No metatarsals are known for abelisaurids.

The patchy distribution of this character within proposed ceratosaurian taxa, its presence in some non-ceratosaurian theropods (caenagnathids: Osmólska 1981; birds), and its high ontogenetic and/or individual variability (Colbert 1990; Raath 1990), makes its use as a ceratosaurian synapomorphy highly questionable.

In summary, the validity of almost all of the characters that were proposed as ceratosaurian synapomorphies by Rowe and Gauthier (1990) is highly questionable. On the other hand, the hypothesis that *Ceratosaurus* and abelisaurids are more closely related to tetanurans than to coelophysids is supported by a high number of synapomorphies (see tree description). The *Ceratosaurus*/Abelisauroidae–Tetanurae clade (node 11) is one of the best supported nodes in the present cladogram. It has a bootstrap value of 90 per cent, while the monophyly of the Ceratosauria *sensu* Gauthier (1986) requires 13 additional steps.

*The phylogenetic position of Dilophosaurus and Shuvosaurus.* One unexpected result of the present analysis is the exclusion of *Dilophosaurus* from the Coelophysoidea. Since the detailed description of this taxon by Welles (1984), it has been compared with *Liliensternus* and coelophysids, and was regarded as a close relative of the latter taxon by the majority of authors (Paul 1988a; Rowe and Gauthier 1990; Holtz



TEXT-FIG. 55. Left distal tibia, fibula, and proximal tarsals of A, *Syntarsus rhodesiensis* (QG 1) and B, *Liliiensternus liliiensterni* (MB R. 2175) in anterior view, showing differences in the development of the distal end of the fibula and its connection with the ascending process of the astragalus. Abbreviations: asc proc, ascending process of the astragalus; astr, astragalus; calc, calcaneum; fib, fibula; tib, tibia. Scale bars represent 10 mm.

1994; Sereno 1997). However, most of the characters shared by *Dilophosaurus* and *Liliiensternus* represent symplesiomorphies, and a close relationship between these two taxa is not supported by any unequivocal synapomorphies.

Rowe and Gauthier (1990, p.165) listed four proposed synapomorphies to unite *Dilophosaurus*, *Liliiensternus*, and coelophysids: presence of a subnarial gap, loss of axial diapophyses, reduction of axial parapophyses, and loss of the axial pleurocoels. None of these characters is unequivocally preserved in *Liliiensternus*, so the following discussion will focus on *Dilophosaurus* and coelophysids.

The reduction or loss of the axial diapophyses and parapophyses is difficult to evaluate since these structures are only poorly defined in many basal saurischians. Virtually no diapophysis and parapophysis is present in the prosauropod *Plateosaurus* (SMNS 13200, MB Skelett 25), and they seem to be poorly developed in *Herrerasaurus* (Sereno and Novas 1993), so the weak development or absence of these structures probably represents a symplesiomorphy in coelophysids and *Dilophosaurus*. The absence of axial pleurocoels clearly represents a symplesiomorphy, since axial pleurocoels are absent in all neotheropodan outgroups.

The only remaining possible synapomorphy of *Dilophosaurus* and Coelophysidae proposed by Rowe and Gauthier (1990) is the presence of a subnarial gap. However, the structure of the subnarial gap in these two taxa is slightly different. In *Syntarsus rhodesiensis* (QG 194, 202, 205, 245, unnumbered) the posterior end of the premaxilla is forked into a dorsal subnarial posterior process and a ventral posterior process. The rather slender and short medial anterior process of the maxillary fits into the posterior notch of the premaxillaries that is formed by the two processes. The situation in *Coelophysis* seems to be very similar (Colbert 1989). In *Dilophosaurus* (UCMP V 6468) the posterior end of the premaxilla tapers posterodorsally underneath the nares. The long and broad medial anterior process of the maxillary is covered laterally by the posterior part of the premaxilla and almost reaches the level of the alveolar margin, where it is bound laterally by a ventral lamina that arises out of the parodontal lamina. This situation is quite similar to the construction of the premaxillary-maxillary articulation in baryonychids (MNN GDF 501). A low ventral lamina is also present in *Syntarsus*. It is uncertain whether these slight differences between *Dilophosaurus* and *Syntarsus* in the construction of the snout indicate convergence, or if one morphology might be derived from the other.

The present analysis found several other possible synapomorphies of a coelophysid–*Dilophosaurus* clade (see node 5 in the tree description): premaxillary body in front of external nares longer than body below the nares, and angle between anterior margin of the premaxilla and alveolar margin less than 70 degrees; presence of a constriction between the articulated premaxillaries and maxillaries; the lateral rims of the nasals are pronounced and form raised edges; no contact between the squamosal and quadratojugal; presence of enlarged, fang-like teeth in the anterior part of the dentaries; posterior dorsal vertebrae considerably elongated; articular facet of the pubic peduncle of the ilium subdivided into an anterior part that faces anteriorly, and a posterior part that faces ventrally. However, *Dilophosaurus* also shares many derived characters with tetanurans and ceratosaurs (see tree description). The systematic position of *Dilophosaurus* is thus equivocal and depends on the inclusion of *Shuvosaurus* in the analysis. If *Shuvosaurus* is included, the inclusion of *Dilophosaurus* in the Coelophysoidea requires three additional steps more than the shortest tree. If *Shuvosaurus* is not included, the phylogenetic position of *Dilophosaurus* as presented above is as parsimonious as inclusion of this taxon in the Coelophysoidea.

*Shuvosaurus* is a problematic taxon, because of its extremely apomorphic skull structure (Chatterjee 1993; Rauhut 1997). The genus is included in the Coelophysoidea mainly because of two characters that it shares with coelophysids, most notably *Syntarsus*: the forked posterior end of the premaxilla and the considerably elongated basisphenoid. The inclusion of *Shuvosaurus* in the Coelophysoidea results in a re-evaluation of several possible synapomorphies that may unite *Dilophosaurus* and coelophysids, and thus leads to the exclusion of the latter taxon from the Coelophysoidea. In contrast to *Dilophosaurus* and coelophysids, *Shuvosaurus* lacks a subnarial gap and a constriction between the premaxillaries and maxillaries, the lateral margins of the nasals are not raised, and the squamosal contacts the quadratojugal (Chatterjee 1993; Rauhut 1997). However, the morphology and configuration of the premaxilla, maxilla, jugal, nasal, and quadratojugal in *Shuvosaurus* are unlike those in any other theropod, or even archosaur, which makes even a positional, or structural homologization of cranial characters very difficult. Since several of the characters that unite *Dilophosaurus* and the ceratosaur–tetanuran clade may be at least partially size-related (e.g. development of the axial and cervical epiphyses), it seems possible that further detailed studies of this taxon and coelophysoids might result in the inclusion of the genus in the Coelophysoidea.

*Carnosaur monophyly and character distribution in basal tetanurans.* In contrast to most recent analyses (e.g. Novas 1992a; Holtz 1994, 2000; Sereno *et al.* 1996; Sereno 1997, 1999), the present study supports a monophyletic Carnosauria that consists of two monophyletic clades, the Spinosauroida and the Allosauroida (Text-fig. 54). Sereno *et al.* (1996, 1998) and Sereno (1997, 1999) also recognized monophyletic Spinosauroida and Allosauroida that are very similar in taxonomic content to the clades recovered in the present analysis, but regarded them as successively closer outgroups to coelurosaurs.

In the present analysis carnosaur monophyly is supported by three unambiguous synapomorphies: ascending process of the maxillary offset from the anterior rim of the maxillary body and anterior projection of the maxillary body longer than high; cervical vertebrae strongly opisthocoelous; metacarpal I very stout and approximately as broad as long. The arrangement of spinosauroids and allosauroids advocated by Sereno *et al.* (1996, 1998) and Sereno (1997, 1998, 1999) requires three additional steps.

One of the problems that accounts for the relative phylogenetic instability in basal tetanurans is the high amount of homoplasy exhibited by these taxa. The problems also at least partially reflect the still poor knowledge of the anatomy of many basal tetanurans, especially the Middle Jurassic, and thus stratigraphically oldest, representatives of this group. Thus, several characters that were used by Holtz (1994) and Sereno *et al.* (1996) to diagnose the clade consisting of allosauroids and coelurosaurs (Avetheropoda in Holtz 1994; Neotetanurae in Sereno *et al.* 1996) are unknown or very difficult to assess in many taxa (e.g. Sereno *et al.* 1996, characters 23–25). Other characters have a more complex distribution among basal tetanurans than previously recognized, or are interpreted differently if the sister-group relationship between ceratosaurs (restricted to neoceratosaurs) and tetanurans, as proposed here, is accepted. Furthermore, the choice of taxa included in the analysis can make a difference in the interpretation of the characters. For example, Holtz (1994, p. 1106) considered the absence of an enclosed obturator foramen as an avetheropodan synapomorphy. However, the obturator foramen is open ventrally in the

spinosauroids *Magnosaurus* and baryonychids, whereas an enclosed foramen is also found in the basal allosauroid *Monolophosaurus*. Thus, the ventral opening of the foramen either evolved separately in several clades of basal tetanurans, or it represents a synapomorphy of spinosauroids, allosauroids and coelurosaurs that is reversed in the spinosauroid *Torvosaurus* and the allosauroid *Monolophosaurus* (the interpretation supported in the present analysis). Likewise, the promaxillary recess extends into the anterior ramus of the maxillary (Serenó *et al.* 1996, p. 991, character 22) in the baryonychid *Suchomimus* (MNN GDF 501), in the even more basal tetanuran *Piatnitzkysaurus* (MACN CH 895; this taxon was not included in the analyses of either Holtz or Sereno *et al.*) and in abelisaurids (*Majungatholus*: FMNH 96202-44C); thus the lack of this character in *Torvosaurus* (Britt 1991) almost certainly represents an apomorphic reversal in this taxon.

In summary, the high amount of homoplasy in basal tetanurans makes phylogenetic interpretations of the interrelationships of these taxa very difficult. More detailed studies of character distributions, character definitions, and phylogenetic relationships are badly needed in this part of the theropod tree.

*Coelurosaur interrelationships.* Since coelurosaur interrelationships were not the main subject of the present study, only a few comments will be made.

The monophyly of the Coelurosauria is only supported by one character (maxillary antorbital fossa more than 40 per cent of the length of the external antorbital fenestra) in the present analysis. However, this reflects the fragmentary nature of the most basal coelurosaur, *Proceratosaurus*; 28 additional possible synapomorphies were found by ACCTRAN, possibly making Coelurosauria one of the best supported clades within theropod phylogeny.

A monophyletic family of basal coelurosaurs, the Coeluridae, is recognized (Text-fig. 54). This clade comprises Late Jurassic and Early Cretaceous taxa, and might thus represent a first radiation of coelurosaurs. However, the monophyly of this clade is only supported by two synapomorphic reversals that might both be at least partially size-related (cervical epiphyses not overhanging the postzygapophyses; posterior dorsal neural spines lower than long). The fact that all basal tetanurans known, and well-known members of the succeeding clade on the cladogram, the tyrannosauroids, are large animals makes further evaluation of these characters difficult. Thus, more material of basal coelurosaurs might show that coelurids are paraphyletic.

The current analysis also supports the inclusion of tyrannosaurids in the Coelurosauria, as advocated by Matthew and Brown (1922), Bakker *et al.* (1988), Novas (1992a), and Holtz (1994), and accepted by most recent authors. However, the phylogenetic position of tyrannosaurids within coelurosaurs is still a matter of debate. Holtz (1994) regarded them as the sister-taxon to his Bullatosauria (ornithomimosaur and troodontids), but they were considered to be more basal coelurosaurs by Novas (1992a), Sereno (1997, 1999), Sues (1997), Forster *et al.* (1998), and Makovicky and Sues (1998). The latter papers differ in the position of ornithomimosaur relative to the tyrannosaurids; whereas Sereno (1997, 1999) placed ornithomimosaur as more basal coelurosaur below tyrannosaurids, they were regarded as being closer to maniraptorans by Sues (1997), Forster *et al.* (1998), and Makovicky and Sues (1998). The latter view is well supported in the present analysis, since placement of ornithomimosaur below tyrannosaurids requires 12 additional steps. Characters shared by tyrannosaurids and maniraptorans that are absent in ornithomimosaur (e.g. presence of a sagittal crest formed by the parietals, distally tapering ischium) are interpreted as reversals in the latter clade.

The placement of *Deltadromeus* as a sister taxon to ornithomimosaur is only supported by two synapomorphies: the straight humerus in lateral view and the presence of a deep and wide groove on the medial side of the proximal end of the fibula. However, straight humeri are found in a variety of theropods (ceratosaurs, advanced spinosauroids, tyrannosaurids), and the morphology of the humerus in *Deltadromeus* is otherwise unlike that of ornithomimosaur. Likewise, the distribution of a deep groove in the proximal fibula is patchy in theropods, and more information on the detailed morphology and probable biological significance of this character is needed for a better evaluation of its value for phylogenetic reconstructions. Several plesiomorphic characters indicate that *Deltadromeus* might be a much more basal coelurosaur: the mid-caudal chevrons show an intermediate morphology between the rod-like to L-shaped chevrons of basal tetanurans and the skid-like chevrons of almost all other coelurosaurs, the pubic boot is

broadly triangular in ventral view, as in all basal neotheropodans and tetanurans, but unlike the narrow boot with subparallel margins as found in all other coelurosaurs, and a horizontal groove is present anteriorly on the astragalar condyles. Such a groove is known in ceratosaurs and carnosaurids, but it is not found in other coelurosaurs. Since placement of *Deltadromeus* at the base of Coelurosauria only requires one additional step, it seems likely that more material of this taxon might show it to be a basal coelurosaur rather than a sister-group to ornithomimosaurids.

Another aspect of coelurosaur phylogeny that has been a matter of debate is the taxonomic contents and interrelationships of Maniraptora. The Maniraptora was named by Gauthier (1986) for a clade that included oviraptorosaurs, dromaeosaurids, troodontids, birds, and several other, poorly known taxa. Holtz (1994) changed the taxonomic contents considerably in that he also placed tyrannosaurids and ornithomimosaurids in the Maniraptora. As noted later by Holtz (1996), this was in contradiction to the definition of this taxon given by Gauthier (1986, p. 35), who defined Maniraptora as a stem-based taxon to include all theropods closer to birds than to ornithomimosaurids. Thus, Holtz (1996) changed the name of the clade named Maniraptora in his 1994 paper to Maniraptoriformes, and restricted the Maniraptora to a clade that only contained dromaeosaurids and birds. Sereno (1997, 1998, 1999) presented a new phylogenetic hypothesis in which he used the name Maniraptora for a clade that included oviraptorosaurs, dromaeosaurids, troodontids, and birds. Although the taxonomic contents of this clade were thus very similar to those of the Maniraptora as devised by Gauthier (1986), it was not in agreement with Gauthier's definition of this clade since it did not include the tyrannosaurids, which, according to Sereno's phylogeny, were more closely related to birds than ornithomimosaurids. Makovicky and Sues' (1998) analysis found a monophyletic clade that consisted of a deinonychosaur–bird clade and an oviraptorosaur–therizinosaur clade, plus the genera *Coelurus* and *Ornitholestes*, and thus also corresponded closely to the original concept of the Maniraptora of Gauthier (1986).

The present analysis supports the phylogenetic relationships of the larger clades of coelurosaurs advocated by Makovicky and Sues (1998). Differences are only found in the exclusion of *Coelurus* and *Ornitholestes* from the Maniraptora. The arrangement published by Makovicky and Sues requires seven more steps in the present analysis. An arrangement similar to that proposed by Holtz (1994) results in a tree that is 55 steps longer than the shortest tree found, rendering this phylogenetic hypothesis highly unlikely. Apart from the phylogenetic position of the Ornithomimosauria (see above), the main difference between coelurosaur interrelationships as seen here and the arrangement of taxa advocated by Sereno (1997, 1999) is the inclusion of the Therizinosauridae as a sister group to oviraptorosaurs in the Maniraptora in the present analysis. Sereno (1997, 1999) regarded the therizinosaurids as a sister group to ornithomimosaurids. However, inclusion of this clade in the Maniraptora is well supported by character data from the recently described, basal therizinosaur *Beipiaosaurus*.

### *The theropod fossil record*

*Stratigraphic consistency of the present cladogram.* Several measurements for the stratigraphic consistency of cladograms have been proposed (e.g. Gauthier *et al.* 1988; Norell and Novacek 1992; Huelsenbeck 1994). Although some of these methods might be influenced by other parameters than stratigraphic consistency alone (Sidall 1996; Sidor 1999), they are usually regarded as reasonably accurate methods for testing the quality of the fossil record by the means of comparison of independently acquired stratigraphic and phylogenetic data (Hitchin and Benton 1997).

Two commonly used indices were used here to investigate the stratigraphic consistency of the cladogram: the Spearman rank correlation (SRC; Norell and Novacek 1992) and the stratigraphic consistency index (SCI; Huelsenbeck 1994).

For the calculation of the indices, the cladogram was turned into a phylogram by mapping the branches against the known stratigraphic ranges of the taxa (Text-fig. 56). Only the ages of first occurrences of taxa were used for the calculation of the indices. Possible differences in the occurrence of sister taxa within one stage were not taken into consideration because of the often imprecise dating of terrestrial tetrapods.

Norell and Novacek (1992) argued that the SRC should only be calculated for pectinate cladograms to avoid redundant clade ranks, so a non-pectinate cladogram has to be reduced to its pectinate components.



However, this procedure is only needed in order to avoid a signal from one pectinate component being masked by noise from other parts of the tree (Norell and Novacek 1992, p. 321). Although this problem certainly exists if branches with widely differing time intervals between taxa are considered together, calculating the SRC for the complete cladogram still gives some information about the quality of the fossil record of the given clade. Thus, SRC values were calculated for all the major lineages of the present cladogram (leading towards coelophysoids, abelisauroids, spinosauroids, allosauroids, coelurids, Aves, and oviraptorosaurs) and for the pooled data set of all pectinate components (Text-fig. 57).

All correlations between age rank and clade rank of the pectinate components are significant at  $P < 0.001$ , with the exception of the SRC for the coelophysoid lineage, which is, however, still significant at  $P < 0.01$ . SRC values are especially high for the abelisauroid lineage (0.961), oviraptorosaurs (0.943), and birds (0.93). This result indicates that the theropod fossil record accurately reflects the evolutionary history of this group, despite several gaps that are nevertheless present (see below).

The slightly poorer SRC for coelophysoids can be explained by three main factors: the low number of taxa that constitute this lineage, their rather short duration as a lineage in total (originating stages for included taxa only range from Norian to Hettangian) and the apparently rapid evolution of dinosaurs in the Late Triassic. Since all taxa are coded at stage level, many Late Triassic taxa have equal age ranks, which lowers the SRC for this lineage.

One of the constant outliers in all correlations (except in their own) are the ceratosaurs, which appear too late in the fossil record for their clade rank. This emphasizes the poorly known origin and early evolution of this group.

The SRC for the complete cladogram (0.862) is also significant at  $P < 0.001$ . As for the SRC values for the separate pectinate components, this high value reflects the accurate representation of theropod evolution in their fossil record. This result is also supported by the high SCI of 0.75 for the present cladogram. This index is higher than the average SCI for tetrapods of 0.66 found by Benton and Hitchin (1996), which might indicate that the theropod fossil record is better than that of other tetrapod groups. There are a number of possible reasons for this. The relatively large average size of theropods makes their preservation more likely than that of smaller animals such as squamates. Another reason for our comparably good knowledge of the theropod fossil record might be the great popularity of these animals; more researchers work on theropods than on most other groups of fossil tetrapods.

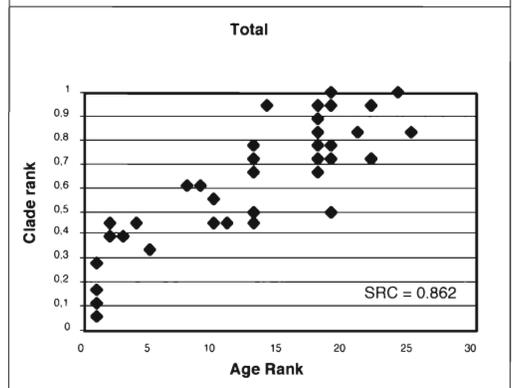
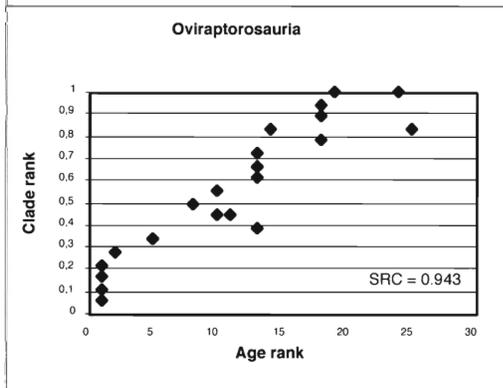
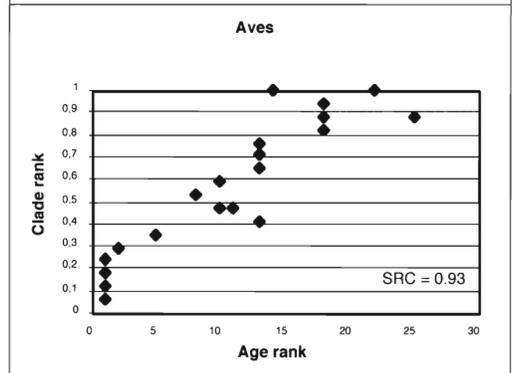
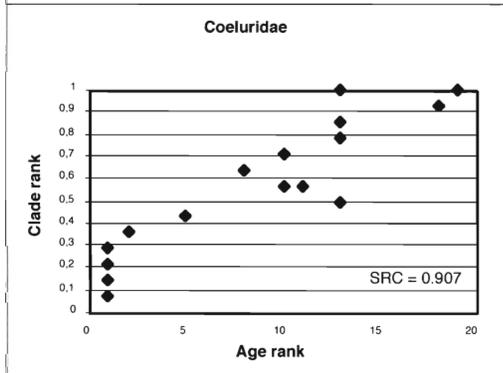
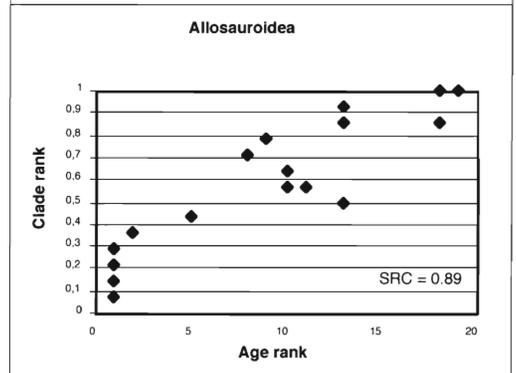
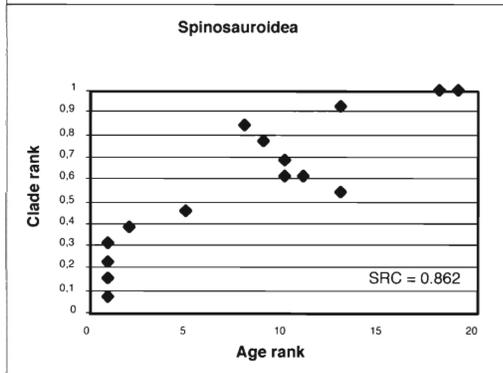
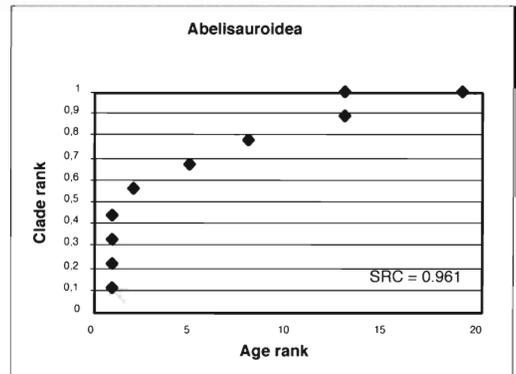
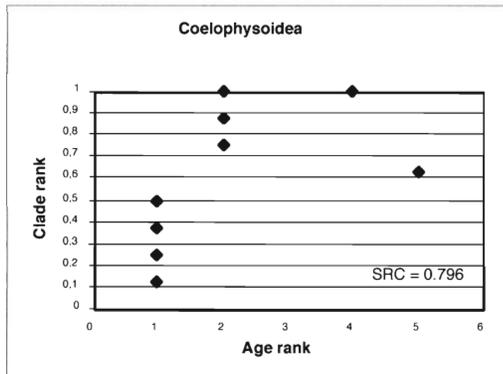
However, it should be noted that new discoveries might, of course, change our picture of the theropod fossil record drastically. If the Lower Jurassic dinosaur *Eshanosaurus* really proves to be a therizinosaur this would retract the ghost lineages of all major theropod lineages to at least that time (Xu *et al.* 2001), making a re-evaluation of the theropod fossil record necessary.

*Distribution of ghost lineages.* Having established that the branching pattern of the present cladogram is generally consistent with the stratigraphic occurrences of theropod clades, the following section explores the completeness of the theropod fossil record, as indicated by the distribution and length of ghost lineages.

One problem of calculating ghost lineage duration for terrestrial tetrapods is the often imprecise dating of terrestrial vertebrate localities. In fact, very few theropod localities have been dated radiometrically, and often even the dating to stage level is uncertain, especially for localities outside Europe or North America. Thus, the first occurrence of taxa was assumed to be at the beginning of the stage they occur in for taxa that are found in formations that can be allocated to a certain stage, and in the middle of the earlier stage for taxa that come from formations that span more than one stage. To calculate the duration of ghost lineages, the 1999 geologic time scale of the Geological Society of America (Palmer and Geissman 1999) was used.

The mean ghost range duration for all taxa under the assumptions stated above is 9.3 myr. However, whereas the mean ghost range for Laurasian taxa is 7.6 myr, that for Gondwanan theropods is almost twice as long, at 13.7 myr. This is a strong indicator that the Gondwanan theropod fossil record is much more poorly known than the Laurasian fossil record.

However, several long ghost ranges are also found in theropods from the Northern Hemisphere. Most notably among these are *Bagaraatan* (67.5 myr; probably slightly overestimated, since *Bagaraatan* forms a polytomy with the deinonychosaur–bird clade and the oviraptorosaur–therizinosaur clade), *Avimimus* (32 myr), and oviraptorosaurs (30.5 myr). All of these taxa are Late Cretaceous in age. *Bagaraatan* and



*Avimimus* are only known from central Asia (Gobi desert). Oviraptorosaurs are known from both North America and Asia (Barsbold *et al.* 1990; Currie *et al.* 1993; Sues 1997), but most of their representatives and most of their close relatives (*Avimimus*, *Caudipteryx*, therizinosaurs) are found in Asia. Thus, the long ghost ranges in these taxa reflect the poor fossil record of Early Cretaceous theropods in Asia.

Tyrannosaurids are a good example of how new finds can drastically reduce the ghost range of a group. Only few years ago the then oldest known member of this group, *Alectrosaurus*, came from the Senonian, giving a ghost lineage of approximately 60 myr. New finds of material representing this lineage from the Lower Cretaceous in Asia (Manabe 1999) and Europe (Hutt *et al.* 2001) have considerably reduced this gap.

*Gaps in the fossil record as predicted from character distribution.* Apart from the stratigraphic consistency of a cladogram and distribution of ghost lineages, gaps in the fossil record of a given group might be predicted by evaluating character distributions in the cladogram. If a gradual acquisition of characters during evolution is assumed, one would predict that many transitional taxa must be missing in the stem lines of clades that are supported by a high number of synapomorphies. In other words, a high number of synapomorphies at a given node in a cladogram indicates that there is a gap in the fossil record of the stem line of the clade (Text-fig. 58).

Practical problems in applying this idea mainly stem from the incompleteness of many fossil taxa that leads to ambiguity of character transformations at many nodes. Nevertheless, an attempt was made to identify major gaps in the theropod fossil record from the character distribution on the present cladogram in the following section.

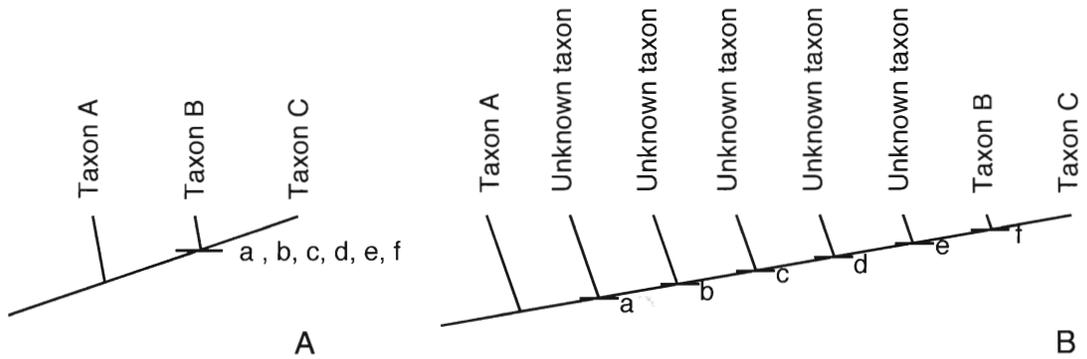
The best supported clade in the present cladogram is the Neotheropoda, diagnosed by 18 unambiguous synapomorphies, and possibly more than 30 in total (see tree description). The changes that occur at this node affect all parts of the skeleton. The great morphological disparity between the most basal neotheropods known, the coelophysoids, and the basal theropod clade Herrerasauridae is especially noteworthy since it is not correlated with any substantial ghost lineage; herrerasaurids are known from the Middle Carnian of the Ischigualasto Formation of Argentina (Rogers *et al.* 1993) while the first coelophysoid neotheropods come from the uppermost Carnian of the Chinle Group of North America (Hunt *et al.* 1998). In the Norian, coelophysoids were widely distributed on the northern continents (see Rowe and Gauthier 1990; Rauhut and Hungerbühler 2000) and they are abundant in some localities (e.g. Colbert 1989).

Two possible explanations that are not necessarily exclusive may account for these observations. First, the evolutionary history of this group might reach back into the Middle Triassic or even earlier times. In this case, the reason that they have not been recognized in the fossil record might be that the origin and early diversification of neotheropodans might have taken place in an area that is poorly, or not at all represented in the sedimentary record. An objection against this hypothesis may be the palaeogeographic situation in Late Triassic times with the relative uniformity of the Late Triassic Pangean faunas. However, some local isolation of populations can never be excluded. A further, and perhaps more severe objection to the extension of the ghost lineage of this clade is that no other group of dinosaurs is known from sediments older than the Carnian, and dinosauriforms first appear in the Ladinian in the fossil record. If the evolutionary history of the Neotheropoda reached back to the Middle or even Early Triassic, the relationships of this clade predicts that dinosauriforms, ornithischians, sauropodomorphs, and more basal theropods must also have existed since then.

A second possible explanation is that very rapid evolution and radiation of neotheropods took place possibly after an extinction event at around the Carnian/Norian boundary, as suggested by Benton (1984, 1993). As noted above, these two possibilities are not necessarily exclusive: a small, isolated population of neotheropods that had a longer evolutionary history than currently recognized might have rapidly radiated

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TEXT-FIG. 57. Diagrams showing the relations between age rank and clade rank and the SRC for pectinate components of the cladogram figured in Text-figure 55 and the total cladogram. Names of the diagrams refer to the terminal taxa to which the pectinate components lead.



TEXT-FIG. 58. Diagrams showing how character distribution in a cladogram indicates gaps in the fossil record. A, arrangement of three taxa in a cladogram; synapomorphies a–f support the monophyly of the clade (B–C). B, if gradual acquisition of characters is assumed, several taxa must be missing in the phylogeny between taxon A and clade (B–C). The number of taxa missing is positively (though not necessarily linearly) correlated with the number of synapomorphies that diagnose any given node.

into the ecological niches left over from extinct groups after a major extinction in the latest Carnian. The high morphological variability that is found in Norian coelophysoids (e.g. *Shuvosaurus*) also indicates a broad and probably rapid adaptive radiation of this group.

Another clade that is supported by a high number of synapomorphies is the Ceratosauria. In contrast to the Neotheropoda, a substantial ghost lineage is associated with this morphological gap in ceratosaur (26 myr). Most ceratosaur are found in the Southern Hemisphere; thus the poor fossil record of this group probably reflects the generally poor fossil record of Gondwanan theropods. The high number of apomorphies of *Elaphrosaurus* and the relatively high number of synapomorphies of abelisauroids and apomorphies of *Ceratosaurus* furthermore indicate that the separation of the latter two clades happened earlier than the contemporaneous Kimmeridgian age of their oldest members suggests.

Coelurosaur monophyly is also supported by a substantial number of synapomorphies, although this is not as obvious as in the other clades discussed above because the most basal member of the Coelurosauria, *Proceratosaurus*, is only represented by a partial skull. However, a high number of character state changes occur between the branching point of carnosaurs and coelurosaurs, and the origin of tyrannosaurids and other higher clades of coelurosaurs. In this case, the relatively long ghost lineage of node 25 might indicate that many of the changes occurred between nodes 24 and 25. On the other hand, the relatively high number of synapomorphies for node 29 indicates that there might be a longer ghost lineage associated with either coelurids and tyrannosauroids than the contemporaneous occurrence of the earliest members of these clades suggests.

#### *Theropod phylogeny: problems and possible solutions*

Owing to the great popularity of theropods, more cladistic studies of the phylogeny of this group have been published than for most other groups of fossil vertebrates. All of these analyses differ substantially. So far, these differences were especially noteworthy within the interrelationships of coelurosaurs, but the present analysis casts strong doubt on the apparent phylogenetic stability at the base of the theropod tree. Questions arising from this observation are: What are the reasons for the differences in the results of cladistic analyses of theropod interrelationships? What needs to be done in the future to solve these problems?

*Possible reasons for differences in proposed theropod phylogenies.* Apart from differences in methodology, character and taxa choice between different palaeontologists, results of phylogenetic analyses might

be influenced by taxonomic effects (grouping of species and genera into higher categories, basing taxa on very fragmentary and often undiagnostic material) and the quality of the fossil record.

Two fundamentally different cladistic methodologies can be recognized in the reconstruction of theropod phylogeny. Most older analyses (e.g. Thulborn 1984; Gauthier 1986), but also several recent analyses (e.g. Sereno *et al.* 1996) are based on a choice of characters that were identified as synapomorphies prior to the actual analysis, thus representing a traditional Hennigian approach. These analyses have a good resolution, high consistency indices and all characters are used to define a clade. A positive aspect of these analyses is that often much consideration is given to character choice, definition and description. However, these analyses do not reflect the high amount of homoplasy that certainly exists in theropod phylogeny, and only partially represent a test of homology by congruence, which is currently regarded as the most reliable method for testing homology (e.g. de Pinna 1991; Rieppel 1992, 1994).

The other methodology is to use as many characters as possible in order to test character congruence and thus establish synapomorphies. Consistency indices and often resolution of the cladograms are poorer than in the approach described above, and the phylogenies exhibit abundant homoplasy. Many recent analyses tend towards this approach (e.g. Holtz 1994, 2000; Makovicky and Sues 1998; this paper). The advantage of this approach is that it is (in theory at least) not dependent on preconceptions of the phylogeny of the group under study and thus represents a more objective analysis of the relationships of the group. Furthermore, by acknowledging the high amount of homoplasy in a cladogram, it more precisely reflects problems in the phylogeny of a given group, such as parallel evolution and incompleteness of the fossil record. One of the major problems in this approach is character choice, definition and description: the degree of familiarity with the anatomy of many different clades of theropods required to identify and evaluate the significance of very high numbers of characters takes more time than is usually available for the completion of a project. Thus, character choice is often biased in favour of characters that are found in taxa that the systematist is most familiar with, or characters that are part of a character complex that they have studied in detail.

In either methodology, character choice will always be a source of contention. Some of the problems stem from our still poor understanding of aspects such as individual and ontogenetic variation, or size dependency of characters. A principal problem is the question: 'Which type of characters should be used?' Several workers have, for example, rejected the use of metric, or generally continuous characters (e.g. Pimentel and Riggins 1987). However, I agree with Rae (1998) that continuous characters can and should be used in phylogenetic reconstructions, since they contain potential phylogenetic information. Furthermore, if a gradual change from one species to the next is accepted as a major pattern of evolution, one would expect that most characters change gradually, if the fossil record were good enough to reveal all changes.

Another factor that accounts for the differences in current theropod cladograms is the choice of taxa that were used as OTUs. Different workers have used different genera as OTUs, or included higher rank taxa with different taxonomic contents in the analysis. The considerable effects that taxon choice can have on a cladogram that is based on the same characters is shown in the present analysis by the dependency of the phylogenetic position of *Dilophosaurus* on the inclusion or exclusion of *Shuvosaurus*. The very unusual anatomy of *Shuvosaurus* and its impact on the phylogeny of basal theropods also emphasizes how little is yet known about early theropod evolution.

Another taxonomic problem is the use of higher rank taxa. The monophyly of many higher rank taxa that are frequently used in analyses (e.g. dromaeosaurids, troodontids, tyrannosaurids) has only rarely been tested by cladistic analyses, and the exact taxonomic contents of many of these clades are uncertain. The inclusion of *Dromaeosaurus* and velociraptorines in a monophyletic Dromaeosauridae, for example, has never been demonstrated in a cladistic analysis. *Dromaeosaurus* is only known from a skull and some fragmentary postcranial remains, and the skull shows several features that are different from velociraptorines (degree of pneumatization of the braincase, morphology of the teeth). Thus, the monophyly of the Dromaeosauridae might be doubted. However, the braincase and mandible of *Dromaeosaurus*, which are the best preserved elements in the holotype, have often been used for coding dromaeosaurid characters, since these elements of the skull are by far the best described and most easily accessible of any dromaeosaurid so far. This highlights another problem in the use of higher rank taxa: character codings for these clades are often

based on the best known, or best described taxon included in it, and might thus not represent the true morphological diversity within that clade.

The interrelationships of taxa within higher rank taxa have also not been established for most of these clades. This is a problem since character codings should, ideally, be based on the basal condition of a higher rank taxon and not on character distributions found in crown group taxa within this group. Thus, the proposed phylogenetic relationships of taxa within ornithomimosaurs (see discussion of OTUs), for example, imply that the presence of an arctometatarsalian pes is not the plesiomorphic condition for this clade (as assumed by Holtz 1994), but arose within it independently from the arctometatarsalian condition found in tyrannosaurids, caenagnathids, and troodontids.

Gaps in the fossil record of theropods present another problem for phylogenetic reconstruction. Taxa that are separated from other taxa by large morphological or temporal gaps are difficult to fit into a phylogeny. One example of this is *Elaphrosaurus*, an African taxon that is, furthermore, only represented by a partial postcranial skeleton. *Elaphrosaurus* combines many plesiomorphic characters with a variety of features that are otherwise only found in coelurosaurs, especially ornithomimosaurs. This combination of characters makes *Elaphrosaurus* a problematic taxon in theropod phylogeny, and this problem reflects the fact that this genus is the only African theropod from the Upper Jurassic that is represented by diagnosable skeletal material. As discussed above, this morphological gap between *Elaphrosaurus* and its closest relatives (*Ceratosaurus* and abelisaurids) also indicates that this genus has a much longer ghost range than is implied by the assumed sister-group relationship of the abelisauroids with *Ceratosaurus*.

*Possible solutions.* Several suggestions follow from the observations presented above. To agree on a single methodology it would be useful to combine data used by different scientists to construct a large data set. Several prerequisites are necessary for an analysis of such a large data set.

A rigorous taxonomic review of theropod dinosaurs is necessary to identify valid and invalid genera and species. All genera and species that are considered valid should be included in the analysis, and the analysis should be only based on species-level taxa. The effects of large amounts of missing data, which would certainly be present in an analysis of all valid taxa, could be at least partially reduced by safe taxonomic deletion (Wilkinson 1995) and reduced consensus methods (Wilkinson 1994). If genera, families, or even higher-level taxa, are included in the analysis, their monophyly and the interrelationships of taxa within this clade should be established by separate cladistic analyses prior to the analysis of all theropods.

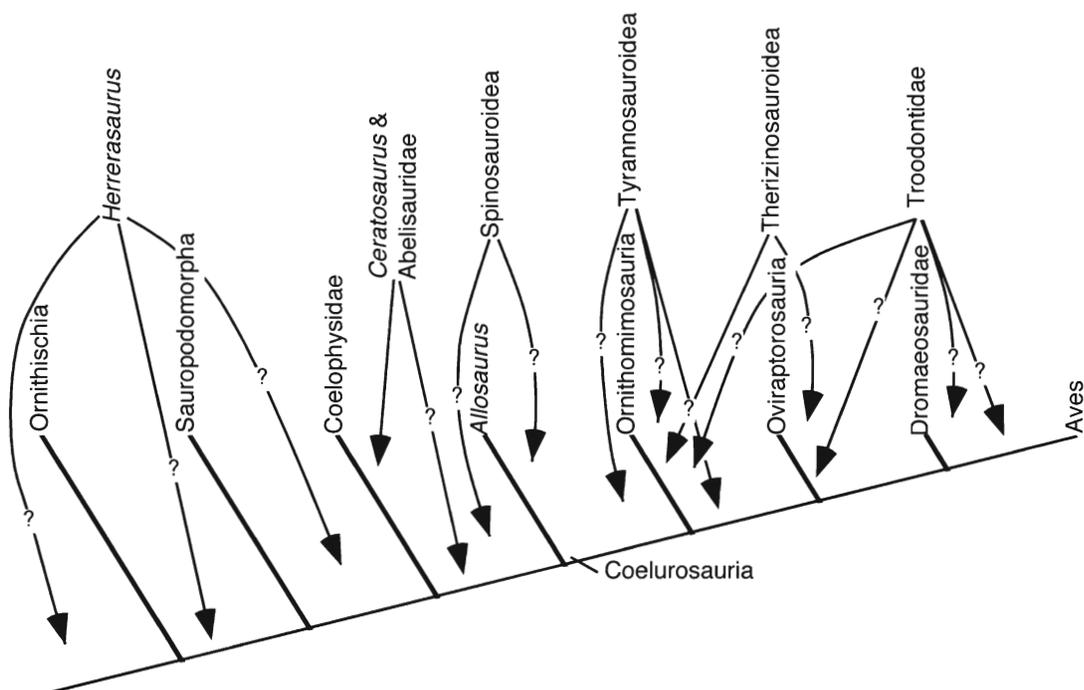
Detailed studies of character complexes must be carried out for a better understanding of character interdependency, variability and better character definition. These analyses should include both investigations of character ontogeny and individual variation in large samples of a single taxon (e.g. *Coelophysis*, *Allosaurus*), as well as detailed comparisons of character complexes between different taxa of theropods. These studies provide different lines of evidence for the formation of hypotheses of homology, which can then be tested by a congruence analysis (de Pinna 1991; Rieppel 1992, 1994).

New discoveries will, of course, always have an effect on the outcome of a cladistic analysis. The results presented above strongly suggest that especially the fossil record of Gondwanan theropods needs to be improved for a better understanding of theropod phylogeny and evolution.

#### *Consensus in current phylogenies and the evolutionary history of theropods*

*Consensus in theropod phylogeny.* Despite the many disparities found in the different hypotheses of theropod phylogeny, there are also consistent similarities. If the data taken from recent hypotheses are combined, several patterns of theropod evolution emerge.

One way of combining phylogenetic information from several analyses is to identify taxa that create problems in phylogenetic reconstructions (Gower and Wilkinson 1996; Holtz 1999). An examination of current theropod cladograms (Novas 1992a; Holtz 1994; Sereno *et al.* 1994, 1996; Sereno 1997, 1999; Makovicky and Sues 1998; Forster *et al.* 1998; this paper) revealed an underlying agreement in the arrangement of several taxa (Text-fig. 59; see also Holtz 1999, 2001b; Farlow *et al.* 2001). All analyses



TEXT-FIG. 59. Consensus cladogram of theropod relationships, showing relationships between several theropod taxa common to all recent cladistic analyses. Possible phylogenetic positions of several important problematic taxa are also indicated.

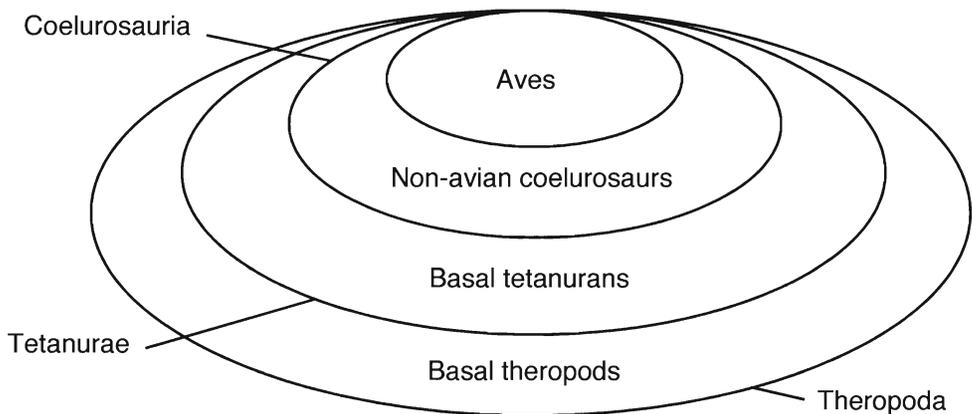
support neotheropodan monophyly, and coelophysids are considered to be more basal than *Allosaurus* and coelurosaurs. Within coelurosaurs, birds are constantly regarded as more closely related to dromaeosaurids than oviraptorosaurs, and the latter taxon is considered to be more closely related to birds than ornithomimosaurids (see also Holtz 1999). A number of taxa create the ‘noise’ that accounts for the apparent differences in different cladograms.

At the base of the theropod tree these are principally the herrerasaurids, which have variously been regarded as being outside the Ornithischia-Saurischia-dichotomy, as basal saurischians, or as basal theropods. This most probably reflects our still poor knowledge of the anatomy of early dinosaurs and basal dinosauriforms.

Recently, another problem with the phylogenetic position of abelisaurids and *Ceratosaurus* was recognized: these taxa are variously regarded as a sister group to coelophysoids (e.g. Holtz 1994; Sereno 1997, 1999), as separate successive outgroups of tetanurans (Rauhut 1998; Carrano and Sampson 1999), or as a monophyletic group that represents the sister-group to tetanurans (present analysis). The reason for these problems in placing *Ceratosaurus* and its close relatives may be the poor fossil record of Gondwanan theropods.

Apart from several poorly known taxa, the phylogenetic position of the Spinosauroidae shows greatest uncertainty among basal tetanurans. Whereas Sereno *et al.* (1996) and Sereno (1997, 1999) regarded this clade as the sister group to an allosauroid-coelurosaur clade, it is included in a monophyletic Carnosauria here, together with allosauroids. As noted above, more detailed analyses of character distribution within early tetanurans are needed to solve this problem.

Within coelurosaurs three larger clades create problems in phylogenetic reconstructions: the tyrannosaurids, the therizinosauroids and the troodontids. There are several reasons for the problems with these taxa. In tyrannosaurids, the considerably larger size of most of the members of this clade in comparison with other coelurosaurs makes the evaluation of several, probably size-related characters difficult. The



TEXT-FIG. 60. Consensus of recent phylogenetic analyses. All recent analyses agree that Theropoda is a monophylum, and within Theropoda, a monophyletic clade Tetanurae exists. There is further agreement that Tetanurae includes a monophyletic Coelurosauria and that Aves is part of the latter clade.

strong modifications of the skull and skeleton in therizinosaurs and our still poor knowledge of basal members of this clade account for the problems with the relationships of this clade within coelurosaurs. In troödontids, the differences in the phylogenetic placement of this clade at least partially stem from the combination of an ornithomimosaur-like skull with a dromaeosaurid-like postcranium in these animals. This problem might have been solved by the recent discovery of *Sinovenator*, which shows a character combination intermediate between dromaeosaurids and troödontids (Xu *et al.* 2002).

Another way of identifying consensus within current theropod phylogenies is to determine the taxonomic contents of clades. All current phylogenies agree in neotheropodan monophyly, in the existence of a monophyletic Tetanurae, and a monophyletic Coelurosauria (Text-fig. 60). Regardless of the detailed relationships of taxa within these clades, the taxonomic content of each of these clades is also constant in current phylogenies.

Neotheropoda includes several basal taxa ('non-tetanuran neotheropods') and Tetanurae. The non-tetanuran neotheropods are coelophysoids, *Dilophosaurus* and ceratosaurs in all analyses. Within these non-tetanuran neotheropods, two monophyletic clades are recognized by the vast majority of analyses: coelophysoids, including at least coelophysids and other, mainly Late Triassic theropods, and Ceratosauria, which include *Ceratosaurus* and abelisaurids. Only Rauhut (1998) and Carrano and Sampson (1999) argued for more distant relationships between the latter two taxa; however, the results presented in these two abstracts were preliminary, and the present analysis does not support my earlier (Rauhut 1998) assumption of the paraphyly of the *Ceratosaurus*–abelisaurid clade. Likewise, the inclusion of new characters in their data matrix will probably change the hypothesis of the interrelationships of these taxa advocated by Carrano and Sampson (1999; Carrano, pers. comm. 1999).

Comparable to the situation found in neotheropodans, Tetanurae includes several basal taxa ('non-coelurosaurian tetanurans') and coelurosaurs. All current phylogenies agree on the taxonomic contents of Tetanurae, and also on which taxa are non-coelurosaurian tetanurans. Among non-coelurosaurian tetanurans, two monophyletic clades are recognized by all analyses that include a higher number of basal tetanurans (Sereno *et al.* 1994, 1996, 1998; Sereno 1997, 1999; this paper): the Spinosauroida, mainly including baryonychids (= spinosaurids), *Torvosaurus*, and *Magnosaurus* (including *Eustreptospondylus*), and the Allosauroida, including *Monolophosaurus*, *Allosaurus*, sinraptorids, and carcharodontosaurids. The analyses differ in the relationships of these two clades to each other and in the placement of several other genera (e.g. *Afrovenator*).

Coelurosaurs are recognized as a monophyletic clade in all cladistic analyses of theropods (Gauthier 1986; Benton 1990; Novas 1992a; Holtz 1994; Sereno 1997, 1999; Forster *et al.* 1998; this paper), with surprisingly little differences in the taxonomic contents of this clade. The only major change in taxonomic

content from the coelurosaur concept proposed by Gauthier (1986) is the inclusion of tyrannosaurids in all current analyses.

*The evolutionary history of theropod dinosaurs.* Theropod origins are still poorly understood, despite recent discoveries in South America (Serenó and Novas 1992; Sereno *et al.* 1993). As discussed above, this is partially a result of our still inadequate knowledge of the immediate dinosaur outgroups; the intensive discussion about whether *Herrerasaurus* represents a basal dinosaur, a basal saurischian, a basal sauropodomorph, or a basal theropod highlights this problem. If the inclusion of *Eoraptor* and herrerasaurids in the Theropoda, as advocated here, is accepted, it seems probable that theropod origins are to be found in South America. This conclusion is supported by the observation that basal ornithomirans and dinosauriforms are known from South America (Romer 1971, 1972; Bonaparte 1975; Arcucci 1986, 1987; Sereno and Arcucci 1993, 1994) and Europe (Benton 1999; Rauhut and Hungerbühler 2000), but the oldest and most basal theropods are exclusively known from the Carnian of South America (Reig 1963; Colbert 1970; Sereno and Novas 1992; Sereno *et al.* 1993). Claims that herrerasaurids were also present in the uppermost Carnian–Norian of North America (Long and Murry 1995; Hunt *et al.* 1998) have yet to be substantiated. Another indication that theropod history began in South America is the occurrence as well of the oldest members of their sister-group, the sauropodomorphs, in the Carnian of this continent (Langer *et al.* 1999).

Whereas the first theropods were most probably small animals (as indicated by the small size of basal dinosauriforms and the most basal theropod known, *Eoraptor*), larger taxa appeared early in theropod evolution: *Herrerasaurus* was an animal of up to 6 m in length (Serenó and Novas 1992) with a weight of 100–400 kg (Peczkis 1994). The reason for this increase in size is uncertain, but the relatively large size of possible prey taxa might be a possible explanation.

These most basal theropods appeared in the fossil record in the Middle–Late Carnian, and probably died out before the Middle Norian (Text-fig. 56). Whether they were replaced because of competition with the more advanced neotheropods, or their extinction had different reasons remains unclear. They might have been victims of a late Carnian extinction event, which set the stage for the radiation of other groups of dinosaurs in the Norian (Benton 1984, 1993).

The first neotheropods, coelophysoids, first appeared in the latest Carnian (Hunt *et al.* 1998) and were widely distributed in the Norian/Rhaetian and the Early Jurassic. Thus, coelophysoids represent the first successful radiation of neotheropods. As discussed above, this radiation appears to have been rapid after the end of the Carnian.

Curiously, no coelophysoids are known from South America; the earliest members of this clade come from North America, and they are well known from the Norian of the latter continent (Colbert 1989; Chatterjee 1993; Carpenter 1997) and Europe (Rauhut and Hungerbühler 2000). The only Triassic neotheropod from South America seems to be an already more derived theropod, not a member of the Coelophysoidea (Arcucci and Coria 1998). Thus, whereas the origin of theropods will probably be found in South America, the early diversification of neotheropods might have taken place in Laurasia. In the Lower Jurassic, coelophysoids are known from North America (Rowe 1989), Africa (Raath 1969), and possibly Europe (*Sarcosaurus*; Andrews 1921). Thus, the Late Triassic and Early Jurassic theropod faunas seem to have been similar in Laurasia and Gondwana.

Coelophysoids include both small (*Segisaurus*: length less than 2 m, weight probably less than 10 kg; Peczkis 1994) and large taxa (*Liliensternus* and *Gojirasaurus*: length more than 5 m, weight more than 100 kg; Peczkis 1994), which renders it difficult to determine the probable size of the most recent common ancestor of all neotheropods. However, the fact that the sister group to neotheropods, the herrerasaurids, and the basal members of the Coelophysoidea (*Liliensternus* and *Gojirasaurus*), are relatively large animals might indicate that this ancestor was also considerably larger than the basal dinosauriforms, and probably the most basal dinosaurs.

No member of the Coelophysoidea is known from sediments younger than the Early Jurassic. Unfortunately, however, the Middle Jurassic theropod fossil record is very poor (Text-fig. 56); this is particularly true of North America and the Gondwana continents. It is, therefore, possible that coelophysoids survived on one of these continents until the Middle or early Late Jurassic.

The other major clade of basal neotheropods, the Ceratosauria, is known from the Late Jurassic to the latest Cretaceous (Text-fig. 56). With the exception of *Ceratosaurus* and the abelisaur *Genusaurus*, all known members of the Ceratosauria are from Gondwana. *Genusaurus*, from upper Lower Cretaceous deposits in Europe (Accarie *et al.* 1995), probably represents an immigrant from Gondwana, since all of its closest relatives are found in Gondwana, and there is evidence for faunal links between Europe and Africa in the Early Cretaceous (Charig and Milner 1997; Sereno *et al.* 1998). Thus, ceratosaurs were rare in the Northern Hemisphere, but they represented a considerable element of Gondwanan faunas. As noted above, the evolutionary history of this group probably reaches back to Middle or even Early Jurassic times, but the origin and early evolution of this group is unknown because of our poor knowledge of Early and Middle Jurassic Gondwanan theropods.

Ceratosaurs were medium-sized to large theropods. Whereas known basal members of this group, *Ceratosaurus* and *Elaphrosaurus*, were animals of moderate size (5–6 m in length), some of the advanced Cretaceous representatives of this clade (*Carnotaurus*, *Abelisaurus*) attained giant size (up to 10 m in length). This increase in size during ceratosaur evolution thus represents a convergent development with the evolution of giant tetanurans in the Late Jurassic–Late Cretaceous.

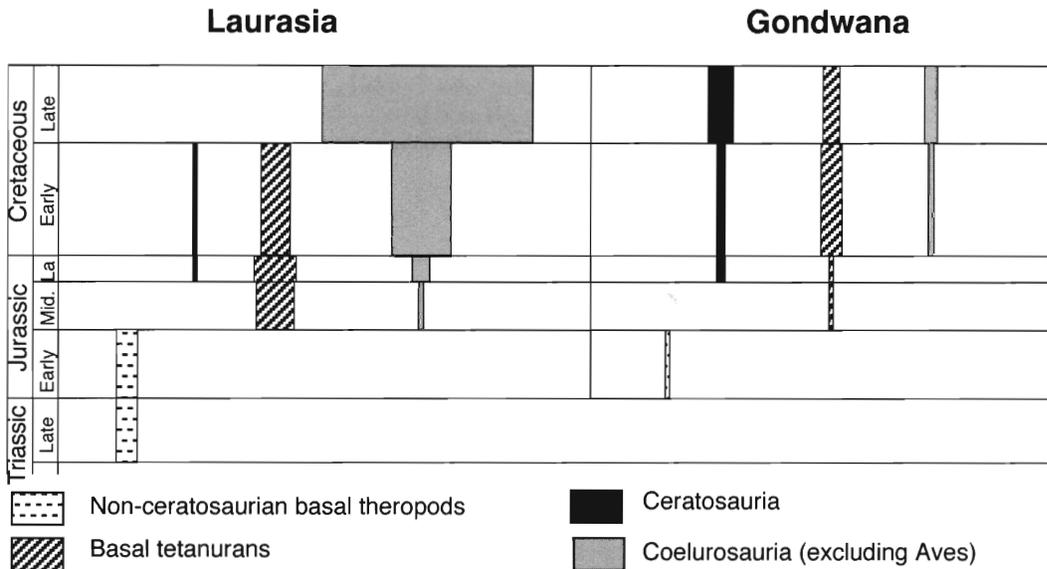
The phylogenetic position of the Ceratosauria has a significant impact on interpretations of the evolutionary history of theropod dinosaurs. If the monophyly of the Ceratosauria *sensu* Gauthier (1986) is accepted, at least two lineages of theropods survived up to the end of the Mesozoic: the tetanurans and the neoceratosaurs (*Ceratosaurus*, *Elaphrosaurus* and abelisaurids). However, if the hypothesis that ceratosaurs are more closely related to tetanurans than to coelophysoids, as advocated in this paper, is accepted, only one lineage of basal neotheropods survived the Early–Middle Jurassic (Text-fig. 56), and theropods might have been on the brink of extinction at some point during this time. Thus, theropod evolution might have followed a pattern of early radiation – extinction – further differentiation of a single surviving lineage. Such a pattern is found in several groups of vertebrates: in birds, for example, among Mesozoic lineages (Enanthiornithes, Hesperornithiformes, Ichthyornithiformes, Neornithes) only Neornithes survived the Cretaceous/Tertiary boundary. In this context, *Cryolophosaurus*, from the Lower Jurassic of Antarctica (Hammer and Hickerson 1994), might prove to be a very interesting animal. If the referral of this taxon to the Allosauroidae (Sereno *et al.* 1996; Sereno 1997, 1999) is correct, this phylogenetic position indicates that other lineages of tetanurans (ceratosaurs, spinosauroids, coelurosaurids) also reach back to at least the Early Jurassic. In this case, no crisis might have occurred in the evolution of theropods during the early Early Jurassic, but coelophysoids might simply have been replaced by a radiation of more advanced neotheropods.

Whereas ceratosaurs flourished in Gondwana throughout the Cretaceous Period, basal theropods did not play a major role in the theropod faunas from the Middle Jurassic onwards in the Northern Hemisphere; they were replaced by tetanurans in these continents (Text-fig. 61).

Basal, non-coelurosaurian tetanurans first appeared in the early Middle Jurassic (*Magnosaurus nethercombensis*) and flourished until the early Late Cretaceous (baryonychids and carcharodontosaurids; Text-fig. 56). Again, the phylogenetic position of ceratosaurs has an important impact on interpretations of the evolutionary history of tetanurans. If ceratosaurs form the sister-group to coelophysoids (Ceratosauria *sensu* Gauthier 1986), at least three lineages of theropods must have been present at the Triassic/Jurassic boundary: the Coelophysoidea, the Neoceratosauria, and the Tetanurae. Tetanuran history would thus reach back to at least the Late Carnian, and all three major lineages of theropods would have been established very early in theropod evolution. If ceratosaurs represent the sister-group to tetanurans (this analysis), only two lineages might have been present at the Triassic/Jurassic boundary, and the diversification of the Ceratosauria–Tetanurae clade could have taken place in the Early–Middle Jurassic, possibly favoured by the decline of the Coelophysoidea.

Basal tetanurans are known from both Laurasia and Gondwana in the Middle–Upper Jurassic, but they become rare in the Lower Cretaceous in the Northern Hemisphere (Text-fig. 61). The two surviving Late Cretaceous clades are exclusively found in Gondwana, and they might have persisted there until the end of the Cretaceous, but are unknown in the poor fossil record of these continents.

Basal tetanurans are medium-sized to large animals, including some of the largest theropods known (*Allosaurus maximus*, *Carcharodontosaurus*, *Giganotosaurus*). It is interesting that the diversification of



TEXT-FIG. 61. Theropod radiations in Laurasia and Gondwana. Column thickness indicates number of taxa. For the Gondwanan columns, some generically indeterminate material has been included for stages for which no generically diagnostic material is known.

these clades seems to coincide with the diversification of sauropod dinosaurs in the Middle–Late Jurassic. Moreover, the decline of basal tetanurans in the Northern Hemisphere also coincides with a decline in the Early Cretaceous of the number of sauropod taxa known from these continents, whereas sauropods were abundant in Gondwana until the end of the Cretaceous (see e.g. Weishampel 1990). This might indicate that large basal tetanurans mainly preyed or scavenged on sauropod dinosaurs (with the exception of some highly specialized representatives, such as the baryonychids), but more detailed studies of the occurrence, functional anatomy, and ecology of these animals are needed to confirm this.

Thus, a world-wide radiation of large basal tetanurans in the Middle–Late Jurassic can be recognized, whether these taxa represent only one, or two or more monophyletic clades. As is the case with ceratosaurs, basal tetanurans were abundant in Gondwana during the Cretaceous Period, but were largely replaced by coelurosaurs in Laurasia during the Early Cretaceous (Text-fig. 61). No basal tetanurans are found on the Laurasian continents in sediments younger than Aptian/Albian.

The first coelurosaur, *Proceratosaurus*, is known from the Middle Jurassic, and the group underwent a rapid radiation in the Late Jurassic and Early Cretaceous (Text-figs 56, 61). The majority of coelurosaur lineages were established by the Late Jurassic, and only further differentiation within these lineages occurred in the Cretaceous. All major lineages were established by the end of the Early Cretaceous (Text-fig. 56), and, at the present state of knowledge, Late Cretaceous non-avian coelurosaur faunas show surprisingly little change in their taxonomic contents and anatomical diversity in Cenomanian–Maastrichtian deposits. Coelurosaurs completely replaced all more basal theropods in the Laurasian continents during the Late Cretaceous, but non-avian coelurosaurs were rare in the Southern Hemisphere. Within coelurosaurs, birds represent another very successful radiation of theropods.

Coelurosaurs include both small and large members. It is noteworthy that within coelurosaurs, giant members seemingly evolved independently in at least three different clades: *Tyrannosaurus* and its closest relatives within tyrannosaurids, *Deinocheirus* within ornithomimosaurids, and *Therizinosaurus* within therizinosauroids. Again, the reasons for this gigantism are unclear.

## CONCLUSIONS

At least four major radiations of theropods (excluding Aves) can be recognized, which show different patterns in Laurasia and Gondwana (Text-fig. 61). In the Late Triassic, coelophysoids represented the first successful group of theropods, and gained a world-wide distribution. They were replaced by ceratosaurs and tetanurans in the Middle Jurassic. Whereas ceratosaurs were mainly restricted to the southern continents, tetanurans established themselves in both Laurasia and Gondwana. Coelurosaurs are first known from the Middle Jurassic. They underwent rapid radiation during the Late Jurassic–Early Cretaceous, almost completely replacing more basal theropods in Laurasia. Very few non-avian coelurosaurs are known from Gondwana, and the Cretaceous theropod faunas of the southern continents were dominated by ceratosaurs and basal tetanurans until the Late Cretaceous. Whereas early Mesozoic theropod faunas were thus rather uniform on all continents, the differences between Laurasia and Gondwana, and between the separate continents that constitute these landmasses, became more marked during the middle–late Mesozoic. This increase in the differences of the faunas can be explained by increased endemism also found in other groups of dinosaurs (Serenó 1997) because of the geographic separation of the continents. Thus, the breakup of Pangea obviously led to an increased differentiation of theropod faunas from different continents. However, Gondwanan theropod faunas are much more poorly known than Laurasian faunas, so conclusions about diversification patterns of theropods on the southern continents must be regarded with caution.

Non-avian theropods seem to have reached their greatest diversity during the Late Jurassic–Early Cretaceous. All major lineages of theropods were established by the end of the Early Cretaceous, and the Late Cretaceous saw only further successions of genera within this lineages, but without the appearance of any major anatomical novelties.

Giant size was attained independently in several lineages of theropods. In this context, it is interesting to note that the maximum size in all these lineages seems to be similar (at a length of 10–15 m and a weight of 6–8 tons), but the reasons for this are unknown. Ecological (prey availability, population/area ratios), physiological (problems of heat transfer and heat loss) and biomechanical (safety factors in the limb bones, stability of the limbs and vertebral column) reasons for this apparent constraint are possible, but further research into theropod gigantism is needed.

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## APPENDIX

### *Institutional abbreviations*

AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; BP/I, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; BYU, Brigham Young University, Provo, Utah, USA; CU, Caen University, Caen, France; DNM, Dinosaur National Monument, Utah, USA; FMNH, Field Museum of Natural History, Chicago, USA; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; IGM, Mongolian Institute of Geology, Ulan Bataar, Mongolia (specimens examined currently housed at the AMNH); IPFUB, Institut für Paläontologie der Freien Universität Berlin, Germany; IVPP, Institute of Vertebrate Palaeontology and Paleoanthropology, Beijing, China; JM, Jura Museum, Eichstätt, Germany; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huinul, Argentina (specimens examined currently housed at the MACN); NMC, National Museum of Canada, Ottawa, Canada (specimens examined currently housed at the TMP); MNN, Musée National du Niger, Niamey, Niger (specimens examined currently housed at the UC); MOR, Museum of the Rockies, Bozeman, Montana, USA; NGMC, National Geological Museum of China, Beijing, China; OUM, Oxford University Museum, Oxford, UK; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; QG, National Museum of Natural History, Harare, Zimbabwe; ROM, Royal Ontario Museum, Toronto, Canada; SGM, S ervice G eologique du Maroc, Minist ere de l' nergie et des Mines, Rabat, Morocco (specimens examined currently housed at the UC); SMNS, Staatliches Museum f ur Naturkunde, Stuttgart, Germany; TMP, Royal Tyrrell Museum of Paleontology, Drumheller,

Alberta, Canada; UA, Université d'Antananarivo, Tananarive, Madagascar (specimens currently housed at State University of New York at Stony Brook, New York, USA); UC, University of Chicago, USA; UCMP, University of California, Paleontological Museum, Berkeley, California, USA; UMNH, Utah Museum of Natural History, Salt Lake City, USA; USNM, United States National Museum, Smithsonian Institution, Washington DC, USA; UUV, University of Utah, Vertebrate Paleontology Collection, Salt Lake City (these are old numbers, which have now been replaced by either UMNH or DNM numbers, but they are frequently found in the literature and therefore given in addition to the new numbers here); YPM, Yale Peabody Museum, New Haven, Connecticut, USA. \*Specimens noted below have only been studied in exhibitions, sometimes behind glass.

### Outgroups

*Euparkeria capensis*; Literature used: Ewer 1965, Gower and Weber 1998.

*Marasuchus lilloensis*; MBR. 2088 (cast of holotype and skeletal reconstruction). Literature used: Bonaparte 1975; Sereno and Arcucci 1994.

Ornithischia. *Dryosaurus lettowvorbecki*: MB, GPIT, SMNS (several hundreds of bones.); *Lesothosaurus diagnosticus*: BMNH RU B 23, R 11956, RU B 17; *Scelidosaurus harrisoni*: BRSMG Ce 12785. Literature used: Marsh 1896; Thulborn 1970, 1972; Galton 1974; Norman 1980, 1986; Colbert 1981; Sereno 1986, 1991b; Coombs *et al.* 1990; Weishampel and Witmer 1990a, b; Haubold 1990; Peng 1992.

Sauropodomorpha. *Thecodontosaurus*: BMNH RU P 24, RU P 51, RU P 59/5, RU P 24/5a, RU P 83/1, RU P 64/1, RU P 77/1, RU P 24/4a; *Plateosaurus*: GPIT Skelett I, Skelett II, Skelett VI; GPIT 18375, SMNS 1986, F 20, F 65, unnumbered, 13200, F 5, MB Skelett I, Skelett XXV, Skelett XXXII, Skelett XXXXV, MB R. 1937; *Sellosaurus gracilis*: GPIT PV 18318a. Literature used: Huene 1926b, 1932; Galton 1976, 1984, 1985c, 1990; Kermack 1984; Attridge *et al.* 1985; Gow 1990; Gow *et al.* 1990; Bonaparte and Pumares 1995.

### Theropoda

*Afrovenator abakensis*: UC OBA 1 (holotype; skull is now housed at the MNN). Literature used: Sereno *et al.* 1994. *Allosaurus* sp.: AMNH 5767 (holotype of *Epanterias amplexus*), AMNH 287, 324, 666, 680, 813, 5750, 6125, BYU Mes 5583, DNM 116, 2560 (originally UUV 6000), MOR 693, UMNH VP 3113, 5316, 5326–5328, 5470, 6365, 6499, 6502, 7408, 7411, USNM 2323, \*4737, 8367, UUV 3304. Literature used: Osborn 1912a; Gilmore 1920; Madsen 1976.

*Avimimus portentosus*: ROM 46144 (cast of the holotype and referred specimens). Literature used: Kurzanov 1982–1983, 1985, 1987.

*Bagaraatan ostromi*: Literature used: Osmólska 1996.

*Caudipteryx zoui*: \*NGMC 97-4-A (holotype), \*NGMC 97-9-A. Literature used: Ji *et al.* 1998.

*Ceratosaurus*: USNM 4735 (holotype of *C. nasicornis*), YPM 4681, UMNH VP 5278 (type of *C. dentisulcatus*), MOR 005, 009 (casts of the type of *C. magnicornis*). Literature used: Marsh 1884, 1896; Hay 1908; Gilmore 1920.

'*Chilantaisaurus*' *maortuensis*: IVPP V 2885 (holotype). Literature used: Hu 1964.

*Chilantaisaurus tashuikouensis*: IVPP V 2884 (holotype). Literature used: Hu 1964.

*Coelophysis bauri*: GPIT 10/2–5, 10/7, 11/1–2, 12/1 (casts of Cope's original material), \*AMNH 7223, 7224, UCMP V 82250–129618. Literature used: Huene 1915; Padian 1986; Colbert 1989; Rowe and Gauthier 1990; Paul 1993.

*Coelurus fragilis*: YPM 1993 (holotype), YPM 1991–1992, 1994–1995, 2010. Literature used: Marsh 1881b, 1884, 1896; Gilmore 1920; Ostrom 1980; Makovicky 1995, 1997.

*Compsognathus longipes*: BSP A. S. I 563 (holotype). Literature used: Huene 1925; Bidar *et al.* 1972; Ostrom 1978. *Compsognathinae* indet.: SMNK 2349 Pal.

*Deltadromeus agilis*: SGM-Din 2 (holotype). Literature used: Sereno *et al.* 1996.

*Dilophosaurus wetherilli*: UCMP V 4214 (holotype and paratype), UCMP V 6468. Literature used: Welles 1984.

*Elaphrosaurus bambergi*: \*MB dd unnumbered (holotype). Literature used: Janensch 1920, 1925, 1929; Russell 1972; Galton 1982; Barsbold and Osmólska 1990.

*Eoraptor lunensis*: PVSJ 512 (skull of the holotype), ROM 44686 (cast of the holotype). Literature used: Sereno *et al.* 1993.

*Gojirasaurus quayi*: MB 1985. G.1–3 (cast of the holotype). Literature used: Parrish and Carpenter 1986; Carpenter 1997.

*Herrerasaurus ischigualastensis*: Literature used: Reig 1963; Brinkman and Sues 1987; Novas 1989, 1992b, 1993; Sues 1990; Sereno and Novas 1992, 1993; Sereno 1993.

*Ligabueino andesi*: MACN-N 42 (holotype). Literature used: Bonaparte 1996.  
*Liliensternus airelensis*: CU unnumbered (cast of the holotype). Literature used: Cuny and Galton 1993.  
*Liliensternus liliensterni*: MB R. 2175 (syntype). Literature used: Huene 1934; Welles 1984; Rowe and Gauthier 1990.  
*Magnosaurus nethercombensis*: OUM J 12143 (holotype). Literature used: Huene 1926a, 1932; Waldman 1974.  
*Magnosaurus oxoniensis* (= *Eustreptospondylus oxoniensis*): OUM J 13558 (holotype). Literature used: Phillips 1871; Nopcsa 1906; Huene 1923, 1926a, 1932; Walker 1964.  
*Metriacanthosaurus parkeri*: OUM J 12144 (holotype). Literature used: Huene 1923, 1926a, 1932; Walker 1964.  
*Microvenator celer*: AMNH 3041 (holotype). Literature used: Ostrom 1970; Makovicky and Sues 1998.  
*Monolophosaurus jiangi*: Literature used: Zhao and Currie 1993.  
*Ormitholestes hermanni*: AMNH 619 (holotype). Literature used: Osborn 1903, 1916; Ostrom 1980; Paul 1988b; Makovicky 1995.  
*Piatnitzkysaurus floresi*: MACN CH 895; MACN unnumbered (cast of braincase of holotype). Literature used: Bonaparte 1986.  
*Poekilopleuron bucklandi*: Holotype and only known specimen was destroyed during the second world war. Literature used: Eudes-Deslongchamps 1838; Huene 1926a.  
*Proceratosaurus bradleyi*: BMNH R 4860 (holotype). Literature used: Woodward 1910; Huene 1932; Paul 1988a, b.  
*Procompsognathus triassicus*: SMNS 12591 (holotype). Literature used: Fraas 1913; Huene 1921; Ostrom 1981; Sereno and Wild 1992.  
*Segisaurus halli*: UCMP V 338 (holotype). Literature used: Camp 1936.  
*Shuvosaurus inexpectatus*: TTU P 9280 (holotype), TTU P 9281, 9282. Literature used: Chatterjee 1993; Rauhut 1997.  
*Siamotyrannus isanensis*: Literature used: Buffetaut *et al.* 1996.  
*Sinosauropteryx prima*: \*NGMC GMV 2123 (holotype), \*?NGMC 65. Literature used: Chen *et al.* 1998.  
*Staurikosaurus pricei*: Literature used: Colbert 1970; Galton 1977; Sues 1990.  
*Stokesosaurus* sp.: UMNH VP 7434 (UUVP 2938; holotype of *Stokesosaurus clevelandi*), UMNH VP 6368 (UUVP 2320), IPFUB Gui Th 1. Literature used: Madsen 1974.  
*Syntarsus rhodesiensis*: QG 1 (holotype), QG 127, 170, 174, 184, 185, 187, 193–197, 200, 202, 205–206, 213, 216, 230, 233–234, 245, 250, 278, 281, 284, 287, 289–290, 292, 577, 691, 781–782, BP/1/5278, 5246. Literature used (both species of *Syntarsus*): Raath 1969, 1985, 1990; Rowe 1989; Rowe and Gauthier 1990.  
*'Szechuanosaurus' zigongensis*: Literature used: Gao 1993.  
*Torvosaurus tanneri*: Literature used: Galton and Jensen 1979; Britt 1991.  
*Unenlagia comahuensis*: MCF PVPH 78 (holotype). Literature used: Novas and Puerta 1997.  
*Xuanhanosaurus qilixiaensis*: IVPP V 6729 (holotype). Literature used: Dong 1984.

Abelisauridae. *Carnotaurus sastrei*: MACN CH 894 (holotype), *Majungatholus atopus*: FMNH 96202–44C, FMNH/UA field 96313–34, field #96300, field #96313, field #95263. Literature used: Bonaparte and Powell 1980; Bonaparte and Novas 1985; Bonaparte *et al.* 1990; Bonaparte 1991b; Sampson *et al.* 1998.

Aves. *Archaeopteryx*: MBI. 027.03 (Berlin specimen), JM (Eichstätt specimen), BSP (Munich specimen); *Confuciusornis sanctus*: GPIT unnumbered, JM unnumbered (two specimens); *Gallus domesticus*: KFC unnumbered; *Rahonavis ostromi*: UA 8656 (Holotype). Literature used: Marsh 1880; Wellnhofer 1974, 1988, 1992, 1993; Elzanowski 1991; Hou 1995; Elzanowski and Wellnhofer 1996; Forster *et al.* 1998.

Baryonychidae. *Baryonyx walkeri*: BMNH R 9951 (holotype); *Irritator challengeri*: SMNS 58022 (holotype); *Suchomimus tenerensis*: MNN GDF 500 (holotype), MNN GDF 501, 503–506. Literature used: Stromer 1915, 1934, 1936; Charig and Milner 1986, 1997; Kellner and Campos 1996; Martill *et al.* 1996; Sereno *et al.* 1998.

Carcharodontosauridae. *Carcharodontosaurus saharicus*: SGM-Din 1. Literature used: Stromer 1931, 1934, 1936; Stovall and Langston 1950; Coria and Salgado 1995; Rauhut 1995; Sereno *et al.* 1996; Harris 1998.

Dromaeosauridae. *Deinonychus antirrhopus*: YPM 5205 (holotype), YPM 5201–5204, 5206–5214, 5217–5218, 5220, 5223, 5226–5228, 5235–5236, 5243–5244, 5263, 5538; *Dromaeosaurus albertensis*: AMNH 5356 (holotype); *Megaraptor namunhuaiquii*: MCF-PVPH 79 (holotype); *Saurornitholestes langstoni*: TMP 74.10.5 (holotype; referral of the non-holotype material to the species *Saurornitholestes langstoni* is tentative; all the material clearly represents dromaeosaurids, and comes from beds of the same age and general geographic vicinity as the holotype) TMP 81.14.34, 85.56.48, 86.78.1, 88.121.39, 91.36.112, 92.36.129, 92.36.333, 93.36.98, 94.12.844, MOR 660; *Velociraptor mongoliensis*: AMNH 6515 (holotype), IGM 100/985, 100/986. Literature used: Matthew and Brown 1922; Osborn

1924; Colbert and Russell 1969; Ostrom 1969*a, b*, 1974, 1976*a, b*, 1990; Sues 1977, 1978; Barsbold 1983; Paul 1988*a*; Currie 1995; Makovicky 1995; Norell and Makovicky 1997; Norell *et al.* 1997; Novas 1998.

Ornithomimosauria. *Archaeornithomimus asiaticus*: AMNH DVP 6565 (lectotype), 6558, 6567, 6569–6570, 6576, 21786–21787, 21790, 21792–21795, 21798–21801, 21884–21887, 21889–21890; *Dromiceiomimus brevitertius*: ROM 797 (holotype), ROM 852 (type of *Struthiomimus ingens*), AMNH 5201; *Dromiceiomimus samueli*: ROM 840 (holotype); *Ornithomimus edmontonicus*: ROM 851; *Struthiomimus altus*: AMNH 5355, 5375, 5385, ROM 1790; Ornithomimosauria indet.: TMP 93.104.1, 93.62.1, cast of TMP 90.26.1, TMP unnumbered, USNM 4736 (holotype of *Ornithomimus sedens*), USNM 5684 (syntype of *Ornithomimus affinis*), USNM 5814 (holotype of *Ornithomimus tenuis*). Literature used: Osborn 1916; Gilmore 1920, 1933; Osmólska and Roniewicz 1969; Osmólska *et al.* 1972; Russell 1972; Nicholls and Russell 1985; Barsbold and Perle 1984; Barsbold 1988; Barsbold and Osmólska 1990; Smith and Galton 1990; Pérez-Moreno *et al.* 1994; Makovicky 1995; Makovicky and Norell 1998.

Oviraptorosauria. *Chirostenotes elegans*: ROM 781 (holotype), TMP 90.56.6, 92.36.390; *Chirostenotes pergracilis*: ROM 43250; unidentified caenagnathid: TMP 82.16.6; *Oviraptor philoceratops*: AMNH 6517 (left manus of holotype); *Oviraptor* sp.: IGM 100/9/72; unidentified oviraptorid: TMP 12.06.88–9. Literature used: Gilmore 1924*a*; Osborn 1924; Sternberg 1940; Cracraft 1971; Barsbold 1976*b*, 1977*b*, 1983; Osmólska 1976; Currie and Russell 1988; Barsbold *et al.* 1990; Currie 1990; Smith 1992; Currie *et al.* 1993; Makovicky 1995; Maryanska and Osmólska 1997; Sues 1997; Makovicky and Sues 1998.

Sinraptoridae. Literature used: Dong *et al.* 1983; Gao 1992; Currie and Zhao 1993*b*.

Therizinosauroida. *Beipiaosaurus inexpectus*: IVPP V 11559 (holotype). Literature used: Barsbold 1976*c*; Barsbold and Perle 1980; Paul 1984; Barsbold and Maryanska 1990; Russell and Dong 1993*a*; Clark *et al.* 1994; Makovicky 1995; Dong and Yu 1997; Xu *et al.* 1999.

Troödontidae. *Sinornithoides youngi*: IVPP V 9612 (holotype); *Troödon formosus*: AMNH 6174, MOR 553S, 563, 748, NMC 12340, 12392, 12433, ROM 1445, TMP 81.37.15, 83.12.11, 86.36.4, 86.49.10, 86.36.457, 88.50.88, 92.36.416, 92.36.575, 93.36.86, 94.12.415, 94.12.438. Literature used: Osborn 1924; Sternberg 1932; L. Russell 1948; D. Russell 1969; Barsbold 1974; Currie 1985, 1987; Wilson and Currie 1985; Barsbold *et al.* 1987; Osmólska 1987; Osmólska and Barsbold 1990; Kurzanov and Osmólska 1991; Currie and Peng 1993; Currie and Zhao 1993*a*; Russell and Dong 1993*b*; Makovicky 1995.

Tyrannosauridae. *Albertosaurus sarcophagus*: ROM 807 (holotype of *A. arctunguis*); *Alectrosaurus olseni*: AMNH 6554 (lectotype); *Daspletosaurus torosus*: AMNH 5346; *Gorgosaurus libratus*: AMNH 5432, \*FMNH PR 308, ROM 1247, USNM 12814, 16745; *Shanshanosaurus huoyanshanensis*: IVPP V 4878 (presacral vertebrae and humerus of the holotype); *Tyrannosaurus rex*: AMNH 973 (braincase of holotype), AMNH 5029; Tyrannosauridae indet. (often labelled as '*Albertosaurus* sp.'): AMNH 5218, 5226–5227, 5232, 5468, ROM 683, 1422, 4591. Literature used: Lambe 1917; Osborn 1905, 1906, 1912*a*, 1916; Gilmore 1933, 1946; Russell 1970; Maleev 1974; Molnar 1980, 1991; Bakker *et al.* 1988; Mader and Bradley 1989; Molnar and Carpenter 1989; Carpenter 1990, 1992; Molnar *et al.* 1990; Makovicky 1995; Makovicky and Currie 1998; Carr 1999.

#### *Other theropod material examined (except unidentified material)*

*Allosaurus* (?) *tendagurensis*: MB Tibia 67 (holotype); *Altispinax altispinax*: BMNH R 1828 (holotype); *Antrodemius valens*: USNM 218 (holotype); *Aristosuchus pusillus*: BMNH R 178 (lectotype); *Calamospondylus foxi*: BMNH R 901 (holotype); *Ceratosaurus* (?) *roechlingi*: type series: MB R. 1934–1935, 2160, 2162, referred material: MB R. 1926, 1938, 2166; *Halticosaurus longotarsus*: SMNS 12353 (Syntype); '*Halticosaurus*' *orbitoangulatus*: SMNS 12353*b* (holotype); *Labrosaurus ferox*: USNM 2513 (holotype); *Marshosaurus bicentesimus*: UNMH VP 6373 (holotype; UUVV 2826), UNMH VP 6372 (UUVV 1845), UNMH VP 6367–6368; *Megalosaurus bucklandi*: type series: OUM J 13505, 13576, 13577, referred material: OUM J 13506, 13559–13563, 13569, 13573–3575, 13579, 29773; '*Megalosaurus*' *hesperis*: BMNH R 332 (holotype); *Phaedrolosaurus ilikensis*: IVPP V (?)4025 (holotype); *Podokesaurus holyokensis*: AMNH DVP 2976 (cast of holotype); *Tugulusaurus faciles*: IVPP V 4025 (holotype).

Data matrix

Matrix	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Euparkeria	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Marasuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Ornithischia	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
4	Eoraptor	0	0	?	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
5	Herrerasaurus	0	0	?	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
6	Staurikosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Sauropodomorpha	0	1	0	0	1	1/2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
8	Coelophysis	0	1	0	1	1	2	0	?	1	0	0	1	1	0	1	0	0	0	0	0	0
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L. lilliensterni	?	?	?	?	?	1/2	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	0	1	0	1	?	1	0	0	0	?	?	1	0	?	0	0	0	0	0	0	0
14	Dilophosaurus	0	1	0	0	1	1/2	0	1	1	?	0	1	0	0	0	1	0	0	0	?	?
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Syntarsus	0	1	0	1	1	2	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0
17	Magnosaurus	0	1	0	0	1	2	0	0	?	?	2	1	0	?	0	1	1	?	?	?	?
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Monolophosaurus	0	0	?	0	1	2	0	0	0	1	2	1	0	0	0	1	?	1	1	1	0
20	Piatnitzkysaurus	?	?	?	?	?	1/2	?	?	?	0	?	1	1	0	?	0	1	1	?	?	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	0	0	0	0	1	1	0	0	0	?	1	1	0	1	0	1	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?
26	Allosaurus	0	0	0	0	2	1	0	0	0	1	2	1	0	0	0	1	1	0	1	1	0
27	Ceratosaurus	1	0	0	0	0	2	1	0	0	?	1	1	0	0	0	1	0	0/1	1	0	1
28	Coelurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Compsognathus	0	1	0	1	0	2	0	?	?	?	0	1	0	1	0	?	1	0	?	?	0
30	Elaphrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	Ornitholestes	0	0	0	0	1	1	0	0	0	?	1	1	0	1	1	1	0	?	0	?	
32	Sinraptoridae	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	0	1	0	0	0	1/2	?	0	0	?	2	1	0	?	0	0	0	?	?	?	?
35	Afrosvenator	?	?	?	?	?	1/2	?	?	0	?	2	1	0	0	0	1	1	?	?	?	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	0	1	?	0	?	2	?	?	0	?	0	?	?	?	?	?	1	0	?	?	?
38	'C.' maortuensis	?	?	?	?	?	1/2	?	?	?	?	0	1	0	0	0	1	0	?	?	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Neovenator	0	1	?	0	2	2	0	0	0	?	2	1	0	0	0	?	1	0	?	1	?
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	0	1	?	?	1/2	?	?	?	?	0	?	?	?	?	?	?	1	?	?	?	?
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
47	Bagaraatan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	1	0	0	0	1	2	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1
52	Aves	0	1	?	0	1	2	0	0	0	?	0	1	0	1	0	1	1	0	0	0	1
53	Baryonychidae	0	1	0	0	3	1	0	1	1	1	2	0	0	0	0	1	0	0	0	0	?
54	Carcharodontosauri	?	0	?	?	?	2	0	?	0	1	1	1	0	0	0	1	0	1	1	1	1
55	Dromaeosauridae	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	1
56	Ornithomimosauria	0	0	1	0	3	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1
57	Oviraptorosauria	1	1	1	0	?	1	0	1	0	1	0	0	0	1	0	?	0/1	0	1	0	0/1
58	Therizinosauroidea	0	1	1	0	?	2	0	0	0	1	0	0	0	1	0	?	0	0	0	0	?
59	Troodontidae	0	0	0	0	1	2	0	0	0	1	0	1	0	1	0	1	1	0	0	0	1
60	Tyrannosauridae	1	0	0	0	1	1/2	0	0	0	1	0	1	0	1	0	1	1	1	0	0/1	1

Matrix	2	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	Euparkeria	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0
2	Marasuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Ornithischia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Eoraptor	0	0/1	1	0	0	0	1	1	0	0	0	0	0	?	?	?	0	0	?	?	0
5	Herrerasaurus	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0
6	Staurikosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Sauropodomorpha	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Coelophysis	1	?	?	0	0	0	1	1	0	0	0	0	0	0	?	?	0	0	0	?	0
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L. lilliensterni	?	1	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	0	1	2	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0
14	Dilophosaurus	1	2	2	0	0	0	1	1	0	?	?	0	1	?	0	0	0	0	0	0	0
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Syntarsus	1	1	0/1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
17	Magnosaurus	?	?	?	?	?	?	1	1	0	1	1	0	1	0	0	0	0	0	0	1	?
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Monolophosaurus	?	2	2	1	1	0	1	1	0	?	?	0	1	0	0	?	0	0	0	?	0
20	Piatnitzkysaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	0
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	?	2	?	1	0	0	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Allosaurus	1	2	1	1	0/1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0
27	Ceratosaurus	0	?	1	?	0	0	1	1	0	1	1	0	1	0	0	?	1	0	1	0	1
28	Coelurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Compsognathus	0	0/1	?	?	0	0	1	1	0	?	?	0	?	0	0	?	0	0	0	?	?
30	Elaphrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	Ornitholestes	0	?	?	1	?	0	1	1	?	1	0	0	0	?	?	?	0	0	0	0	0
32	Sinraptoridae	1	2	2	1	1	0	1	1	0	1	1	0	1	0	0	0	1	0	1	0	1
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	?	2	?	1	0	0	1	1	0	1	1	0	?	?	?	?	?	?	0	1	?
35	Afrovenator	?	?	?	1	1	0	1	1	0	1	1	0	?	?	?	?	?	0	0	1	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	?	0	?	?	?	0	1	?	?	?	?	?	?	?	?	?	0	0	0	?	?
38	'C. maortuensis	?	?	2	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Neovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	?	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	0	?	?	?	?
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	0	0	?	?	0
47	Bagaraatan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	0	2	2	0	0	0	1	1	0	1	?	1	1	1	0	0	1	1	1	0	1
52	Aves	0	0	2	0	0	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0
53	Baryonychidae	0	2	2	?	0	0	1	1	0	1	1	0	1	0	0	0	0	0	?	?	1
54	Carcharodontosauri	0	2	2	1	1	0	1	1	0	1	1	0	1	?	?	0	0	0	1	1	0
55	Dromaeosauridae	0	0	2	0	1	0	1	1	0	0/1	0	1	1	1	0	1	0	0	0	0	0
56	Ornithomimosauria	0	0	2	0	0	0	1	1	1	0	0/1	1	1	0	1	1	0	0	0	0	0
57	Oviraptorosauria	0	0	1	0	0	1	1	1	?	1	0	1	1	1	0	?	0	0	0	?	0
58	Therizinosauroidae	0	0	2	0	0	0	1	1	0	0	0	0	1	0	0/1	1	0	0	0	?	0
59	Troodontidae	0	0	2	0	0	0	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0
60	Tyrannosauridae	0	2	2	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0/1	0	0	0

Matrix	3	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
1	Euparkeria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?
2	Marasuchus	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?
3	Ornithischia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Eoraptor	?	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	Herrerasaurus	0	0	1	0	0	0	1	?	1	1	?	0	0	0	0	0	0	?	?	0	?
6	Staurikosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Sauropodomorpha	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
8	Coelophysis	0	0	0	?	0	?	?	?	0	?	?	0	0	?	1	0	?	?	?	0	?
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L. lilliensterni	?	?	1	?	?	0	1	0	?	1	0	0	?	?	?	?	?	?	?	?	?
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	?	?	0	0	0	0	0	0	2	1	?	0	0	1	1	0	1	1	?	0	?
14	Dilophosaurus	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Syntarsus	0	0	0	1	0	0	?	0	0	1	0	0	0	1	1	0	1	0	0	0	0
17	Magnosaurus	?	0	1	?	?	0	0	0	1	1	0	1	0	0	1	?	1	1	?	0	?
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Monolophosaurus	0	0	1	0	0	0	0	0	1	2	?	1	0	0	1	?	?	?	?	?	?
20	Piatnitzkysaurus	?	?	?	?	?	?	?	?	?	1	?	1	0	0	1	?	1	?	?	?	?
21	Piveteausaurus	0	?	?	?	?	?	?	?	?	0	0	0	0	1	1	?	1	?	0	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	?	?	1	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Allosaurus	0	0	1	0	0	0	1	0	1	2	0	1	1	0	1	1	1	1	1	0	0
27	Ceratosaurus	1	0	1	0	0	0	2	0	1	1	?	1	0	0	1	0	?	?	?	0	0
28	Coelurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Compsognathus	0	0	?	?	?	?	?	?	0	?	?	?	0	0	1	?	?	?	?	0	?
30	Elaphrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	Ornitholestes	2	0	0	?	?	0	1	0	0	1	?	1	?	?	?	?	?	?	?	0	?
32	Sinraptoridae	0	0	1	0	0	0	1	0	1	2	0	1	1	0	1	1	1	?	?	0	0
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
35	Afrovenator	?	?	1	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	?	?	?	0	1	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
38	'C.' maortuensis	2	?	?	?	?	0	0	0	?	1/2	1	1	0	0	1	?	1	1	1	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	Neovenator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	2	1	0	?	?	?	?	?	0	1	?	1	0	0	1	?	?	1	?	0	?
47	Bagaraatan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	1	0	1	1	0	0	2	0	1	1	0	1	0	0	1	?	1	0	1	0	?
52	Aves	?	1	0	1	1	1	?	1	2	1	1	1	0	0	1	1	1	1	0	0	1
53	Baryonychidae	0	1	?	?	?	0	0	0	2	1	?	1	0	0	1	1	1	1	?	0	?
54	Carcharodontosauri	0	0	1	?	?	?	?	?	?	1/2	0	?	?	0	1	1	1	1	?	0	0
55	Dromaeosauridae	2	0/1	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0/1	1	1	0	1
56	Ornithomimosauria	0	1	0	0	1	1	0	0	2	1	1	0	0	0	1	1	1	1	?	1	1
57	Oviraptorosauria	2	0	0	1	1	1	0	1	0	1	1	1	0	0	1	2	?	1	1	0	1
58	Therizinosauroidea	0	0	0	0	1	?	0	?	0	1	1	1	0	0	0	2	?	1	?	0	?
59	Troodontidae	2	1	0	?	?	1	0	0	0/2	1	1	1	0	0	0	1	1	1	1	1	1
60	Tyrannosauridae	2	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	1	1	?	0	0

Matrix		4	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
1	Euparkeria	?	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	?	0	0	0	0	0
2	Marasuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Ornithischia	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
4	Eoraptor	?	?	?	?	?	0	0	0	0	?	?	0	0	?	?	?	?	0	0	?	0	0
5	Herrerasaurus	?	0	0	?	0	1	0	0	0	0	0	0	0	0	?	?	?	?	0	0	0	0
6	Staurikosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?
7	Sauropodomorpha	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
8	Coelophysis	?	?	0	?	?	1	0	0	0	0	0	0	0	0	?	?	?	?	0	0	?	1
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L. lilliensterni	?	?	?	1	?	1	?	0	0	?	?	0	0	?	?	?	?	?	0	1	?	?
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	?	?	?	?	?	?	?	0	?	0	0	0	1	?	?	?	?	1	1	?	?	?
14	Dilophosaurus	0	?	?	?	?	?	1	0	0	0	1	?	0	?	?	?	?	0	0	1	0	0
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Syntarsus	0	1	0	1	?	1	0	0	0	0	0	0	0	?	?	?	?	0	0	0	1	1
17	Magnosaurus	0	?	?	?	?	?	2	0	?	?	?	?	0	?	?	?	?	?	0	0	1	0
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Monolophosaurus	?	?	?	?	?	?	2	0	0	?	?	1	0	1	2	1	0	0	0	0	0	0
20	Piatnitzkysaurus	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	0	0	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	?	?	?	?	?	?	2	0	0	?	1	?	0	?	?	?	?	?	0	0	0	0
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
26	Allosaurus	0	1	0	2	0	1	2	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0
27	Ceratosaurus	0	?	0	0	?	1	1	0	0	?	0	0	0	?	1	0	?	0	0	0	0	0
28	Coelurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Compsognathus	?	?	?	?	?	?	1/2	0	0	?	?	1	0	?	?	?	?	?	0	0	0	1
30	Elaphrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	Ornitholestes	?	?	?	2/3	?	1	2	0	0	1	1	1	0	?	1	?	?	0	0	0	1	0
32	Siraptoridae	?	1	0	2	0	1	2	0	0	?	1	0	0	?	1	1	?	0	0	0	0	0
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0	?	?	?
35	Afrovenator	?	?	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	?	?	?	?	?	?	1	?	?	?	?	?	0	?	?	?	?	0	1	?	1	1
38	'C.' maortuensis	0	?	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	1	?	?	?
42	Neovenator	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0	?	?	?
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	?	?	?	?	?	?	2	0	0	?	?	?	0	?	?	?	?	0	0	?	1	0
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	1	?	?	?	?	1	?	?	1	0	1	0	1	?	?	?	?	1	1	?	?	?
47	Bagaraatan	?	?	?	?	?	?	?	?	?	1	1	?	0	?	?	?	?	?	0	0	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
52	Aves	1	2	0	?	?	1	2	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1
53	Baryonychidae	?	?	?	?	?	?	2	0	0	?	?	?	0	1	1	?	?	0	0	0	1	0
54	Carcharodontosauri	0	1	0	2	?	1	2	0	?	?	?	?	0	?	?	?	?	?	0	0	?	?
55	Dromaeosauridae	1	1	0	3	1	1	2	0	0	1	1	1	0	1	2	1	0	0	0	0	0	0
56	Ornithomimosauria	1	1	0	3	1	1	2	0	0	?	1	1	1	1	0	1	1	0	0	0	0	1
57	Oviraptorosauria	?	0	1	0	0	1	?	1	1	0	1	0	1	0	0	0	1	1	1	?	?	?
58	Therizinosauroidea	1	0	1	?	?	1	2	0	0	1	?	1	1	1	1	0	1	1	0	0	?	?
59	Troodontidae	1	1	0	3	1	1	2	0	?	?	?	?	1	?	2	?	?	0	0	0	0	0
60	Tyrannosauridae	0	1	0	3	1	1	2	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0/1

Matrix	5	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
1	Euparkeria	0	0	0	0	?	?	0	0	0	?	0	?	0	0	?	0	0	0	0	?	0
2	Marasuchus	1	0	0	0	?	?	0	0	0	?	0	?	0	0	?	0	?	0	?	?	?
3	Ornithischia	0	?	1	0	?	?	0	0	0	0	0	0	0	0	1	0	0	1	0	?	0
4	Eoraptor	0	0/1	0/1	0	?	?	0	?	?	?	0	?	?	?	?	0	?	1	?	?	?
5	Herrerasaurus	0	0	0	0	?	?	0	1	0	0	0	?	0	0	0	0	0	1	1	0	0
6	Staurikosaurus	?	?	?	?	0	?	?	?	?	?	0	?	0	0	0	0	1	0	?	?	0
7	Sauropodomorpha	0	1	1	0	?	?	0	0/1	0	0	0	0	0	0	0	0	0	1	1	0	0
8	Coelophysis	0	0	0	1	0	0	0	1	0	?	0	1	?	0	0	0	?	1	?	?	0
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0
10	L.airelensis	?	?	?	1	0	0	?	?	?	?	?	?	?	1	0	0	0	?	1	1	0
11	L.liliensterni	0	0	0	1	1	0	?	?	?	?	0	0	0	1	0	0	0	1	1	0	0
12	Procompsognathus	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	1	?	?	0
13	Shuvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Dilophosaurus	0	0	0	1	0	1	0	2	0	0	0	?	0	0	0	?	1	2	1	0	0
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Syntarus	0	0	0	1	0	0	0	?	0	0	0	?	0	0	?	0	?	1	1	0	0
17	Magnosaurus	0	0	0	1	1	1	0	2	0	0	1	?	1	0	1	0	1	2	1	0	0
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0
19	Monolophosaurus	0	0	0	1	1	1	1	1	1	?	1	?	?	?	?	0	?	2	1	0	0
20	Piatnitzkysaurus	0	0	0	1	1	1	0	2	1	0	0	1	?	0	1	0	1	2	1	0	0
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0
25	'S.' zigongensis	0	0	0	1	1	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?
26	Allosaurus	0	0	0	1	1	1	1	2	1	0	1	1	0	0	1	0	0	2	1	0	0
27	Ceratosaurus	0	0	0	1	0	1	1	2	0	0	0	2	0	0	0	0	0	2	1	0	0
28	Coelurus	?	?	?	1	1	1	?	?	?	?	0	?	1	0	1	1	0	1	1	0	0
29	Compsognathus	0	0	0/1	1	1	1	1	?	0	?	1	?	0	0	?	?	?	1	?	?	?
30	Elaphrosaurus	?	?	?	1	0	0/1	?	?	?	?	0	?	1	0	0	0	1	0	1	0	0
31	Ornitholestes	0	0	0	1	1	1	?	?	?	?	0	?	1	0	1	1	2	2	1	?	0
32	Sinraptoridae	0	0	0	1	1	1	1	2	1	0	1	1	1	0	1	0	0	2	1	0	0
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	0	0	0	1	1	1	?	?	?	?	1	1	0	0	1	0	1	2	1	0	0
35	Afrovenator	0	0	0	1	1	1	0	2	1	0	1	?	0	0	1	0	1	2	1	0	0
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
38	'C.' maortuensis	0	0	0	1	?	1	1	2	1	0	?	?	1	?	?	?	?	?	?	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	1	0	0/1	1	1	0	1	0	?	?	0	1	?	1	1	1	?	1
42	Neovenator	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	0	0	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
46	Avimimus	?	?	?	1	0/1	1	?	1	0	1	0	?	0	0	1	?	0	1	1	0	?
47	Bagaraatan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	0	0	0	1	0	1	1	2	0	0	0	?	1	0	1	0	1	2	1	0	0
52	Aves	1	0	1	1	1	1	?	1	0	1	0	2	1	0	1	1	2	1	1	1	0
53	Baryonychidae	0/1	0	0	1	1	1	1	2	1	0	1	?	0	0	1	0	1	2	1	0	0
54	Carcharodontosauri	0	0	0	1	1	1	1	2	1	0	1	2	0	0	1	0	1	2	1	0	0
55	Dromaeosauridae	0	0	0	1	1	1	1	2	1	1	0	1	1	0	1	1	2	2	1	1	0/1
56	Ornithomimosauria	1	0	1	1	1	1	1	1	0	1	0	2	1	0	1	1	2	1	1	0	0
57	Oviraptorosauria	?	?	?	1	0	1	?	?	?	?	0	2	1	0	1	1	2	0	1	?	1
58	Therizinosauroidae	0	1	1	1	0	1	?	?	?	?	0	?	1	0	?	0	?	1	1	0	0
59	Troodontidae	0	0	1	1	1	1	1	2	1	1	0	2	1	0	1	?	2	2	1	1	0
60	Tyrannosauridae	0	0	0	1	1	1	1	2	1	0	0	2	?	0	1	0	0	2	1	0	0

Matrix	6	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126
1	Euparkeria	0	0	0	0	0	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?
2	Marasuchus	0	0	0	0	1	?	2	0	0	0	?	0	0	?	?	?	?	0	0	0	0
3	Ornithischia	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Eoraptor	0	0	?	0	0	?	?	1	?	?	?	?	0	0	?	?	?	0	?	?	?
5	Herrerasaurus	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0
6	Staurikosaurus	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	?	0	0	0
7	Sauropodomorpha	0	0	0	0	0	0	1	0/1	0	0	0/2	0	0	0	0	0	0	0	0	0	0/1
8	Coelophysis	0/1	0	0	0	0	0	2	2	0	?	1	0	0	0	1	0	0	0	0	0	0
9	Gojirasaurus	0/1	?	?	1	0	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	0/1	?	?	?	?	?	2	?	0	0	?	?	?	?	1	0	1	?	?	?	0
11	L. lilliensterni	1	0	0	?	0	0	2	?	0	0	0	0/1	0	0	1	0	?	?	0	0	0
12	Procompsognathus	0/1	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Dilophosaurus	1	0	0	1	0	0	2	2	0	0	0	0	0	1	0	0	0	0	0	0	0
15	Segisaurus	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	?	?
16	Syntarsus	1	0	0	0	0	0	2	2	1	0	1	0	0	0	1	0	1	0	0	0	0
17	Magnosaurus	1	0	0	1	0	0	2	?	0	0	?	?	0	?	0	0	?	?	0	0	0
18	Metriacanthosaurus	1	0	1	1	0	1	1	?	0	0	?	?	?	?	1	1	?	?	?	?	?
19	Monolophosaurus	1	0	1	1	0	?	1	2	0	?	?	?	?	?	1	?	?	?	?	?	?
20	Piatnitzkysaurus	1	0	1	1	0	0	1	2	0	0	0	?	?	?	?	?	?	?	?	?	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0	0	0	0
23	Proceratosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	1	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S. zigongensis	1	?	1	?	?	?	?	2	0	?	?	?	?	?	?	?	1	?	0	?	0
26	Allosaurus	1	0	1	1	0	1	0	2	0	0	0	0	0	0	1	1	1	1	0	1	0
27	Ceratosaurus	1	0	0	1	0	?	1	2	0	0	1	0	0	0	1	0	0	0	2	0	0
28	Coelurus	1	0	1	0	0	1	1	?	?	?	?	?	?	0	?	?	?	0	?	1	0
29	Compsognathus	0/1	?	?	0	1	?	1	?	?	0	?	?	?	0	?	?	?	?	0	0	0
30	Elaphrosaurus	0	0	0	0	1	0	2	3	1	0	1	?	?	0	0	0	1	?	1	0	0
31	Ornitholestes	1	1	1	?	0	1	1	2	1	0	?	?	?	0	1	1	1	?	?	0	0
32	Sinraptoridae	1	1	1	1	0	1	1	2	0	0	0	0	0	0	1	1	1	?	0	1	0
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	2	0	1	1	0	?	1	2	?	?	?	?	0	0	1	1	?	0	0	?	?
35	Afrovenator	0/1	?	?	?	?	?	?	1	?	?	?	?	?	0	0	?	?	1	?	0	1
36	Aristosuchus	?	?	?	?	?	?	?	2	0	0	0	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	0/1	?	?	?	?	?	?	2	?	?	?	2	1/2	?	?	?	?	0	0	?	0
38	'C. maortuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
41	Microvenator	2	0	?	?	?	?	1	?	?	?	?	?	0	?	?	?	0	?	?	?	1
42	Neovenator	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
43	Siamotyrannus	0/1	?	?	?	?	?	?	2	0	?	?	?	?	0	?	?	?	?	1	0	1
44	Sinosauropteryx	?	?	?	0	1	?	?	?	?	?	?	0	0	0	?	?	1	?	1	0	0
45	SMNK 2349Pal	0/1	?	?	0	1	?	2	2	0	0	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	0	1	1	0	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?
47	Bagaraatan	?	?	?	?	?	?	?	?	?	?	0	?	1	0	?	?	1	0	1	0	0
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	1	0	0
49	Unerlagia	2	?	?	1	0	1	1	3	1	0	0	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	1	0	0	1	0	?	1	3	0	0	1	?	0	0	0	0	1	0	2	0	0
52	Aves	?	1	1	1	0	1	1	2/3	1	?	1	2	2	1	1	0	0/1	0	?	?	0
53	Baryonychidae	1	0	1	1	0	1	1	?	0	0	0	?	?	?	0	0	?	0	?	?	?
54	Carcharodontosauri	2	0	1	1	0	?	?	?	0	1	0	?	?	0	0	1	1	?	1	0	1
55	Dromaeosauridae	1/2	1	1	1	0	1	1	2/3	1	0/1	0	2	2	1	1	0	1	0	?	0	0
56	Ornithomimosauria	1	0	0	?	0	1	2	3	1	1	0	1	1	0	0	0	1	0	1	0	0
57	Oviraptorosauria	2	1	1	1	0	?	1	3	1	1	0	1/2	0	0	1	0	0	0	?	0	1
58	Therizinosauroidea	1	?	?	1	0	1	1	2/3	1	?	?	?	1	?	?	?	0	?	?	?	1
59	Troodontidae	1	1	1	1	0	1	1	3	1	0	0	2	2	1	1	0	1	0	?	0	0
60	Tyrannosauridae	2	0	1	1	0	1	1	2	0	0	0	1	1	0	1	0	1	0	1	0	0





Matrix	9	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189			
1	Euparkeria	0	0	0	0	?	?	?	?	?	0	0	0	1	0	1	0	?	?	?	?	0	0		
2	Marasuchus	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?	?	0	0		
3	Ornithischia	1	0	0	0	?	0	0	0	0	?	0	0	0	?	0	0	?	?	?	?	0	0		
4	Eoraptor	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0		
5	Herrerasaurus	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0		
6	Staurikosaurus	0	0	0	0	?	?	?	?	1	0	0	?	?	0	0	1	?	?	?	?	?	0	0	
7	Sauropodomorpha	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0		
8	Coelophysis	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	?	?	?	?	0	0	
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	?	?	
10	L. airelensis	?	?	?	?	?	?	?	?	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	
11	L. lilliensterni	0	0	0	0	?	0	0	1	0	1	0	0	0	0	0	0	?	?	?	?	?	0	0	
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	0	?	?	?	?	?	?	?	
13	Shuvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
14	Dilophosaurus	?	0	0	0	?	0	0	0	0	1	0	?	?	1	0	1	0	0	0	0	0	0	0	
15	Segisaurus	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	1	?	0	0	?	?	?	0	0
16	Syntarsus	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	?	?	?	?	?	0	0	
17	Magnosaurus	?	?	0	0	?	0	0	0	1	0	0	1	0	?	0	1	0	0	0	?	?	?	0	0
18	Metriacanthosaurus	0	?	?	?	?	?	?	?	0	?	0	0	?	?	1	?	1	?	?	0	?	?	?	?
19	Monolophosaurus	0	0	0	0	0	0	0	0	0	1	0	0	0	?	?	1	?	?	?	?	?	?	0	0
20	Piatnitzkysaurus	0	?	0	0	?	?	?	?	?	0	0	0	0	0	?	0	1	?	?	0	0	0	0	0
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Proceratosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	1	?	0	1	0	0	0	0	
26	Allosaurus	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0/2	1	0	0	0	1	0	0	1	0
27	Ceratopsus	0	0	0	0	?	?	?	?	0	0	0	0	0	0/1	1	1	?	?	?	?	?	?	0	0
28	Coelurus	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	1	0	0	?	?	?	?	
29	Compsognathus	1	0	?	?	?	0	0	?	?	1	?	?	?	?	?	0/1	1	?	0	2	1	0	0	
30	Elaphrosaurus	1	0	0	0	0	0	0	0/1	0	0	0	0	2	0	?	0	?	?	?	?	?	0	0	
31	Ornitholestes	1	0	?	0	?	1	1	0	1	0	1	2	0	?	0	?	?	?	?	?	?	?	1	0
32	Sinraptoridae	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0
33	Stokesosaurus	1	0	1	1	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	Afrovenator	0	0	0	0	?	0	0	0	1	0	0	?	?	1	0	1	0	0	0	0	1	0	0	0
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	2	?	?	?	?
37	Caudipteryx	1	1	?	?	?	0	1	?	?	1	0	0	?	?	?	?	1	?	?	?	?	1	1	1
38	'C.' maortuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	Chilantaisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40	Ligabueino	?	0	?	0	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	?	1	1	0	?	?	?	1	0	1	0	0	?	?	?	2	1	?	1	0	?	?	?	?
42	Neovenator	?	?	?	?	?	?	?	?	?	1	?	?	1/2	0	?	?	1	0	0	0	1	0	0	0
43	Siamotyrannus	0	0	0	1	0	0	?	0	?	0	0	1	0	?	0	1	?	?	?	?	0	1	0	0
44	Sinosauropteryx	1	0	?	0	0	?	?	?	?	1	?	?	?	?	?	0	1	?	0	1	1	0	0	0
45	SMNK 2349Pal	?	?	?	?	?	?	1	?	?	?	0	1	0/1	0	1	0	1	1	0	2	1	0	0	0
46	Avimimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	?	1	1	1	1	0	?	?
47	Bagaraatan	?	?	?	?	?	?	1	?	?	0	1	?	?	2	0	?	0	?	?	?	?	?	?	?
48	Deltadromeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	1	0	?	?	?
49	Uhenlagia	2	0	?	0	0	1	1	0	1	0	0	2	0	1	0	1	1	0	1	1	0	1	1	1
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51	Abelisauridae	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	1	0	0	0	0	0	0	0	0
52	Aves	2	0	1	0	0	1	1	0	1	0	0	2	0	1	0	1	1	0	1	1	0	1	1	1
53	Baryonychidae	0	0	0	0	?	0	0	0	1	0	?	1/2	0	1	0	0	?	?	?	?	?	?	?	0
54	Carcharodontosauri	?	0	?	?	?	?	0	0	?	0	0	1	0	1	0/2	1	0	0	0	1	0	0	0	0
55	Dromaeosauridae	2	0	0	0	0	1	1	0	1	0	0	2	0	1	0	1	0	1	1	0	1	1	1	1
56	Ornithomimosauria	1	0	1	0	0	0	1	1	1	1	1	2	0	1	0	1	1	0	1	1	0	0	1	0
57	Oviraptorosauria	1	0/1	1	0	0	1	1	0	1	0	0	2	0	?	2	1	?	1	0	1	0	1	1	1
58	Therizinosauroida	1/2	1	0	0	0	1	0	?	0	0	0	2	0	?	0	1	?	1	0	1	0	1	1	1
59	Troodontidae	?	0	1	0	?	1	?	0	?	?	?	?	2	0	?	0	?	?	?	?	?	?	?	?
60	Tyrannosauridae	1	0	1	1	1	0	1	0	1	0	1	2	0	1	0/2	1	1	1	0	1	0	1	0	0

Matrix	10	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	
1	Euparkeria	0	0	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	?	?	0	?	?
2	Marasuchus	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	?	?
3	Ornithischia	0	0	0	0	1	0	1	0	?	2	0	0	0	0	0	0	0	0	2	0	0	0
4	Eoraptor	0	0	0	0	0	?	?	?	0	?	0	?	0	0	?	?	0	?	?	?	?	?
5	Herrerasaurus	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Staurikosaurus	0	?	0	?	0	0	0	?	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Sauropodomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Coelophysis	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0	0
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	?	?	?
10	L.airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L.liliensterni	?	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0
12	Procompsognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Shuvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Dilophosaurus	1	?	0	?	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1
15	Segisaurus	?	?	0	0	0	?	?	?	?	?	?	?	1	?	0	?	1	?	?	?	1	0
16	Syntarsus	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0/1	1	1	0	1	1	0	0
17	Magnosaurus	0	0	0	?	0	1	0	1	2	1	0	0	1	1	1	1	2	0	2	0	0	0
18	Metriacanthosaurus	?	?	?	?	0	1	0	1	2	1	0	0	1	1	1	?	2	?	?	?	?	?
19	Monolophosaurus	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	Piatnitzkysaurus	1	0	0	0	0	0	0	1	2	1	0	0	?	1	1	1	2	0	2	0	?	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	2	?	?
23	Proceratosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	1	0	0	1	0	0	?	1	?	?	?	?	1	1	?	?	2	0	?	0	1	?
26	Allosaurus	1	0	0	0	0	1	0	1	2	1	0	0	1	1	1	1	2	0	2	0	1	?
27	Ceratosaurus	1	0	0	1	0	0	0	1	2	0	0	0	1	1	1	1	1	0	1/2	0	1	?
28	Coelurus	?	?	?	?	0	?	0	1	2	1	0	0	1	1	?	?	2	2	3	0	1	?
29	Compsognathus	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?
30	Elaphrosaurus	0	?	0	1	0	0	0	1	2	0	0	0	1	1	0	1	1	2	2	0	1/2	?
31	Ornitholestes	0	?	0	2	?	?	?	?	?	?	?	1	?	1	?	?	?	?	?	0	1	?
32	Sinraptoridae	1	0	0	1	0	1	0	1	2	1	0	0	1	1	1	1	2	0	2	0	1	?
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1	1	2	0	2	0	1
35	Afrovenator	1	0	0	0	0	1	0	?	2	1	0	0	?	1	?	?	?	0	2	0	0/1	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	0	1	0	2	?	1	1	?	2	1	0	?	?	1	?	?	?	2	2/3	?	?	?
38	'C.' maortuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	Chilantaisaurus	?	?	?	?	0	1	0	?	2	1	0	0	1	1	?	?	2	1	2	?	?	?
40	Ligabueino	?	?	?	?	0	0	0	1	2	0	0	0	1	1	?	?	?	?	?	?	?	?
41	Microvenator	?	?	?	?	1	1	1	?	2	2	0	1	0	1	?	?	2	2	2/3	0	0	?
42	Neovenator	?	?	?	1	0	?	0	?	2	1	?	0	1	1	?	?	?	?	?	?	?	?
43	Siamotyrannus	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	?	1	0	0	0	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
45	SMNK 2349Pal	0/1	?	0	?	?	1	0	?	2	1	?	1	1	1	1	1	2	?	?	?	0	1
46	Avimimus	?	?	?	?	1	1	1	0	2	2	?	0	0	1	1	0	2	2	3	0	?	?
47	Bagaraatan	?	?	0	?	1	1	1	1	3	2	0	?	?	1	1	0	2	2	2/3	0	?	?
48	Deltadromeus	?	?	0	?	?	1	0	?	2	1	0	1	1	1	1	1	2	2	0	2	?	?
49	Unenlagia	0	1	1	?	1	1	1	1	3	2	0	1	?	1	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	2	?	?
51	Abelisauridae	1	?	0	1	0	0	0	0	2	0	0	0	1	1	0	1	1	?	2	0	?	?
52	Aves	0	1	1	2	1	1	1	1	3	2	1	1	0	1	1	1	2	2	3	0	0	?
53	Baryonychidae	1	0	0	0	0	1	0	1	2	1	0	0	0	1	1	1	2	1	2	0	2	?
54	Carcharodontosauri	1	0	0	0/1	0	1	0	1	2	1	0	0	1	1	?	?	2	0	2	0	1	?
55	Dromaeosauridae	0	1	0	2	1	1	1	1	3	2	1	1	1	1	1	?	2	2	3	0	2	?
56	Ornithomimosauria	0	0	0	1	1	1	0	1	2	2	0	1	1	1	1	1	2	2	2	0	2	?
57	Oviraptorosauria	0	0	0	2	1	1	1	?	2	2	?	1	?	1	?	?	2	2	2/3	?	?	?
58	Therizinosauroidae	0	0	0	?	1	1	1	?	2	2	?	?	?	?	?	?	2	?	?	?	?	?
59	Troodontidae	0	1	0	2	1	1	1	1	3	2	1	1/2	0	1	1	?	2	2	3	0	0	?
60	Tyrannosauridae	0	0	0	2	1	1	0	1	2	2	0	0	1	1	1	1	2	2	2	0	2	?

Matrix	11	2 1 1	2 1 2	2 1 3	2 1 4	2 1 5	2 1 6	2 1 7	2 1 8	2 1 9	2 2 0	2 2 1	2 2 2	2 2 3	2 2 4
1	Euparkeria	?	0	0	?	?	?	0	?	0	0	?	0	0	0
2	Marasuchus	0	0	0	0	0	0	0	0	0	0	?	0	1	?
3	Ornithischia	0	0	0	0	0	0	0	0	1	0	0/1	0	?	0
4	Eoraptor	0	?	?	?	?	?	?	?	?	0	?	0	?	?
5	Herrerasaurus	1	0	0	0	0	0	0	0	0	0	?	0	0	0
6	Staurikosaurus	0	0	?	?	?	?	?	?	?	?	?	?	?	?
7	Sauropodomorpha	0	0	0	0	0	0	0	0	0	0	?	1	0	0
8	Coelophysis	1	0	0	0	0	0	0	0	0	0	0	1	1	0
9	Gojirasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	L. airelensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	L. liliiensterni	1	0	0	0	0	0	0	0	0	0	0	?	?	0
12	Procompsognathus	?	0	?	?	?	?	?	?	?	0	0	1	1	0
13	Shuvosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Dilophosaurus	1	0	0	0	0	0	0	0	0	0	0	1	2	0
15	Segisaurus	1	0	?	?	?	?	?	?	?	0	0	1	1	0
16	Syntarsus	1	0	0	0	0	0	0	0	0	0	0	1	1	0
17	Magnosaurus	1	0	0	0	1	0	1	1	?	0	0	?	?	0
18	Metriacanthosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Monolophosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	Piatnitzkysaurus	?	0	?	?	?	?	?	?	?	0	?	?	?	?
21	Piveteausaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Poekilopleuron	?	?	?	0	1	0	1	?	?	?	?	?	?	?
23	Proceratosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Xuanhanosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25	'S.' zigongensis	1	0	?	?	?	?	?	?	?	?	?	?	?	?
26	Allosaurus	1	0	0	0	1	0	1	1	1	0	0	2	2	0
27	Ceratosaurus	1	0	0	0	0	0	0	1	1	0	?	?	?	?
28	Coelurus	1	?	?	?	?	?	?	?	?	?	?	?	?	?
29	Compsognathus	?	0	?	?	?	?	?	?	?	0	0	2	2	0
30	Elaphrosaurus	1	0	0	?	?	?	0	1	1	0	?	?	?	0
31	Ornitholestes	?	0	?	?	?	?	?	?	?	0	?	?	?	?
32	Sinraptoridae	1	0	0	0	1	0	1	1	1	0	0	2	2	0
33	Stokesosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Torvosaurus	?	0	0	0	1	0	1	1	1	0	?	?	?	?
35	Afrovenator	?	?	0	?	?	?	1	1	1	0	?	2	2	?
36	Aristosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
37	Caudipteryx	?	?	1	1	2	1	1	?	1	1	0	?	?	0
38	'C.' maortuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
39	Chilantaisaurus	?	0	?	?	?	?	?	?	?	0	?	?	?	?
40	Ligabueino	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	Microvenator	1	1	1	1	2	1	1	0	1	?	?	?	?	?
42	Neovenator	?	?	?	?	?	?	?	?	?	0	?	?	?	0
43	Siamotyrannus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	Sinosauropteryx	?	?	?	1	2	?	1	?	?	0	?	1/2	1/2	0
45	SMNK 2349Pal	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46	Avimimus	1	1	1	1	2	1	1	0	1	1	0	1/2	1	0
47	Bagaraatan	1	1	?	1	2	1	1	0	1	?	?	?	?	?
48	Deltadromeus	1	?	1	1	?	1	1	1	1	0	?	?	?	?
49	Unenlagia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	Velocisaurus	?	?	?	?	?	?	0	?	?	0	0	?	?	0
51	Abelisauridae	1	0	0	0	0	0	0	1	1	?	?	?	?	?
52	Aves	1	1	1	1	2	1	1	0	1	0	0	2	1	0/1
53	Baryonychidae	1	0	?	0	1	0	1	?	1	?	?	?	?	?
54	Carcharodontosauri	1	0	0	?	?	?	?	?	?	0	?	?	?	?
55	Dromaeosauridae	1	1	1	1	2	1	1	0	1	0	1	2	1	1
56	Ornithomimosauria	1	0	1	1	2	1	1	0	1	0/1	0	2	2	0
57	Oviraptorosauria	1	1	1	1	2	1	1	?	1	0/1	0	2	1	0
58	Therizinosauroidae	?	?	1	1	2	?	?	?	1	0	?	0/1	1/2	0
59	Troodontidae	1	1	1	1	2	1	1	0	1	1	1	2	1	1
60	Tyrannosauridae	1	0	1	1	2	1	1	0	1	1	0	2	2	0