The Phylogeny of Ceratosauria (Dinosauria: Theropoda)

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SYNOPSIS Recent discoveries and analyses have drawn increased attention to Ceratosauria, a taxonomically and morphologically diverse group of basal theropods. By the time of its first appearance in the Late Jurassic, the group was probably globally distributed. This pattern eventually gave way to a primarily Gondwanan distribution by the Late Cretaceous. Ceratosaurs are one of several focal groups for studies of Cretaceous palaeobiogeography and their often bizarre morphological developments highlight their distinctiveness. Unfortunately, lack of phylogenetic resolution, shifting views of which taxa fall within Ceratosauria and minimal overlap in coverage between systematic studies, have made it difficult to explicate any of these important evolutionary patterns. Although many taxa are fragmentary, an increase in new, more complete forms has clarified much of ceratosaur anatomy, allowed the identification of additional materials and increased our ability to compare specimens and taxa. We studied nearly 40 ceratosaurs from the Late Jurassic–Late Cretaceous of North and South America, Europe, Africa, India and Madagascar, ultimately selecting 18 for a new cladistic analysis. The results suggest that *Elaphrosaurus* and its relatives are the most basal ceratosaurs, followed by *Ceratosaurus* and Noasauridae + Abelisauridae (= Abelisauroidea). Several additional forms were identified as noasaurids, including *Genusaurus*. Within Abelisauridae, our analysis reveals a clade including *Majungasaurus* and the Indian forms, as well as a more weakly supported clade comprising *Carnotaurus* and *Ilokelesia*. These results greatly clarify the sequence of character acquisition leading to, and within, Abelisauroidea. Thanks to new noasaurid materials (particularly *Masiakasaurus*), numerous formerly ambiguous characters can now be resolved as either abelisaurid, noasaurid or abelisauroid synapomorphies. Skull and forelimb shortening, for example, now appear to be features confined to Abelisauridae. Nevertheless, a great deal of phylogenetic resolution is lacking, particularly among noasaurids, which hampers attempts to glean meaningful biogeographical information from the phylogeny. As a result, temporal and geographical sampling biases are probably contributing to the apparent patterns in the data and we suggest that definitive answers must await new discoveries. None of the recent ceratosaurian discoveries bear directly on the controversy surrounding latest Cretaceous ceratosaur biogeography.

KEY WORDS systematics, dinosaur, Saurischia, evolution, Abelisauroidea, Abelisauridae, Noasauridae, biogeography, morphology

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INTRODUCTION

In 1999, we began an extensive phylogenetic study of Theropoda (Dinosauria: Saurischia), to elucidate the detailed interrelationships of the basal (i.e. non-coelurosaurian) members of this clade. In the intervening years, this task has involved firsthand examination of hundreds of specimens representing more than 70 taxa and the critical review of more than 600 published characters and character state observations. The results of our broader study are now in preparation and will be published elsewhere. In this paper, we focus on the phylogeny of Ceratosauria, particularly the primarily Gondwanan radiations of the families Abelisauridae and Noasauridae.

Most previous systematic studies of Ceratosauria (e.g. Coria & Salgado 2000; Coria *et al.* 2002; Lamanna *et al.* 2002; Wilson *et al.* 2003) have focused on the placement of individual – usually new – taxa. As such, they typically employ relatively complete taxa with the goal of achieving the greatest possible resolution. By contrast, other works (e.g. Novas 1997; Tykoski & Rowe 2004) have attempted to resolve relationships within ceratosaurs as a whole. Not surprisingly (see below), the latter studies tend to achieve more limited resolution, with rather less agreement between them.

Much of the problem stems from the highly incomplete nature of many ceratosaur taxa, resulting in generally poor resolution and/or the tendency of researchers to exclude numerous taxa. In addition, discrepancies can arise when studies employ different taxon samples, using only a stable core group to which selected taxa of interest are added. This paper attempts to alleviate several of these difficulties by presenting a character and taxon-rich analysis of ceratosaur theropods, which is then analysed in several different iterations.

We begin with the presumption, supported in several recent analyses (Carrano & Sampson 1999; Forster 1999; Rauhut 2000, 2003; Carrano *et al.* 2002; Wilson *et al.* 2003; Sereno *et al.* 2004), that ceratosaurs form a clade that was derived independently from coelophysoids and represents the sister group to Tetanurae. Therefore, we do not include a diverse sample of coelophysoids in this analysis and our analyses do not test this supposition. However, by including both tetanuran (*Allosaurus*) and coelophysoid (*Syntarsus*) taxa as outgroups, as well as the more basal *Herrerasaurus*, we allow for several possible arrangements of the basal topology.

This paper is concerned primarily with ingroup relationships within Ceratosauria. A well resolved phylogeny of this group is a prerequisite for any comprehensive view of ceratosaur evolution, including patterns of temporal and geographical dispersal. Phylogenetic resolution is also necessary to evaluate the placement of numerous fragmentary taxa, as well as to suggest new assignments for several other forms.

HISTORICAL BACKGROUND

Constituency and Placement of Ceratosauria

Ceratosauria was diagnosed over a century ago by Othniel Charles Marsh (1884*a, b*) based on a single theropod taxon – indeed, a single specimen – from the Upper Jurassic Morrison Formation of Colorado, *Ceratosaurus nasicornis*. Marsh noted certain characteristics of *Ceratosaurus* (fused pelvic elements, a coossified metatarsus: Marsh 1884*c*) that were then unknown elsewhere among theropods, but were also found in birds. Other features (midline dorsal osteoderms, a median nasal horn) were apparently unique. *Ceratosaurus* seemed to occupy a distinct position among theropods that deserved formal recognition and, therefore, he set it apart from taxa such as *Allosaurus*, *Megalosaurus* and the 'coelurosaurs' in its own infraorder, Ceratosauria (Marsh 1884*b*). Later, the group was informally allied with Ornithomimidae (Marsh 1892).

For nearly half a century thereafter, the distinctiveness of *Ceratosaurus* among theropods was either explicitly or implicitly supported (e.g. Gilmore 1920). When Huene (1914, 1923, 1926) formally reorganised Theropoda into two largely size-based suborders (Coelurosauria and Carnosauria), he specifically exempted both *Tyrannosaurus* and *Ceratosaurus* from 'typical' positions among the other large carnosaurs (although citing different reasons for each). He allied *Ceratosaurus* with the smaller *Proceratosaurus bradleyi* from the Bathonian Great Oolite of England, based on the supposed presence of a nasal 'horn' in the latter. This relationship was recently supported by Madsen & Welles (2000), but has been questioned by most other workers (Paul 1988*a, b*; Holtz 2000; Rauhut 2000, 2003).

Very few additional taxa have been referred to Ceratosauria *sensu* Marsh, 1884*b*. Among these were the fragmentary materials described as *Ceratosaurus* (?) *roechlingi* (Kimmeridgian–Tithonian, Tendaguru Beds, Tanzania: Janensch 1925) and *Chienkosaurus ceratosauroides* (Tithonian, Kyangyuan Series, China: Young 1942). Other poorly known species (e.g. *Megalosaurus ingens*: Janensch 1920) have also been referred to the genus *Ceratosaurus*, but without much cause. Over time the term 'Ceratosauria' fell into disuse and *Ceratosaurus* was generally considered to be merely an aberrant, primitive carnosaur.

A significant change came when Gauthier (1986) used the results of a cladistic analysis to reorganise theropod phylogeny and taxonomy. His study separated most theropods into one of two clades: Tetanurae, which included most 'carnosaurs' and 'coelurosaurs' as well as birds, and its sister taxon Ceratosauria (Fig. 1). Gauthier resurrected the latter term to encompass *Ceratosaurus* and more the primitive 'coelurosaurs' *Coelophysis*, *Segisaurus*, *Dilophosaurus* and *Syntarsus*. *Liliensternus* and *Procompsognathus* were primitive forms that occupied an unresolved polytomy with Ceratosauria and Tetanurae. In formalising the diagnosis of Ceratosauria, Gauthier also reconfirmed its distinctiveness from all other theropods, both large and small.

Once established, the morphological links between coelophysoids and *Ceratosaurus* were soon expanded (Rowe 1989*a, b*; Rowe & Gauthier 1990), allowing the inclusion of additional taxa. In their description of *Abelisaurus comahuensis*, Bonaparte & Novas (1985) commented on numerous similarities between it, *Ceratosaurus* and the Indian theropods *Indosaurus matleyi* and *Indosuchus raptorius*. Similarly, Bonaparte (1985) discussed the resemblances
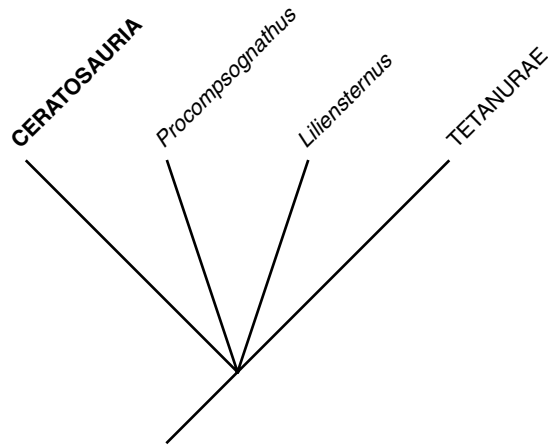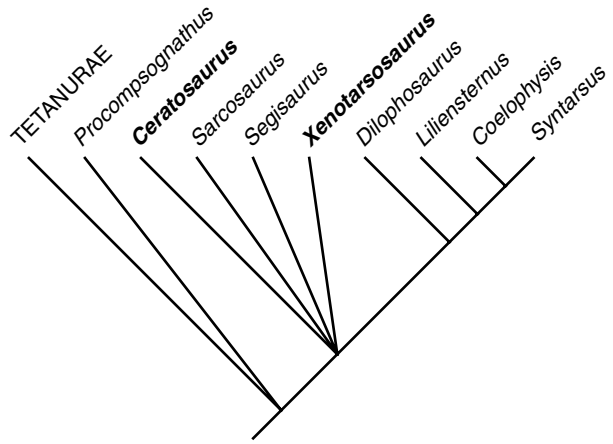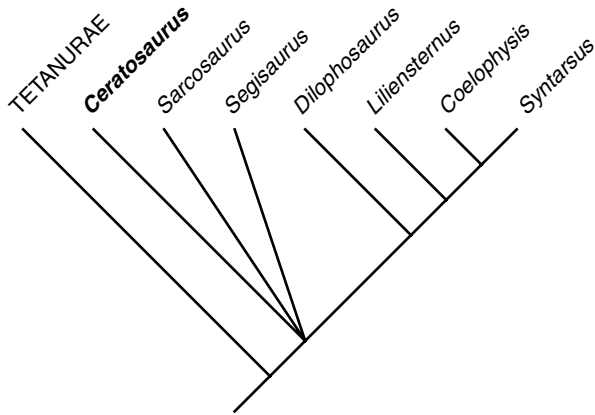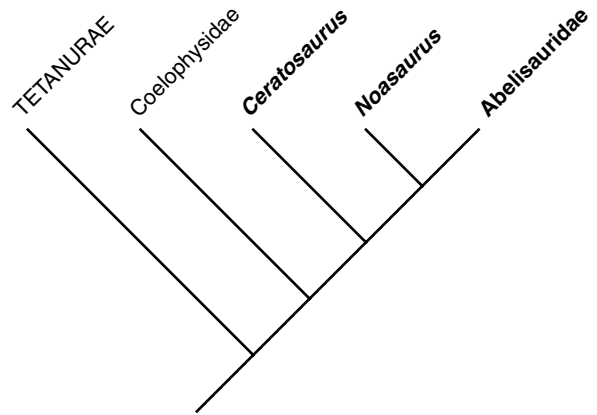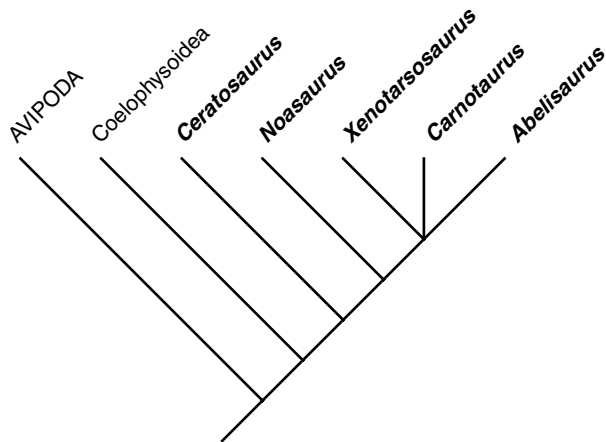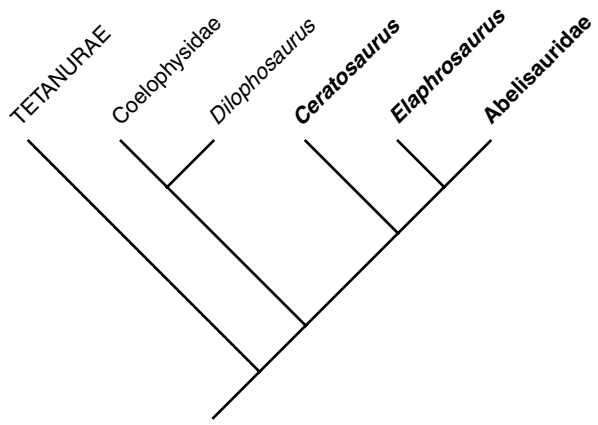
Figure 1 Previously published phylogenies of Ceratosauria, 1986–1994. Taxa in bold are those considered to belong to Ceratosauria in the present study.

between *Carnotaurus sastrei*, *Abelisaurus* and *Ceratosaurus*, thus implying an even wider membership for Ceratosauria. Rowe (1989b) remarked on similarities in the tarsus between ceratosaurs and the unusual South American theropod *Xenotarsosaurus bonapartei* (Martínez *et al.* 1986), while Molnar *et al.* (1990) suggested that the Madagascan taxon

Majungasaurus crenatissimus might be an abelisaurid. Abelisauridae was first given formal recognition as a component of Ceratosauria by Bonaparte (1991*a*), accompanied by the smaller bodied Argentine form *Noasaurus leali* (Bonaparte & Powell 1980).

For the next decade, Ceratosauria was accepted as comprising *Ceratosaurus*, coelophysoids and abelisauroids. As the morphology of abelisauroids became better understood, additional taxa were referred to this group from Europe (*Tarascosaurus salluvicus*, *Betasuchus bredai*: Le Loeuff & Buffetaut 1991), South America (*Ilokelesia aguadagrandensis*: Coria & Salgado 2000), Africa (*Elaphrosaurus bambergi*: Holtz 1994*a*, 2000) and Madagascar (*Majungatholus atopus*, *Masiakasaurus knopfleri*: Sampson *et al.* 1998, 2001). At the same time, newer cladistic phylogenies (e.g. Holtz 1994*a*, 2000; Sereno 1999; Tykoski & Rowe 2004) continued to support the Ceratosauria–Tetanurae dichotomy. In this view, abelisauroids were a late radiation of a predominately Triassic–Jurassic clade, most of whose evolutionary history was therefore missing from the fossil record.

However, with these new data came the recognition that some ceratosaurs – specifically, *Ceratosaurus* and the abelisauroids – shared many features with tetanurans that were not found in coelophysoids. Furthermore, fewer synapomorphies linked ceratosaurs with coelophysoids than had been thought previously. By including additional taxa and new morphological information, recent phylogenetic analyses (Carrano & Sampson 1999; Forster 1999; Rauhut 2000, 2003; Sampson *et al.* 2001; Carrano *et al.* 2002; Wilson *et al.* 2003; Sereno *et al.* 2004) instead supported dissolving Ceratosauria *sensu* Gauthier (1986) into two clades: Coelophysoidea and Ceratosauria *sensu stricto*, the latter including *Ceratosaurus* and Abelisauroidea. These two clades were arranged as successive sister taxa to Tetanurae. Under this hypothesis, the abelisauroid radiation had a more recent origin, with a considerably shorter missing lineage.

Ingroup Relationships of Ceratosauria

Although Gauthier (1986) did not detail ceratosaur interrelationships, several subsequent analyses did achieve some consistent ingroup resolution. Rowe (1989*a*) and Rowe & Gauthier (1990) proposed that *Ceratosaurus* was the most primitive member of Ceratosauria, the outgroup to the coelophysoids (Fig. 1). This position reflected the fact that *Ceratosaurus* lacked many derived 'ceratosaur' synapomorphies, despite its relatively late appearance in the fossil record. Rowe (1989*b*) made the first explicit connection between abelisaurs and coelophysoids by placing *Xenotarsosaurus* as part of an unresolved trichotomy with *Ceratosaurus* and Coelophysoidea (Fig. 1).

Novas (1991) hypothesised that in fact a diverse 'neoceratosaur' clade existed as the sister taxon to coelophysoids within Ceratosauria (Fig. 1), listing several supporting synapomorphies. Holtz (1994*a*) was the first to include abelisaurs and coelophysoids in a formal cladistic analysis and resolved Ceratosauria into two clades: Abelisauroidea (*Ceratosaurus*, *Elaphrosaurus* and Abelisauridae) and Coelophysoidea (Fig. 1). This general arrangement was supported by other studies (Sereno 1997, 1999; Holtz 2000; Tykoski & Rowe 2004; Figs 2 & 3), although Novas (1992*a*, *b*) suggested that *Elaphrosaurus* was probably a coelophysoid, not an abelisauroid.

A few workers have concentrated on relationships within Abelisauroidea. Most have supported the existence, albeit often with reservations, of two constituent clades: the large-bodied Abelisauridae and the smaller-bodied Noasauridae (this latter usually included only *Noasaurus*, but occasionally also *Ligabueino andesi*) (Bonaparte 1991*a*, 1996; Novas 1991, 1992*a*, 1997). Abelisauridae typically included *Abelisaurus*, *Carnotaurus*, *Majungasaurus* (*Majungatholus*), *Indosaurus*, *Aucasaurus* and *Indosuchus*. More recent works have described new discoveries of both noasaurid and abelisaurid taxa (e.g. Carrano *et al.* 2002; Wilson *et al.* 2003; Calvo *et al.* 2004). *Xenotarsosaurus* has remained problematic due to the incomplete nature of the type and only specimen; it has alternately been described as an abelisaurid (Martínez *et al.* 1986; Novas 1992*a*; Fig. 1) and an indeterminate neoceratosaur (Coria & Rodríguez 1993). More recently, Coria & Salgado (2000) placed the fragmentary *Ilokelesia* as the sister taxon to Abelisauridae + Noasauridae (Fig. 2).

Although there is considerable agreement among these analyses with regard to the general topology of abelisauroid phylogeny, little consensus exists concerning its details. Resolution is poor within Abelisauridae, for example, with different authors favouring *Majungasaurus* (*Majungatholus*) (Sereno 1998, 1999; Sampson *et al.* 2001; Wilson *et al.* 2003; Tykoski & Rowe 2004; Figs 2 & 3), *Abelisaurus* (Coria & Salgado 2000; Fig. 2), or *Aucasaurus* (Coria *et al.* 2002) as the sister taxon to *Carnotaurus*. The recent assignment of *Masiakasaurus* and *Laevisuchus* to the Noasauridae (Sampson *et al.* 2001; Carrano *et al.* 2002) was accompanied by only limited support and resolution for that clade as well (Fig. 3). More recent studies have added taxa to the Noasauridae but not resolution (Wilson *et al.* 2003; Sereno *et al.* 2004; Fig. 3).

One problem in comparing these studies is that most include only a small core group of overlapping taxa, generally comprising *Ceratosaurus*, *Carnotaurus*, *Abelisaurus*, *Majungasaurus* (*Majungatholus*) and occasionally *Noasaurus* and *Elaphrosaurus*. To these are usually added one or two taxa of interest, depending on the focus of the study. A further complicating matter is the fragmentary nature of many ceratosaur specimens, making it difficult to make direct comparisons between taxa and, thus, to identify characters and character states. As a result, cladistic matrices are largely incomplete and the evolutionary history of ceratosaurs has yet to be described in detail.

MATERIALS AND METHODS

Outgroup Relationships

For this analysis, we rely on the results of several recent works in assuming that ceratosaurs are more closely related to tetanurans than to coelophysoids (Rauhut 2000, 2003; Carrano *et al.* 2002; Wilson *et al.* 2003). Our outgroup taxa include a basal theropod (*Herrerasaurus ischigualastensis* Reig, 1963), a coelophysoid (*Syntarsus rhodesiensis* Raath, 1969) and a tetanuran (*Allosaurus fragilis* Marsh, 1877). Although some controversy exists concerning the theropod nature of *Herrerasaurus* (e.g. Langer 2004), it is certainly the most primitive taxon included here and has never been
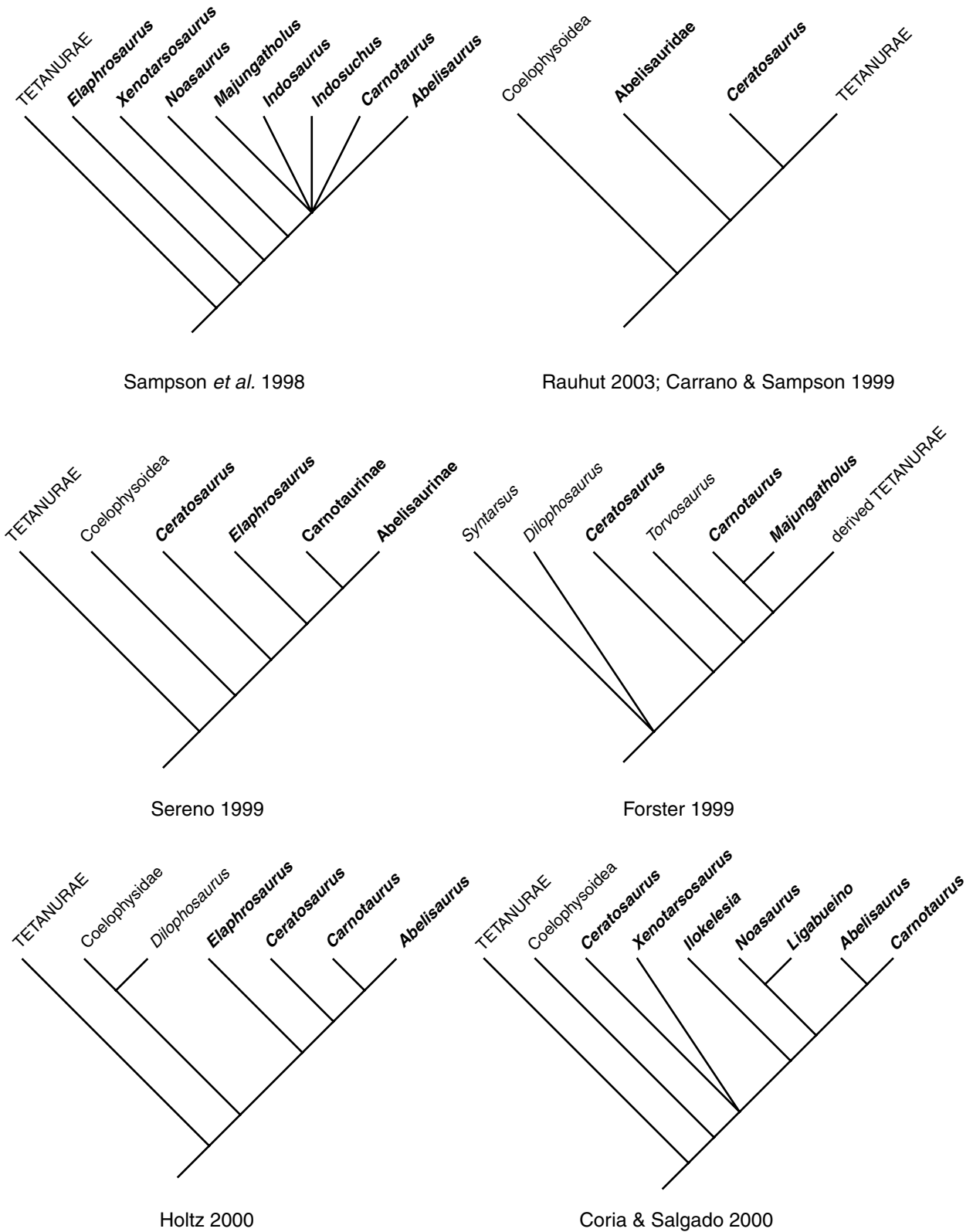
Figure 2 Previously published phylogenies of Ceratosauria, 1998–2000. Taxa in bold are those considered to belong to Ceratosauria in the present study.

considered a member of any of the other clades represented in our study. Likewise, the coelophysoid relationships of *Syntarsus* (Rowe 1989a; Tykoski & Rowe 2004) and the teta-

nuran affinities of *Allosaurus* (Gauthier 1986; Holtz 2000), are firmly established and allow these taxa to serve as representatives of these respective clades.
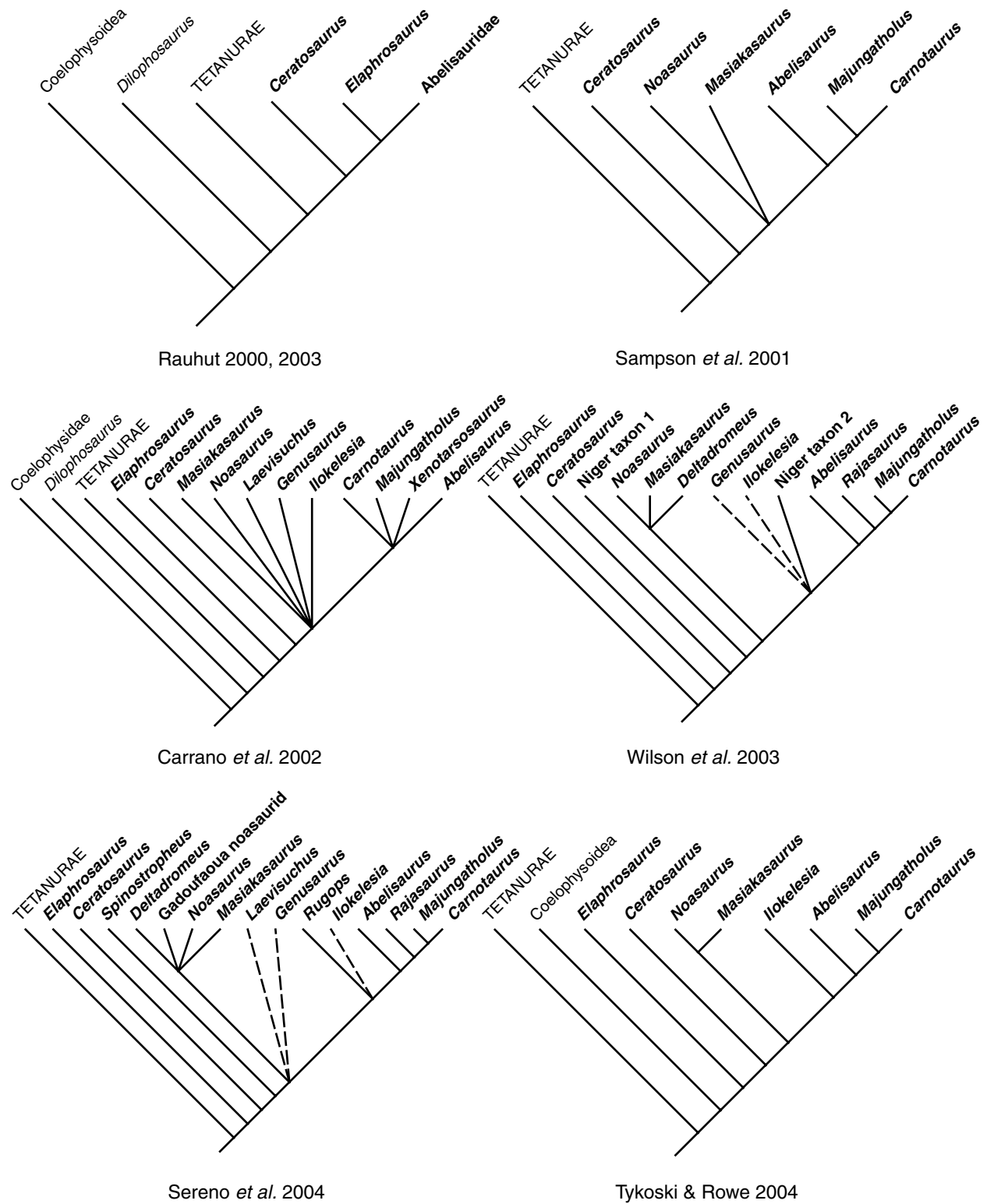
Figure 3 Previously published phylogenies of Ceratosauria, 2000–2004. Taxa in bold are those considered to belong to Ceratosauria in the present study. Dashed lines indicate taxa placed into the phylogeny *a posteriori*.

In choosing these three taxa, we allow for the possibility that our selected ingroup (or any of its putative members) might be more closely related to any one (or combin-ation) of them. By selecting individual taxa, we have tried to avoid the problems associated with suprageneric taxon codings, although we also acknowledge that our sample only

imperfectly represents the primitive conditions in each clade. Multiple outgroups also allow for greater resolution of character states at root nodes (Barriel & Tassy 1998).

Operational Taxonomic Units

Our goal in selecting ingroup taxa was to create a compromise between maximal inclusiveness and productive (i.e. at least partly resolved) analysis. Several forms (e.g. the Morrison 'Elaphrosaurus sp.' and the 'Gondwanan' maxilla from Porcieux, France; Galton 1982; Buffetaut et al. 1988; Chure, 2001) are so fragmentary and preserve so few codable characters that their inclusion would swamp the matrix with missing data. Nevertheless, it is insufficient to exclude taxa simply on the basis that they are not complete. Incomplete forms can preserve important data, including unique combinations of character states that may significantly impact the phylogenetic results. However, because the forms mentioned above (as well as several others; see Fragmentary Taxa, below) preserve no unique character combinations, but merely duplicate those present in more complete forms, they can be 'safely' excluded (Wilkinson 1995).

Other taxa (e.g. *Laevisuchus*) are probably distinct forms despite their incompleteness and may also represent important stratigraphical and geographical data points. In many cases, however, the preserved remains do not record features that can be usefully described as autapomorphies. Rather than consider these as true 'metataxa' – which would imply a genuine lack of definable features in the original organism – we provisionally accept them as valid and include them in our analysis. These taxa are identified below by the lack of a formal diagnosis; instead, we include our comments on the potential diagnosability of the taxon and our reasons for considering it valid.

Certain problems of association pose a significant frustration. In particular, *Indosaurus* is known from a formation that also preserves additional, but non-overlapping, abelisaurid materials. Some of these specimens might pertain to *Indosaurus* and would thereby enhance the morphological data available for phylogenetic analysis. However, because these associations cannot be unequivocally demonstrated, we do not use them for character codings. Similar problems associated with other ceratosaurs, not included in our phylogenetic analysis, are reviewed later (see Fragmentary Taxa, below). In total, we analysed 18 from among the nearly 40 non-coelophysoid theropods that have at one time been classified as 'ceratosaurs.' These operational taxonomic units (OTUs) are listed and discussed below.

Institutional abbreviations

AMNH = American Museum of Natural History, New York
ANSP = Academy of Natural Sciences, Philadelphia
BMNH = The Natural History Museum, London
BSP = Bayerische Staatssammlung für Paläontologie und historische Geologie, München
BYU = Brigham Young University, Provo
DGM = Departamento Nacional da Produção Mineral, Rio de Janeiro
DMNH = Denver Museum of Nature and Science, Denver
FMNH = Field Museum of Natural History, Chicago
FSL = Faculté des Sciences, Université Claude Bernard, Lyon
GSI = Geological Survey of India, Kolkata
HMN = Humboldt Museum für Naturkunde, Berlin
ISI = Indian Statistical Institute, Kolkata
MACN = Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires
MCF = Museo Municipal 'Carmen Funes', Plaza Huincul
MLP = Museo de La Plata, La Plata
MNHN = Muséum National d'Histoire Naturelle, Paris
MNN = Musée National du Niger, Niamey
MPCA = Museo Provincial 'Carlos Ameghino', Cipoletti
MPCM = Museo Paleontologico, Cittadino di Monfalcone, Gorizia
MPEF = Museo Paleontológico 'Egidio Feruglio', Trelew
MPM = Museo Regional Provincial 'Padre Manuel Jesús Molina', Padre Molina
MUCP = Museo de la Universidad Nacional del Comahue, Neuquén
MWC = Museum of Western Colorado, Fruita
NMC = Canadian Museum of Nature, Ottawa
PVL = Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán
SGM = Ministère de l'Énergie et des Mines, Rabat
UA = Département de Paléontologie, Université d'Antananarivo, Antananarivo
UCPC = Department of Organismal Biology and Anatomy, University of Chicago, Chicago
UFRJ-DG = Museu Nacional, Universidade Federal de Río de Janeiro
UMNH = Utah Museum of Natural History, University of Utah, Salt Lake City
UNPSJB = Universidad Nacional de la Patagonia 'San Juan Bosco', Comodoro Rivadavia
URC = Museu de Paleontologia e Estratigrafia 'Prof. Dr. Paulo Milton Barbosa Landim', Rio Claro
USNM = National Museum of Natural History, Smithsonian Institution, Washington
WDC = Wyoming Dinosaur Centre, Thermopolis
YPM = Peabody Museum of Natural History, Yale University, New Haven

See also Table 2

Abelisaurus comahuensis Bonaparte & Novas, 1985
1985 *Abelisaurus comahuensis* Bonaparte & Novas: 260, figs 1, 2C.

HOLOTYPE. MPCA 11908, an incomplete skull.

DIAGNOSIS. Abelisaurid with: (1) a prominent ventral quadratojugal flange that overlaps the quadrate posteriorly and (2) a tall dorsal bump on the lateral edge of the skull roof formed from the postorbital, squamosal and parietal (new diagnosis).

OCCURRENCE. Lago Pellegrini stone quarries, General Roca department, Río Negro Province, Argentina; Anacleto Formation, Río Colorado Subgroup, Neuquén Group; early–middle Campanian, Late Cretaceous (Bonaparte & Novas 1985; Heredia & Salgado 1999; Dingus et al. 2000).

REMARKS. Most of the original diagnosis (e.g. contact of lacrimal and postorbital lateral to frontal, orbital 'overhang', nasal rugosities; Bonaparte & Novas 1985) now pertains to Abelisauridae or even more inclusive groups, but *Abelisaurus* is quite distinct from other members of the clade and its validity is not in question. Once considered primitive among abelisaurids for its flattened dorsal skull roof, other taxa (e.g. *Indosuchus*) share this feature and its plesiomorphic status deserves re-evaluation.

Unfortunately, the holotype skull was reconstituted and heavily reconstructed, the original materials having been found in a very fragmentary condition (R. A. Coria, pers. comm.). Postmortem distortion has altered the proportions of the skull and several important contacts between elements (e.g. all the jugal articulations) are missing. There is no compelling anatomical reason to articulate the quadrate as sloping strongly laterally and posteroventrally (as originally shown in Bonaparte & Novas (1985) and frequently reproduced thereafter), especially given that such an arrangement is not apparent in close relatives such as *Carnotaurus* and *Majungasaurus*. On the contrary, the left and right quadrate–articular contacts have been asymmetrically distorted and it is not possible to determine with certainty which (if either) accurately represents the original condition (see Fig. 7D).

Aucasaurus garridoi Coria et al., 2002
2002 *Aucasaurus garridoi* Coria *et al*.: 460, figs 1–4.

HOLOTYPE. MCF-PVPH 236, a nearly complete skull and skeleton with preserved soft tissues and skin impressions.

DIAGNOSIS. Abelisaurid with (1) complete lateral exposure of the maxillary fenestra and (2) frontal swells instead of horns (modified from Coria *et al.* 2002).

OCCURRENCE. Auca Mahuevo, near La Escondida Mine, northeastern Neuquén Province, Argentina; Anacleto Formation, Río Colorado Subgroup, Neuquén Group; early–middle Campanian, Late Cretaceous (Heredia & Salgado 1999; Dingus *et al.* 2000; Coria *et al.* 2002; Leanza *et al.* 2004).

REMARKS. *Aucasaurus* has been described only preliminarily (Coria *et al.* 2002) and the specimen is currently being prepared and studied in more detail (R. A. Coria & L. M. Chiappe, pers. comm.). We confine our discussion to the published materials, although our character codings were obtained from direct examination of the specimen.

Aucasaurus is similar to, but distinct from, *Carnotaurus*, sharing numerous skull features along with a proportionally slender appendicular skeleton (unlike *Majungasaurus* or *Lametasaurus*). Although the original diagnosis includes several features present in other abelisaurids, further work will undoubtedly reveal numerous distinctive characters. In addition, the well preserved forelimb materials will allow significant clarification of these puzzlingly reduced and modified elements, while the presence of muscle impressions and other soft tissue remains will also add to our knowledge of these anatomical structures.

Carnotaurus sastrei Bonaparte, 1985
1985 *Carnotaurus sastrei* Bonaparte: 149–150, fig. 1.

HOLOTYPE. MACN-CH 894, a nearly complete skull and skeleton, lacking the distal hindlimbs and tail.

DIAGNOSIS. Abelisaurid with (1) proportionally shorter skull with a deeper snout than other abelisaurids, (2) an accessory pneumatic opening in the maxillary ascending ramus (excavatio pneumatica?; Witmer 1997; Sampson & Witmer 2007), (3) large frontal horns, (4) extremely short and stout radius and ulna, the former bearing a large ulnar process and both provided with large, convex distal ends (modified from Bonaparte *et al.* 1990).

OCCURRENCE. Estancio Pocho Sastre, near Bajada Moreno, Telsen department, Chubut Province, Argentina; Lower section, La Colonia Formation; Maastrichtian, Late Cretaceous (Ardolino & Delpino 1987; Bonaparte *et al.* 1990; Bonaparte 1996).

REMARKS. *Carnotaurus* has long been the emblematic taxon for Abelisauridae, because (until the discovery of *Aucasaurus*) the holotype represented the most complete associated skull and skeleton for any member of this clade. It is also the largest known abelisaurid, nearly twice the size of the largest known specimens of either *Majungasaurus* or *Aucasaurus* (although the incompletely known *Abelisaurus* may have been even larger). The descriptions of *Carnotaurus* (Bonaparte 1985; Bonaparte *et al.* 1990) have formed the main basis for most discussions of abelisaurid morphology and greatly aided the identification of more fragmentary specimens. Much of the original diagnosis (Bonaparte 1990: 3) now includes more inclusive synapomorphies, but the taxon is clearly distinct and valid.

Now, as additional taxa have been brought to light, some details of the morphology of *Carnotaurus* can be re-evaluated. The skull is perhaps the best known feature, primarily due to its extremely short, tall proportions and prominent frontal horns. Although generally well preserved, postmortem distortion has apparently exaggerated several features. Distortion is manifested primarily as mediolateral compression, but also in the form of dorsoventral displacement. The anterior portion of the skull has suffered more than the posterior portion, probably because it lacks significant internal mediolateral buttressing (which would have been provided by the braincase more posteriorly).

As a result, the premaxillae and maxillae have been pushed closer to the midline than they would have been in life, as evidenced by separation along the anterior portion of the inter-premaxillary suture. This has, in turn, compressed the ventral nasals, similarly opening the dorsal internasal suture and causing each nasal to rotate slightly outward. The premaxillae have ridden up dorsally onto the nasal, above the true dorsal margin of the nasal–premaxilla suture. This has created an artificially pronounced curvature to the ventral margin of the upper jaw. Nevertheless, the dorsal margin of the dentary suggests that the jaws were more strongly curved than in other abelisaurids, with the possible exception of *Rugops* (see Fig. 7C).

The sacrum was originally described as including seven vertebrae, including three dorsosacrals and two caudosacrals (Bonaparte *et al.* 1990). However, the first 'sacral' of this series is a nearly unmodified dorsal vertebra 12, whose centrum is articulated but not attached to the remainder of the sacrum. Furthermore, its transverse process is not modified for contact with the ilium, nor is its neural arch fused to that of the next vertebra. Therefore, only six true sacrals appear to exist in *Carnotaurus*, as in *Ceratosaurus*.

Ceratosaurus nasicornis Marsh, 1884*a*

1884*a* *Ceratosaurus nasicornis* Marsh: 330, pls 8–14.
  1892 *Megalosaurus nasicornis* Cope: 241.
  2000 *Ceratosaurus magnicornis* Madsen & Welles: 2–3, figs 1, 3, pls 1–8.
  2000 *Ceratosaurus dentisulcatus* Madsen & Welles: 21, figs 2–5, 10, pls 9–23.

HOLOTYPE. USNM 4735 (including YPM 1933), a complete skull and partial skeleton.

HYPODIGM. Holotype and MWC 1.1 (type, *Ceratosaurus magnicornis*), complete skull and partial skeleton; UMNH VP 5278 (type, *Ceratosaurus dentisulcatus*), partial skull and skeleton; BYU-VP 5010, left metatarsal III; BYU-VP 5008, left metatarsal III; BYU-VP 4838, 4853, 4908, 5092, 8937–8, 8974, 8982, 9099, 9108, 9141, 9152, 9161–3, 9165, caudal vertebrae; BYU-VP 4951–2, 8907, 9142–4, dorsal vertebrae, 12893, pelvis and sacrum.

DIAGNOSIS. Ceratosaur with: (1) mediolaterally narrow, rounded midline horn core on the fused nasals, (2) medial oval groove on nasals behind horn core, (3) pubis with large, rounded notch underneath the obturator foramen, (4) small median dorsal osteoderms (modified from Rauhut 2003: 24).

OCCURRENCE. Garden Park Quarry 1, Cañon City, Fremont County, Colorado; near Fruita, Mesa County, Colorado; Cleveland–Lloyd Quarry, Emery County, Utah; Dinosaur National Monument, Uintah County, Utah; Quarry 9, Como Bluff, Albany County, Wyoming; Dry Mesa Quarry, Montrose County, Colorado; USA; Lower Brushy Basin Member, Morrison Formation; Kimmeridgian–Tithonian, Late Jurassic (Madsen & Welles 2000; Turner & Peterson 2004).

REMARKS. A nearly complete skeleton of this theropod has been known since the end of the nineteenth century (Marsh 1884*a*), but only fragmentary additional specimens were added during several subsequent decades. More recently, three new specimens have been discovered that include two adult skulls (Madsen & Welles 2000) and one juvenile (Britt *et al.* 2000), all with associated postcranial materials. A fourth specimen (BYU-VP 12893) represents the largest adult individual and includes a well preserved, articulated pelvis and sacrum.

Two of the new adult specimens have been designated as holotypes of new species, *C. dentisulcatus* (UMNH VP 5278) and *C. magnicornis* (MWC 1.1) (Madsen & Welles 2000). However, the purported diagnostic characters of these two species are based almost entirely on proportional differences that are probably attributable to individual and/or ontogenetic variation; many can be specifically attributed to differences in body size. For example, *C. magnicornis* is supposedly distinguished from *C. nasicornis* by its 'more massive' lacrimal, dentary and ventral part of the quadratojugal, all of which may simply be the result of allometric scaling. Likewise, *C. dentisulcatus* is distinguished by its 'more massive' premaxilla, maxilla, dentary, teeth and tibia – all of which might again be due to allometry. Other diagnostic characters relate only to the absolute size of elements, which in larger individuals cannot be interpreted to have systematic meaning. Finally, the genotype specimen of *C. nasicornis* is an overly fused and pathological individual; some of its features should be interpreted with caution. Accordingly, we

agree with Rauhut (2003) that only one species of *Ceratosaurus* can be documented in the Morrison Formation.

A femur and tibia from the Late Jurassic of Rodela do Volmitão, near Lourinhã, Portugal have also been referred to *Ceratosaurus*, along with isolated teeth from other localities (Mateus & Antunes 2000; Antunes & Mateus 2003; Mateus *et al.* 2006). The tibia apparently more closely resembles that of *C. dentisulcatus* than *C. nasicornis* (Mateus & Antunes 2000; Antunes & Mateus 2003; Mateus *et al.* 2006). However, the supposed similarities are with distorted features of the right tibia of *C. dentisulcatus*; the left tibia of the same individual is identical to those of other *Ceratosaurus* 'species'. Thus we refer to the Portuguese specimen as *Ceratosaurus* sp. or *Ceratosaurus* cf. *nasicornis*.

Deltadromeus agilis Sereno *et al.*, 1996

1996 *Deltadromeus agilis* Sereno *et al.*: 991, fig. 3.

HOLOTYPE. SGM Din-2, a very incomplete postcranial skeleton, including several anterior caudal neural spines and mid-caudal vertebrae; the left scapulocoracoid, humerus and forearm; a partial mold of the left iliac blade; fused distal ischia; the right femur, proximal tibia and distal tibia with partial tarsus; the left fibula; the left and right metatarsus and several pedal phalanges.

HYPODIGM. Holotype, BSP 1912 VIII 60, 69, 70 and 81 (a partial postcranial skeleton originally referred to *Bahariasaurus ingens*) and BSP 1912 VIII 78 (a right tibia originally referred to as aff. *Erectopus sauvagei*). The referred specimens are now destroyed and exist only as lithographic plates and their accompanying descriptions (Stromer 1934).

DIAGNOSIS. Ceratosaur with: (1) broad quadrangular neural spines on anterior caudal vertebrae, (2) coracoid with shallow, concave notch in anterior margin, (3) dorsoventrally compressed ischial midshaft and (4) reduced metatarsal IV distal condyles (modified from Sereno *et al.* 1996: 991; Rauhut 2003: 32).

OCCURRENCE. Kem Kem region, southwestern Morocco, lower unit, Kem Kem Beds (Sereno *et al.* 1996); Baharîje oasis, west central Egypt, beds m and p, Baharîje Formation (Stromer 1934); early Cenomanian, Late Cretaceous (Sereno *et al.* 1996; Cavin *et al.* 2001).

REMARKS. *Deltadromeus* remains a problematic taxon due to its extremely fragmentary nature. Although parts of the skeleton bear some resemblance to coelurosaurs (Sereno *et al.* 1996; Rauhut 2000, 2003; Holtz *et al.* 2004), other recent analyses have placed it as a ceratosaur (Carrano & Sampson 2002; Wilson *et al.* 2003; Sereno *et al.* 2004). The latter two studies reinterpreted *Deltadromeus* as a basal noasaurid, largely on the basis of the strongly reduced distal condyles on the fourth metatarsal, a character also present in *Masiakasaurus*. Several of the putatively autapomorphic features identified by Sereno *et al.* (1996) occur in other taxa: the well developed medial ridge on the femur characterises all abelisauroids to some degree but especially noasaurids, the expanded coracoid and acromion can be observed in abelisauroids; and the 'accessory trochanter' is, in fact, an unusually strongly developed insertion scar for the M. adductor femoris 1 (cf. *Tyrannosaurus* in Carrano & Hutchinson 2002).

In addition, the status of *Bahariasaurus ingens* (Stromer 1934) complicates this situation. Sereno *et al.* (1996) removed several elements that Stromer (1934) had referred to this genus and placed them in *Deltadromeus*. In particular, they noted that one of the referred pubes (BSP 1912 VIII 81) differed from the holotype pubis of *Bahariasaurus* (BSP 1922 × 47) and more closely resembled that of the holotype of *Deltadromeus* (SGM Din-2), while the proximal ischium of SGM Din-2 differed from that of BSP 1922 × 47 (Sereno *et al.* 1996: 991). However, the differences between these ischia are subtle, especially considering the poorly preserved condition of this bone in *Deltadromeus*. In addition, the element originally described as the distal pubis of *Deltadromeus* is probably the distal ischium, rendering the stated distinctions with the pubes of *Bahariasaurus* meaningless. Although not all of the specimens referred to *Bahariasaurus* may belong there (as noted by Stromer 1934: 38, himself), the holotypes of *Bahariasaurus* and *Deltadromeus* (as well as the specimens referred to the latter by Sereno *et al.* 1996) cannot be confidently distinguished at this time. More complete materials from Egypt and Morocco are required before this issue can be settled.

It is interesting that Stromer (1934:24) noted the similarities between the holotypic sacrum of *Bahariasaurus* and that of *Ceratosaurus*, specifically commenting that both shared an unusual constriction of the vertebral centra. This feature is now known to occur commonly among abelisaurs and may hint at such affinities for *Bahariasaurus*.

Elaphrosaurus bambergi Janensch, 1920

1920 *Elaphrosaurus bambergi* Janensch: 225, figs 1–5.

HOLOTYPE. HMN Gr. S. 38–44, partial skeleton lacking the skull, distal forelimbs, ribs, pubis and ischium, and distal caudals.

HYPODIGM. Holotype, HMN MB.R.1762 (manual phalanx) and HMN MR.R.1755 (left radius). HMN MB.R.1756, a distal left ischium, may also pertain to this taxon.

DIAGNOSIS. Ceratosaur with: (1) a thin ventrolateral lamina bordering the posterior cervical pleurocoel ventrally, (2) a strongly concave ventral border of the cervical vertebrae, whose apex is above the midheight of the anterior articular face, (3) scapular blade breadth exceeding the height of the vertebral column, and (4) an extremely wide iliac brevis fossa, with a nearly horizontal brevis shelf (Rauhut 2003: 26).

OCCURRENCE. RD, dd and *Dysalotosaurus* Quarries, Kindope, north of Tendaguru, Mtwara, Tanzania; Middle and ?Upper Saurian Beds, Tendaguru Formation; late Kimmeridgian–?late Tithonian, Late Jurassic (Janensch 1920, 1925; Aberhan *et al.* 2002; Schrank 2005).

REMARKS. The holotype skeleton of *Elaphrosaurus* is relatively complete, missing the skull and distal forelimbs but containing much of the remainder of the skeleton. Janensch (1925, 1929) referred a few additional bones to the taxon, but no other specimens are known. Fusion between the bases of the cervical ribs and their respective parapophyses, closure of the neurocentral sutures of the dorsal vertebrae and extensive sacral fusion seem to indicate that the holotype individual was mature, although we cannot determine whether it had reached its maximum size. *Elaphrosaurus* has relatively long distal limb bones, but there is no evidence of locomotor specializations such as those seen in the metatarsi of many coelurosaurs (Holtz 1994*b*). The potential functional implications of the unusually prominent metatarsal III, seen in this taxon as well as other ceratosaurs, remains to be studied.

The phylogenetic affinities of *Elaphrosaurus* have been debated almost since its original description. The slender build of the skeleton led Janensch (1920, 1925) to describe it as a coelurosaur, which at that time referred to any lightly built theropod. Few subsequent works addressed the relationships of this taxon at all until Galton (1982) suggested that it might represent the earliest ornithomimid. He additionally referred USNM 8415, a humerus from the Late Jurassic Morrison Formation, to *Elaphrosaurus* sp. and, later, Chure (2001) referred a proximal tibia to this form. Although these bones do appear to derive from a ceratosaur, we cannot find specific features to ally them with *Elaphrosaurus*. Indeed, the tibia (DMNH 36248) bears a greater resemblance to isolated Tendaguru abelisauroid tibiae (Rauhut 2005) than to the tibia of *Elaphrosaurus*.

Paul (1988*a*) noted several primitive features in the skeleton of *Elaphrosaurus* and suggested that it was a ceratosaur. This has been supported in nearly all subsequent cladistic analyses (Holtz 1994*a*, 2000; Rauhut 2000, 2003; Carrano *et al.* 2002; Wilson *et al.* 2003; Sereno *et al.* 2004; Tykoski & Rowe 2004). Raath (1977), Novas (1992*a*), and Holtz (2000) also noted several morphological similarities between *Elaphrosaurus* and primitive theropods such as *Coelophysis* and *Syntarsus*.

Stromer (1934) referred three specimens from the Baharîje Formation (BSP 1911 XII 29, 1912 VIII 76, 192; all now destroyed) to cf. *Elaphrosaurus*, but we can identify no features to ally them specifically with this taxon. Two additional species have been assigned to *Elaphrosaurus*, both from the Early Cretaceous of Niger: *E. iguidiensis* and *E. gautieri* (Lapparent 1960). The former is extremely fragmentary, based primarily on small theropod teeth and isolated caudal vertebrae collected from several different localities. We regard it as a *nomen dubium* and these specimens as Theropoda indet. *Elaphrosaurus gautieri*, however, is represented by considerably more material and appears to be a valid taxon. It is discussed in greater detail below (see *Spinostropheus gautieri*).

Ekrixinatosaurus novasi Calvo *et al.*, 2004

2004 *Ekrixinatosaurus novasi* Calvo *et al.*: 557, figs 2–8.

HOLOTYPE. MUCPv-294, an incomplete skeleton with parts of the skull, axial and appendicular regions.

COMMENTS ON DIAGNOSIS. The original diagnosis of *Ekrixinatosaurus* includes both diagnostic and descriptive characters. This abelisaurid taxon appears to be diagnosed minimally by the presence of a posteriorly directed protuberance at the contact between the parietal and paroccipital process. Other features are shared by other abelisaurid taxa. However, other listed features are not accompanied by illustrations, so they have not been evaluated here, but further study may reveal them to be diagnostic.

OCCURRENCE. Approximately 34 km northwest of Añelo, Neuquén Province, Argentina; Candeleros Formation, Río Limay Subgroup, Neuquén Group; late? Cenomanian, Late Cretaceous (Corbella *et al.* 2004; Leanza *et al.* 2004).

REMARKS. Only recently described, *Ekrixinatosaurus* is a relatively early member of Abelisauridae. It appears to share a mixture of features with several other abelisaurids, highlighting the homoplastic, and probably ontogenetic, nature of many of these character states. The remains document a significant portion of the skeleton, but it has been only briefly described as of this writing.

Genusaurus sisteronis Accarie *et al.,* 1995
1995 *Genusaurus sisteronis* Accarie et al.: 330, fig. 4.

HOLOTYPE. MNHN Bev-1, a partial pelvis, femur, proximal tibia and fibula, distal tarsal and several vertebral centra.

COMMENTS ON DIAGNOSIS. The published diagnosis of *Genusaurus* (Accarie *et al.* 1995) no longer serves to distinguish it from other ceratosaurs. The skeleton is very fragmentary and we were unable to identify any autapomorphies on the preserved materials without canonizing obvious morphological minutiae. However, the provenance and small size of the animal strongly suggests that it represents a taxon distinct from other ceratosaurs (as opposed to a genuine 'metataxon') and we provisionally accept its validity while awaiting the discovery of additional specimens.

OCCURRENCE. Bevons, 4.25 km southwest of Sisteron, Alpes de Haute-Provence, France; 'greenish clays and glauconitic sands of Bevons,' (translated from Accarie *et al.* 1995); Albian, Early Cretaceous.

REMARKS. Accarie *et al.* (1995) described *Genusaurus* as a ceratosaur, which at that time did not necessarily include abelisaurs. Thus it represented an important extension of this mainly Triassic–Jurassic clade into Early Cretaceous times. The authors particularly noted the expansive development of the tibial cnemial crest, citing it as the only autapomorphy of the species. Subsequent discoveries have revealed that this is a feature common to abelisauroids (e.g. Carrano *et al.* 2002) and, further, that *Genusaurus* possesses several other characteristics of that clade and Ceratosauria. These include fusion of the pelvic elements (also present in some coelophysoids), a deep, posteriorly directed fossa on the medial surface of the proximal fibula, an enlarged iliofibularis tubercle, a prominent anteromedial flange along the distal femoral shaft and the nearly horizontal dorsal margin of the ilium.

Other putative 'ceratosaur' features are more equivocal and now serve to distinguish *Genusaurus* from coelophysoids in general. The femur does not have a trochanteric shelf, but instead possesses a distinct lesser trochanter that flanks a mound for the insertion of M. iliofemoralis externus, not M. puboischiofemoralis internus pars dorsalis (Hutchinson 2001; Carrano & Hutchinson 2002; *contra* Accarie *et al.* 1995). This mound is more transversely orientated than in derived tetanurans. The base of the tibiofibular crest bears only a moderate lateral sulcus, comparable in depth to that seen in many other theropods and considerably shallower than the condition in *Syntarsus* (Rowe & Gauthier 1990).

The original description of *Genusaurus* highlighted that several areas of the iliac blade appeared to be unossified. The authors suggested that this might be a preservational artifact due to corrosion, or perhaps a natural reduction, citing the example of the extant ratite *Casuarius casuarius* (Accarie *et al.* 1995: 333). The preserved vertebral centra are entirely separated from their neural arches, suggesting that the holotype represents a subadult individual despite the fused pelvic bones. The apparent incomplete ossification of the iliac blade might, therefore, also be due to the ontogenetic status of this individual.

Ilokelesia aguadagrandensis Coria & Salgado, 2000
2000 *Ilokelesia aguadagrandensis* Coria & Salgado: 90–91, figs 2–14.

HOLOTYPE. MCF-PVPH 35, one left and two right postorbitals, right quadrate, left? pterygoid, occipital condyle, ?paroccipital process, two anterior cervical vertebrae, a posterior dorsal vertebra, five middle caudal vertebrae and fragments of others, three ribs including one posterior cervical or anterior dorsal, eight proximal chevrons, eight non-ungual pedal phalanges, two pedal unguals, and other fragments, including limb shafts.

DIAGNOSIS. Abelisauroid possessing: (1) quadrate with very reduced lateral condyle and posterior border of the articular surface formed completely from medial condyle, (2) square rather than rectangular cervical vertebra in dorsal view, (3) posterior dorsal vertebrae with ventrally concave anterior centroparapophyseal laminae and (4) distal edge of caudal transverse processes slightly concave in their middle portion (modified from Coria & Salgado 2000: 90–91).

OCCURRENCE. Aguada Grande, 15 km south of Plaza Huincul, Neuquén Province, Argentina; Huincul Formation, Río Limay Subgroup, Neuquén Group; Turonian–Santonian, Late Cretaceous (Coria & Salgado 2000; Dingus *et al.* 2000; Corbella *et al.* 2004; Leanza *et al.* 2004).

REMARKS. *Ilokelesia* was originally described as a primitive abelisaurian theropod (Coria & Salgado 2000), based primarily on the morphology of the postorbital. Unlike in more derived abelisaurids, this element appeared to lack a suborbital process and had a relatively straight, rather than oblique, ventral ramus. However, the type materials of *Ilokelesia* actually include three postorbitals, thus representing at least two individuals. The postorbital described by Coria & Salgado (2000) is damaged and incomplete, but both of the remaining elements show a more characteristic abelisaurid morphology that includes the suborbital process, numerous pronounced vessel traces and an anteroventral fossa similar to that seen in *Carnotaurus* (Sampson *et al.* 1998).

The remainder of the specimen is very fragmentary but confirms the abelisauroid nature of *Ilokelesia*. The pedal phalanges are similar to those of *Aucasaurus*, differing in subtle features of proportion. One pedal ungual displays (faintly) the double vascular grooves that characterise all abelisauroids.

Interestingly, the two individuals of *Ilokelesia* from this site were found along with a third specimen, MCF-PVPH 36, that was described as a juvenile of this taxon (Coria & Salgado 1993). MCF-PVPH 36 is represented by a dorsal and sacral series in which the neural arches and centra have detached from one another along nearly the entire length of the column, yet retained their serial articulations. This specimen can be identified an abelisauroid but cannot be ascribed specifically to *Ilokelesia* on morphological grounds. Nevertheless, it remains possible that three individuals of this abelisaurid were deposited together.

Indosaurus matleyi Huene & Matley, 1933

1933 *Indosaurus matleyi* Huene & Matley: 44, pl. 9, figs 3–4, pl. 10, fig. 1.

HOLOTYPE. GSI IM K27/565, a partial braincase.

ORIGINAL DIAGNOSIS. '. . . much stouter and thicker bones. The parietals . . . are short and broad . . . there seems to have been a transverse crest above and behind the orbits, and the frontals are concave and decline in front; on the post-frontals there were apparently horn-like tuberosities' (Huene & Matley 1933: 46).

OCCURRENCE. Bara Simla Hill, Jabalpur, Madhya Pradesh, India; 'Carnosaur Bed', 'infratrappean beds' of the Lameta Formation; Maastrichtian, Late Cretaceous (Matley 1921).

REMARKS. The theropod materials from the Lameta Formation have been problematic nearly since their original discovery and description (see Matley 1918 *et seq.*). The disassociation of the materials in the assemblage has made taxon identification and diagnosis difficult, particularly because multiple similar-sized taxa appear to be present (Huene & Matley 1933; Wilson *et al.* 2003; Novas *et al.* 2004). Furthermore, in the years since their original description, many specimens have been lost and cannot now be studied. Thus, recent advances in our understanding of theropod anatomy and systematics have had limited application to the Lameta theropods.

The collection described in detail by Huene & Matley (1933) was recovered from an outcrop of the Lameta Formation located on the estate of a gun carriage factory on Bara Simla Hill, on the east side of Jabalpur in present day Madhya Pradesh (then the Central Provinces), India. The theropod specimens derived from a single layer in the formation, termed the 'Carnosaur Bed' (Matley 1921) and were concentrated within an area of about 20 square yards (Huene & Matley 1933). Because all the elements were disarticulated and intermixed, Huene & Matley resisted grouping disassociated specimens under a single taxonomic name and many of the specimens were not associated with any of the nine new taxa they eventually erected. In the same paper, they opined that a tenth Lameta theropod, *Orthogoniosaurus matleyi* Das-Gupta, 1930, had been founded on insufficient materials (a single tooth) and was probably a *nomen dubium*. Interestingly, several years previously Matley (1924) had named the 'stegosaur' *Lametasaurus indicus* based on materials from the same 'Carnosaur Bed' (originally described as a theropod; Matley 1921) which he had presumably united based on their proximity in the quarry. Once Chakravarti (1934, 1935) reidentified these materials as a theropod, *Lametasaurus* became the eleventh theropod taxon from the Jabalpur site.

At least some of these theropods probably represent the same taxa, but such determinations are exceedingly difficult because most were founded on different skeletal elements (see Novas *et al.* 2004 for a thorough review). Therefore the type braincase is the only specimen that can be assigned unequivocally to *Indosaurus* at this time. To many authors this braincase has appeared distinct from the type braincase of *Indosuchus*, also from the Bara Simla site (e.g. Huene & Matley 1933; Walker 1964; Chatterjee 1978; Molnar 1990). More recently, it was also distinguished from the type braincase of *Rajasaurus* (Wilson *et al.* 2003). However, the preservation of the Bara Simla materials is not optimal; at times it can be difficult to identify even the original external bone surface (our pers. obs.). Therefore discriminations between these forms must be viewed with caution.

Despite being the most fragmentary specimen, the type of *Indosuchus* would seem to be the most distinct of the three, particularly in exhibiting a thin and non-ornamented skull roof. *Rajasaurus* and *Indosaurus* are more similar to one another than either is to *Indosuchus* and, in fact, the apparent differences may be artefacts of preservation. In addition, the ilium of *Rajasaurus* bears a prominent ridge between the supra-acetabular crest and the lateral edge of the brevis fossa, as in *Lametasaurus*. We believe that these three taxa – *Indosaurus*, *Lametasaurus* and *Rajasaurus* – are the most likely candidates for synonymy (in which case the name of priority would be *Lametasaurus*). However, in the absence of definitive information, we analyse the two most informative taxa (*Indosaurus* and *Rajasaurus*) separately here.

Laevisuchus indicus Huene & Matley, 1933

1933 *Laevisuchus indicus* Huene & Matley: 60–61, pl. 20, figs 2–5.

HOLOTYPE. GSI IM K20/613, 614, K27/588, 696, three cervical and one dorsal vertebrae.

COMMENTS ON DIAGNOSIS. *Laevisuchus* is extremely fragmentary and only a single vertebra remains of the four original type specimens, although it is quite likely that many of the small Lameta theropod specimens pertain to *Laevisuchus*. Thus we face the same problem as with *Genusaurus*, and tentatively accept the validity of *Laevisuchus* while acknowledging that it cannot be diagnosed at this time.

OCCURRENCE. Bara Simla Hill, Jabalpur, Madhya Pradesh, India; 'Carnosaur Bed', 'infratrappean beds' of the Lameta Formation; Maastrichtian, Late Cretaceous (Huene & Matley 1933).

REMARKS. *Laevisuchus* and the other small theropods described from the Lameta Formation by Huene & Matley (1933) have remained incomplete and problematic since their discovery. Most of these materials are non-diagnostic and many have now been lost (Novas *et al.* 2004), but subsequent discoveries from elsewhere in Gondwana have offered some illumination. The four vertebrae of *Laevisuchus* are very similar to those of *Noasaurus* and *Masiakasaurus* (Sampson *et al.* 2001), but unfortunately no other skeletal elements are known for comparison.

The small Lameta theropods pose persistent nomenclatural and phylogenetic problems. Among the many unnamed materials are distinctively abelisauroid pedal unguals and noasaurid second metatarsals (cf. Carrano *et al.* 2002). There is little to suggest the presence of multiple small (< 3 m length) taxa. It is tempting to refer most of these materials to *Laevisuchus*, but we cannot be certain without additional associated materials.

Majungasaurus crenatissimus (Depéret, 1896) Lavocat, 1955

1896 *Megalosaurus crenatissimus* Depéret: 188, pl. 4, figs 4–8.
1928 *Dryptosaurus crenatissimus* Depéret & Savornin: 263.
1955 *Majungasaurus crenatissimus* Lavocat: 259, fig. 1.
1979 *Majungatholus atopus* Sues & Taquet: 634, fig. 1.

HOLOTYPE. MNHN MAJ-1, a left dentary.

HYPODIGM. Holotype and FSL 92.289, 92.290, 92.306 and 92.343 (type series, *Megalosaurus crenatissimus* Depéret, 1896), MNHN MAJ-4 (type, *Majungatholus atopus* Sues & Taquet, 1979), FMNH PR 2008, 2100, UA 8678.

DIAGNOSIS. Abelisaurid with: (1) thickened, fused, highly pneumatic nasals bearing large, bilateral foramina, (2) thin nasal lamina separating left and right premaxillary nasal processes, (3) maxilla with 17 teeth, (4) frontals with a median hornlike projection and (5) pronounced median fossa on sagittal crest (modified from Sampson *et al.* 1998; Krause *et al.* 2007).

OCCURRENCE. Meravana and Berivotra, Mahajanga Basin, Madagascar; Anembalemba Member, Maevarano Formation; ?upper Campanian–Maastrichtian, Late Cretaceous (Depéret 1896; Thévenin 1907; Sampson *et al.* 1998).

REMARKS. The history of this taxon, and of *Majungatholus atopus*, is given in detail elsewhere (Sampson *et al.* 1996, 1998; Carrano 2007; Krause *et al.* 2007). The present diagnosis excludes two characters that are now known to occur in at least one other abelisaurid, *Carnotaurus* (cervical ribs bifurcate distally; cervical ribs with multiple enlarged pneumatic foramina proximally (diameter > 10 mm); Sampson *et al.* 1998).

Depéret (1896) described a collection of fragmentary theropod bones as the (unofficial) type series of *Megalosaurus crenatissimus*. Later, Lavocat (1955) referred this species to the new genus *Majungasaurus* and designated an incomplete dentary as the neotype. These materials clearly represent abelisaurid theropods, the earliest described forms from the Maevarano Formation of Madagascar. Indeed, Depéret's specimens include a left pedal IV ungual with distinctive double vascular grooves. Additional materials referred to this taxon (Russell *et al.* 1976) have not been studied or located anytime recently. Sampson *et al.* (1998) described new materials demonstrating the putative Madagascan pachycephalosaur *Majungatholus atopus* to be an abelisaurid theropod, probably conspecific with *Majungasaurus*. Not finding species-specific characters on the neotype dentary specimen of Lavocat, they referred large abelisaur materials from this region to *Majungatholus atopus*. However, more recent examination of these materials (Krause *et al.* 2007) has led to the determination that Lavocat's *Majungasaurus* material is diagnostic and that, therefore, *Majungatholus* is a junior synonym.

Masiakasaurus knopfleri Sampson et al., 2001

2001 *Masiakasaurus knopfleri* Sampson *et al.*: 504, figs 1–2.

HOLOTYPE. UA 8680, a left dentary.

HYPODIGM. Holotype and FMNH PR 2108–2182, UA 8681–8696.

DIAGNOSIS. Abelisauroid with: (1) four most anterior dentary teeth procumbent, with the first set in a large, ventrally expanded alveolus that is almost horizontal in orientation, (2) a strongly heterodont lower dentition, grading from elongate, weakly serrated, apically round with labiolingually positioned carinae (anteriorly) to increasingly recurved, transversely compressed, with mesiodistally positioned carinae (posteriorly) (modified from Sampson *et al.* 2001: 504).

OCCURRENCE. Berivotra, Mahajanga Basin, Madagascar; Anembalemba Member, Maevarano Formation; ?upper Campanian–Maastrichtian, Late Cretaceous (Carrano *et al.* 2002).

REMARKS. This taxon has recently been described in detail (Carrano *et al.* 2002), but several new elements were recovered by the 2001 and 2003 Mahajanga Basin Project expeditions; these are currently under study (Carrano *et al.* 2004, unpublished results). Certain character codings reflect information derived from these new specimens, which now include the postorbital, braincase, scapulocoracoid, ilium, ischium, fibula and numerous vertebrae representing previously unknown positions within the column. *Masiakasaurus* is now by far the best known noasaurid; these new specimens confirm the distinctive nature of the noasaurid skull and postcranium and suggest that these taxa are indeed quite specialised and not merely small-bodied versions of the large-bodied Abelisauridae.

Noasaurus leali Bonaparte & Powell, 1980

1980 *Noasaurus leali* Bonaparte & Powell: 23–24, figs 7–8.

HOLOTYPE. PVL 4061, quadrate, maxilla, cervical vertebral arch, vertebral centrum, cervical rib, manual phalanges and unguals, metatarsal IV.

DIAGNOSIS. Abelisauroid with: (1) maxillary tooth count reduced to 10 at most, and (2) cervical neural arch with anterior epipophyseal prong (modified from Bonaparte & Powell 1980: 23–24).

OCCURRENCE. El Brete, southern Salta Province, Argentina; Lecho Formation; ?upper Campanian–Maastrichtian, Late Cretaceous (Bonaparte & Powell 1980).

REMARKS. *Noasaurus* has remained enigmatic since its original description (Bonaparte & Powell 1980). The incomplete holotype preserves elements from across the skeleton. Numerous authors (e.g. Novas 1991, 1992*a*; Bonaparte 1996; Coria & Salgado 2000) have discussed the abelisauroid affinities of *Noasaurus*, citing the nearly vertical ascending ramus of the maxilla, the lack of a maxillary fenestra, the anteroposteriorly short cervical neural spine and the anterior epipophyseal prongs on the cervical arch. At the same time, *Noasaurus* was considered distinct enough from abelisaurids such as *Carnotaurus* and *Abelisaurus* to warrant placement in its own family, Noasauridae. Nevertheless, for nearly 20 years it remained the sole member of this group, with the occasional exception of *Ligabueino* (e.g. Coria & Salgado 2000; see Discussion, below).

The discovery of *Masiakasaurus* (Sampson *et al.* 2001; Carrano *et al.* 2002, 2004) clarified the morphology of noasaurids and established the group as a widespread clade of small-bodied theropods. Most earlier opinions of *Noasaurus* were confirmed; namely, that it was closely related to Abelisauridae but remained outside that clade. In addition, the more complete pedal materials of *Masiakasaurus* allowed the supposedly 'hyperextensible' pedal phalanx and ungual (Bonaparte & Powell 1980) to be re-identified as an inverted manual phalanx and ungual (Carrano *et al.* 2004). Thus *Noasaurus* and its relatives do not represent an abelisauroid parallel to the generally Laurasian deinonychosaurs, but a bizarre radiation of their own. Its currently understood

affinities indicate that the presence of anterior epipophyseal prongs on the cervicals of *Carnotaurus* are homoplastic.

Rajasaurus narmadensis Wilson *et al.,* 2003

2003 *Rajasaurus narmadensis* Wilson *et al.*: 4–5, figs 2–15.

HOLOTYPE. GSI 21141/1–33, a braincase, cervical, dorsal and sacral vertebrae, left and right ilia, a distal tibia, partial fibula and metatarsals.

DIAGNOSIS. Abelisaurid with: (1) median nasal–frontal prominence with frontal forming the posterior rim, (2) anteroposteriorly elongate upper temporal fenestrae (approximately 150% length of frontal) and (3) a robust ilium with a transverse ridge separating the brevis fossa from the acetabulum (modified from Wilson *et al.* 2003).

OCCURRENCE. Near Rahioli, Narmada Valley, Rajasthan, India; 'infratrappean beds' of the Lameta Formation; Maastrichtian, Late Cretaceous (Wilson *et al.* 2003).

REMARKS. The holotype of *Rajasaurus* is an important Lameta theropod specimen because it is one of the few that provides any overlap between cranial and postcranial elements. The braincase preserves much of the original skull roof – confirming that it is a thick-skulled form – along with a low but distinctive transverse crest on the anterior frontals. This crest rises just posterior to the ridged, shelflike nasal contact, implying its continuation onto the nasals.

As noted previously, the morphology of *Rajasaurus* appears to be closer to *Indosaurus* than to *Indosuchus*. For example, a similar crest was described in *Indosaurus* (Huene & Matley 1933: 45, pl. X: 1a, b) and both taxa show relatively elongate upper temporal fenestrae. The possible presence of the crest in *Indosaurus* has been disputed (Wilson *et al.* 2003; Novas *et al.* 2004), but unfortunately no definitive judgement can be made because the entire dorsal surface has been significantly eroded in this region, rendering even the proper horizontal axis subject to debate.

Rugops primus Sereno *et al.,* 2004

2004 *Rugops primus* Sereno *et al.*: 1326–7, fig. 3.

HOLOTYPE. MNN IGU1, a partial skull.

DIAGNOSIS. Abelisaurid with: (1) a small fenestra in the skull roof between the prefrontal, frontal, postorbital and lacrimal and (2) a concave dorsal surface of the nasals (modified from Sereno *et al.* 2004: 1327).

OCCURRENCE. In Abangarit, Niger; Echkar Formation, Tegama Group; Cenomanian, Late Cretaceous (Sereno *et al.* 2004).

REMARKS. The small size of the holotypic skull of *Rugops* suggests that it may represent a subadult individual, a possibility highlighted by the incomplete fusion between the left and right nasals. Indeed, the fenestra between the prefrontal, frontal, postorbital and lacrimal may be an ontogenetic artifact as well, but this can only be evaluated once subadult specimens of other abelisaurid taxa have been discovered. However, the condition exhibited by *Rugops* lends credence to the hypothesis that the prefrontal of abelisaurids was not lost, but rather fused during ontogeny (and/or phylogeny) to the medial lacrimal, as is the case for carcharodonto-

saurids (including *Carcharodontosaurus*) and tyrannosaurids (Brochu 2002).

In addition, the row of foramina on the dorsal nasal is a feature shared with *Carnotaurus*, although in the latter the dorsal surface of the posterior nasals is convex along the midline, rather than concave. Nevertheless, the slender proportions of many of the skull bones, along with the relatively thin nasals and proportionally large skull fenestrae, demonstrate that *Rugops* is clearly a distinct abelisaurid taxon.

Spinostropheus gautieri (Lapparent, 1960) Sereno *et al.* 2004

1960 *Elaphrosaurus gautieri* Lapparent: 31, pl. 5, figs 5–6, pl. 10, fig. 5, pl. 11, figs 2, 4, 8, 10–11.
2004 *Spinostropheus gautieri* Sereno *et al.*: 1325, fig. 2.

HOLOTYPE. MNHN 1961–28, a series of vertebrae.

HYPODIGM. Holotype, additional MNHN specimens (see below) and MNN TIG6, a complete vertebral series from C3 to the sacrum with associated cervical and dorsal ribs.

DIAGNOSIS. Ceratosaur with: (1) strongly canted anterior articular faces on the mid-cervical vertebral centra (30° to posterior centrum face), (2) partitioned anterior pleurocoels, (3) dorsoventrally flattened epipophyseal processes and (4) broad, subrectangular neural spines (modified from Sereno *et al.* 2004: 1325).

OCCURRENCE. In Tedreft, 250 km northwest of Agadez; and Fako, about 35 km southwest of In Gall, Niger; Tiourarén Formation, Tegama Group; Neocomian, Early Cretaceous (Lapparent 1960; Sereno *et al.* 2004).

REMARKS. Sereno *et al.* (2004) referred to the figured cervical of *Elaphrosaurus gautieri* as the holotype of *Spinostropheus*. Lapparent (1960) described this cervical as coming from a 'lot' of 16 vertebrae from In Tedreft. Although he did not describe the associations of these vertebrae, he later (Lapparent 1960: 31–32) indicated that the remains of a second, associated individual were recovered from the same locality. This second specimen included a cervical neural arch that was not figured. Two points may be deduced from this information. First, the 16 vertebra 'lot' was probably not from a single individual. Second, the overlapping cervical elements between the two specimens make it likely that Lapparent's referral of them all to one species was based on observed similarities. Thus we may infer that the unillustrated cervical was morphologically similar to that illustrated from the 'lot' of 16 (Lapparent 1960: pl. XI, fig. 5). These deductions are important clues because not all of Lapparent's specimens can be located today.

Examination of MNHN 1961–28 confirms that the illustrated cervical possesses a fossa on the dorsal surface of the diapophysis, as in both MNN TIG6 and *Elaphrosaurus*. Unlike *Elaphrosaurus*, the posterior centrum face is quite strongly concave, whereas the anterior face is slightly convex. The ventral surface bears an abbreviated keel anteriorly along with a very prominent anterior pleurocoel complex that extends well onto the posteromedial surface of the parapophysis.

Additional elements of *S. gautieri* add to these morphological data. The fused sacrals of the second specimen (MNHN uncat.) appear in fact to represent the pathologically fused centra of two cervicals, preserving portions of the

parapophyses but none of the neural arches (P. M. O'Connor, pers. comm.). The centra are relatively long anteroposteriorly and the more anterior one bears evidence of a concave posterior face. The dorsal centra are also long, lacking any keels or prominent foramina. The tibia is similar to those of other basal ceratosaurs, with a moderately mediolaterally elongate distal end, a cnemial crest that is large but proportionally smaller than in abelisauroids and a distinct anterior facet for a laminar astragalar ascending process.

Velocisaurus unicus Bonaparte, 1991*b*

1991*b* *Velocisaurus unicus* Bonaparte: 70–71, figs 20–21, 22A.

HOLOTYPE. MUCPv-41, an incomplete lower right hindlimb.

COMMENTS ON DIAGNOSIS. It is not clear whether *Velocisaurus* preserves autapomorphies (Rauhut 2003: 33), but it is probably a distinct taxon based on its provenance.

OCCURRENCE. Campus of the Universidad Nacional del Comahue, Neuquén, Neuquén Province, Argentina; Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group; Coniacian, Late Cretaceous (Bonaparte 1991*b*).

REMARKS. The partial hindlimb of *Velocisaurus* is poorly preserved and both the distal end of the tibial cnemial crest and astragalar ascending process are missing. However, the distal tibia is mediolaterally elongate, as in tetanurans and ceratosaurs. The astragalus and calcaneum are coossified but separate from the tibia and the metatarsals show an antarctometatarsalian condition (see Appendix 1, character 148), resembling other ceratosaurs. Most striking is the reduction of metatarsal II, as in the noasaurids *Masiakasaurus* and *Noasaurus*. Although metatarsal IV is also somewhat reduced, it is much less so than metatarsal II, again resembling the condition in noasaurids. Supposed differences between *Velocisaurus* and *Noasaurus* (Bonaparte 1991*b*; Agnolín *et al.* 2003) are based on the misidentified pedal (actually manual) elements of the latter, as noted earlier.

Characters

This study utilised a taxon/character matrix that included 151 characters, all equally weighted. Characters are described in Appendix 1 and were derived from direct study and a synthesis of prior anatomical work (see Supplementary Data Table 1 available online on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477201907002246). The resultant matrix is listed in Appendix 2. The majority of character scorings were obtained from direct examination, except for those specimens now lost, destroyed, or in distant collections (Appendix 3).

Eighteen characters are new to this study; the majority (133 or 88.1%) derive from some 51 previously published studies, although several have been modified for this study. Of those previous works, 37 represent the original sources for all 133 characters. An examination of the pattern of character use (see Supplementary Data Table 1) illustrates that these characters are relatively evenly derived from the earlier studies, with only five works (Gauthier & Padian 1985; Gauthier 1986; Sereno *et al.* 1994; Sampson *et al.* 1998; Carrano *et al.* 2002) contributing to more than 5% (about 8 characters) of

the current matrix. A number of previously used characters were excluded from this study, most due to their inapplicability – either the original analysis focused on different taxa than those studied here (e.g. coelurosaurs), the characters are invariant or autapomorphic, or we could not confirm the relevant morphological observations.

In the current matrix, 71 (47.0%) characters were cranial, 33 (21.9%) were axial and 47 (31.1%) were appendicular. One character (141) was ordered to reflect an apparent cline of distribution; the remainder were unordered. Numerous characters could not be coded for certain taxa due to missing data; these were tallied as '?'. Missing data accounted for as little as 0% of the total character codings (*Allosaurus*, *Syntarsus*), to over 90% (*Genusaurus*, *Indosaurus*, *Laevisuchus*, *Velocisaurus*). None of the character states were considered to be 'inapplicable' in this matrix.

Phylogenetic methods

Characters were scored using MacClade 4.06 (Maddison & Maddison 2003). We used the branch-and-bound search option in PAUP* 4.0b10 (Swofford 2002), with *Herrerasaurus*, *Syntarsus* and *Allosaurus* rooted as successive outgroup taxa. The matrix was also analysed using NONA (Goloboff 1999) and WinClada (Nixon 2002). We could not use an exhaustive search because of the large number of OTUs, but the methods employed are designed to find all most parsimonious trees (Maddison 1991; Page 1993).

Following the initial analyses, we determined branch support using the 'Decay Index PAUP File' option in MacClade 4.06 for the strict consensus phylogeny. This created a series of constrained trees that were then analysed in PAUP to determine the branch support index for each node. The Kishino–Hasegawa test in PAUP was used to determine the significance of alternative topologies with longer step lengths.

Biogeographical methods

Numerous biogeographical methods are available, but many require a great deal more data (and certainty) than we have available to us for ceratosaurs. Therefore we employed two relatively basic analyses in order to develop a supportable biogeographical history of Ceratosauria.

Our first analysis reconstructed geography as an unordered multistate character. For this we coded geography as a discrete character in MacClade, using polymorphic characters to represent taxa present in multiple locales. The tree topology was taken from the previous phylogenetic analyses and the biogeographical character 'mapped' onto this phylogeny. We then noted the reconstructed 'ancestral states' for this 'character' as potential sites of origin for the included clades.

We also subjected our data to Tree Reconciliation Analysis (TRA) using TreeMap, in a manner analogous to host–parasite codivergence analysis (Charleston & Page 2002). This poses numerous difficulties in the present example. First, the poorly resolved tree necessitates the exclusion of several taxa, even though we used the strict consensus results from our 'pruned' phylogeny. Second, it is not possible to assign relative 'weights' to dispersal, vicariance and regional extinction (Upchurch *et al.* 2002) without resorting to *ad hoc* assumptions and, thus, we are forced to treat all equally.

We examined two taxonomic datasets – (1) all ceratosaurs and (2) all Late Cretaceous ceratosaurs – in order to accommodate concerns about the use of non-contemporaneous taxa (Upchurch *et al.* 2002). The Ceratosauria cladogram represented North America (NA), South America (SA), Africa (AF), Madagascar (MA) and India (IN). We also utilised two area cladograms, reflecting disagreement about the sequence of Gondwanan fragmentation (e.g. Krause *et al.* 1998; Sereno *et al.* 2004): (1) (NA(AF(SA (MA,IN)))), with successive nodes representing Pangaea, Gondwana, SA + Indo-Madagascar and Indo-Madagascar, and (2) (NA((SA,AF)(MA,IN))), with successive nodes representing Pangaea, Gondwana, Afro-South America and Indo-Madagascar. The Late Cretaceous dataset was reduced through the exclusion of one taxon (*Ceratosaurus*) and one area (NA).

RESULTS

Phylogenetic Results

Under PAUP*, the analysis produced 10,560 most parsimonious trees (MPTs), each of 220 steps, Consistency Index (CI) = 0.732 and Retention Index (RI) = 0.821. A strict consensus of these trees produced the cladogram shown in Fig. 4A. Under NONA, island hopping analysis produced identical results. Character support for each node is detailed in Table 1. Ambiguous character states were examined through accelerated (ACCTRAN) and delayed (DELTRAN) optimisation options (Swofford, 2002).

The strict consensus tree supports the monophyly of Abelisauroidea, Abelisauridae and Noasauridae as commonly construed. It places three African taxa, *Elaphrosaurus*, *Deltadromeus* and *Spinostropheus*, in an unresolved polytomy at the base of Ceratosauria. *Ceratosaurus* is more derived than these forms and is the outgroup to a monophyletic Abelisauroidea (= Noasauridae + Abelisauridae). Five taxa are included in Noasauridae, but no internal resolution is achieved. Within Abelisauridae, *Rugops* and *Ekrixinatosaurus* are successive outgroups to a more derived, but largely unresolved clade. *Majungasaurus*, *Rajasaurus* and *Indosaurus* are grouped together in all trees, but the remaining South American abelisaurids form a polytomy.

Adams consensus revealed that *Deltadromeus*, *Abelisaurus* and *Aucasaurus* acted as 'wildcard' taxa at their respective nodes (Fig. 4B). That is, these taxa were placed at the base of resolved nodes that had been reduced to polytomies under the strict consensus (Nixon & Wheeler 1992; Wilkinson 1994). We pruned these taxa from the matrix and re-analysed the dataset. The result was a set of 264 MPTs of 213 steps, with CI = 0.756 and RI = 0.818. The strict consensus cladogram is shown in Figure 4C (identical for PAUP and NONA results). It differs from the full analysis in that it resolves two additional sister-taxon relationships: *Spinostropheus* + *Elaphrosaurus* (at the base of Ceratosauria), and *Carnotaurus* + *Ilokelesia* (within Abelisauridae). The former is rather well supported (decay index = 3), suggesting that it may represent a legitimate clade that was destabilised by the presence of *Deltadromeus*. Adams consensus did not reveal any additional 'wildcards' within the two remaining unresolved clades, Noasauridae and higher Abelisauridae.

Decay analyses reveal that many of the internal nodes are weakly supported (Figs 4A, C), hardly surprising given the amount of missing data and, in particular, the fact that many taxa are known from limited materials that do not overlap with those of other taxa. As a result, even comparatively well-known taxa can belong to weakly supported clades by virtue of missing data. Nevertheless, more basal nodes are quite robust, including those supporting the derived placement of *Ceratosaurus* relative to *Elaphrosaurus* and its relatives.

Biogeographical results

Unfortunately, neither biogeographical analysis achieves much resolution. The character analysis is particularly unresolved. The node representing *Ekrixinatosaurus* + higher abelisaurids is resolved as South American, but biogeography cannot be unambiguously reconstructed at any other node. The same is true when the reduced dataset tree is employed. However, when we added the undescribed African noasaurid (Sereno *et al.* 2004) to the unresolved Noasauridae node, this (along with the basal position of *Rugops* within Abelisauridae) led to the resolution of Africa as the site of origin for Ceratosauria, Abelisauroidea, Noasauridae and Abelisauridae. However, given the paucity of the fossil record of pre-Cenomanian abelisaurs outside of Africa, any such conclusion regarding the origin of the clade must be regarded with extreme caution.

The TRA analysis required the removal of several taxa in order to present fully resolved nodes. These included *Deltadromeus*, all but two of the noasaurids (*Masiakasaurus* and *Noasaurus* were retained), and three abelisaurids (*Indosaurus*, *Aucasaurus* and *Abelisaurus*). Fortunately, only the removal of the noasaurids had the potential to obscure any major biogeographical signals and then only within that group.

Under biogeographical scenario (1), the results were similar between the full and Late Cretaceous datasets, with the latter requiring fewer overall biogeographical events to explain the apparent patterns. For the full dataset, TRA discovered 11 possible biogeographical solutions that were equally congruent with our cladogram. Among them, one solution had the fewest dispersal events (0) and a high degree of vicariance. This solution was highly significant ($p = 0.01$) and involved a high number of regional extinctions (5). A second, equally significant solution involved a single dispersal (the *Rugops* lineage into Africa from the remainder of Gondwana) and only two extinctions. However, several of these 'extinctions' may be viewed as predictions of future discoveries, including the presence of noasaurids throughout pre-breakup Gondwana (as implied by their currently understood distribution). The Late Cretaceous dataset discovered only four possible scenarios, three of which were significant; all of these indicated a high amount of vicariance and little or no dispersal.

The results were broadly similar under biogeographical scenario (2), with those solutions involving greater vicariance and less dispersal tending to be more significant. However, although this scenario was congruent with more possible solutions (11 for the full dataset, 9 for the Late Cretaceous dataset), none of them were statistically significant. The best-case solutions for the full dataset ($p = 0.12$–0.13) involved either no dispersals or a single such event (abelisaurids from South America to Indo–Madagascar). All of the Late Cretaceous solutions have high p-values (0.41–0.99).
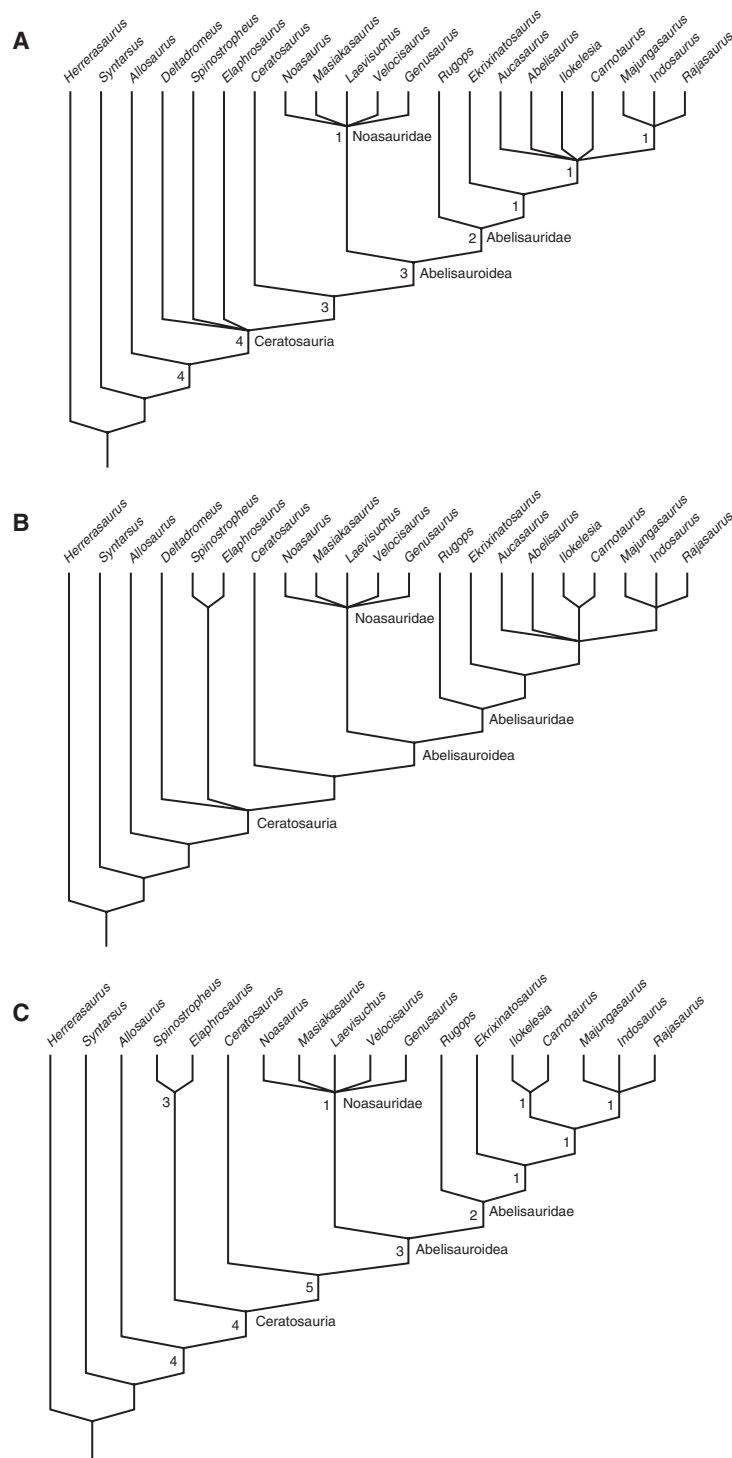
Figure 4 Phylogeny of Ceratosauria, based on present results. (A) Strict consensus tree based on entire data set. (B) Adams consensus tree based on entire data set. (C) Strict consensus based on pruned data set. Numbers indicate the decay index for each node. Character support is given in Table 1.

DISCUSSION

Comparisons with previous analyses

By now at least a dozen cladistic analyses of ceratosaurs and their close relatives have been published (see Supplementary Data Table 2) and it is safe to say that a great many permutations of the basic topology have been explored. Issues

regarding the relationships of ceratosaurs to other theropod groups are reviewed in the Introduction, above. As this study is primarily concerned with ingroup relationships, key issues affecting these aspects are addressed below.

Basal taxa

Although most studies have regarded *Ceratosaurus* and *Elaphrosaurus* as primitive ceratosaurs, there has been some

Table 1 Character support by node for results of the pruned analysis.

Node	Unambiguous	ACCTRAN	DELTRAN
Neotheropoda	73(1), 93(1)		
Tetanurae + Ceratosauria	43, 44, 45, 52, 53, 55, 60, 61, 67, 74, 75, 76, 77, 81, 112, 112, 123, 124, 132, 136, 137(1), 140, 144	47, 84, 127, 142, 145	
Ceratosauria	72, 73(2), 90, 93(2), 94, 96, 98, 108, 110, 111, 113, 118, 128, 138, 141(1)	5, 7, 14, 22, 41, 42, 46, 51, 56, 62, 63, 66, 71, 106, 126, 150	89, 97, 116, 117, 119, 134, 143, 148
Spinostropheus + *Elaphrosaurus*	86, 88, 92(0)		78(1)
Ceratosaurus + Abelisauroidea	85(2), 114, 125, 129, 133(1), 135, 137(2)	41, 79	5, 7, 14, 22, 42, 46, 51, 56, 62, 63, 66, 71, 78(2), 84, 126, 127, 131, 134, 142
Abelisauroidea	2, 4, 26, 33, 50, 58, 59, 87, 95, 100, 103, 109, 120, 139, 149	3, 11, 12, 21, 30, 34, 35, 36, 37, 38, 39, 54, 57(2), 91, 122	6(1), 41, 79, 106, 150
Noasauridae	8, 9, 68, 70, 80, 85(1), 92(0), 94(0), 133(2), 146, 147		
Abelisauridae	1, 16, 20, 31, 69	10, 24, 25, 29, 64, 65, 83, 101, 104, 115	3, 11, 21, 30, 34, 35
Ekrixinatosaurus +higher abelisaurids	17, 23		24, 29, 37, 65, 83, 122
Higher abelisaurids	6(2), 18, 99	19	10, 25, 36, 38, 39, 54, 64, 91, 104, 115
Carnotaurus + *Ilokelesia*	27		101
Majungasaurus + *Rajasaurus* + *Indosaurus*	15, 49, 130		19, 57(2)

Support under accelerated (ACCTRAN) and delayed (DELTRAN) transformations are given, along with unambiguous character support.

disagreement about their exact positions. Specifically, *Ceratosaurus* was considered to be the most primitive ceratosaur by Holtz (1994*a*; Fig. 1), Sereno (1999; Fig. 2) and Rauhut (2000, 2003; Fig. 3), whereas most other studies that included both forms (Holtz 2000; Carrano *et al.* 2002; Wilson *et al.* 2003; Sereno *et al.* 2004; Carrano & Sampson 2004; Tykoski & Rowe 2004; Figs 2, 3) have favoured *Elaphrosaurus* with that distinction. Here we support the latter conclusion. Although we acknowledge that the higher amount of missing data (58%, including 100% of cranial data) allows *Elaphrosaurus* to assume a more primitive position on this basis alone, it does indeed show a more primitive axial morphology than *Ceratosaurus*. In our analysis, six additional steps are required to place *Ceratosaurus* as the most primitive member of Ceratosauria. Unfortunately, we were unable to assess the statistical significance of these added steps; implementing the Kishino–Hasegawa test in PAUP* 4.0b10 exhausted available memory (> 1 GB) before reaching a computational solution.

Deltadromeus

The poorly known theropod *Deltadromeus agilis* was first described as a primitive coelurosaur (Sereno *et al.* 1996) and later placed in the Ornithomimosauria (Rauhut 2000, 2003). However, more recently it has been placed within Ceratosauria (Carrano & Sampson 2002, 2004; Sereno *et al.* 2004), a conclusion supported by features in the limbs and girdles. Although *Deltadromeus* was resolved as a noasaurid based on two synapomorphies (Wilson *et al.* 2003; Sereno *et al.* 2004), our analysis does not support this conclusion. Instead, *Deltadromeus* is a primitive ceratosaur with possible affinit-

ies to *Elaphrosaurus* and *Spinostropheus*; 12 extra steps are needed to place it within Noasauridae.

Noasauridae

Noasauridae has been included in several cladistic analyses of Ceratosauria, but until recently this meant only the type taxon *Noasaurus* (Novas 1991, 1992*a*; Sampson *et al.* 1998). Coria & Salgado (2000) linked *Ligabueino* with *Noasaurus* in the Noasauridae (Fig. 2), supported by two synapomorphies (low, anteroposteriorly elongated cervical neural arches and a square dorsal process on the proximal articular surface of the distal pedal phalanges). We consider the first character to be a by-product of elongate cervical vertebrae; it is subsumed into our character 86 and is also present in *Elaphrosaurus* and its relatives but cannot be confirmed in *Ligabueino*. We were unable to observe the second character in *Noasaurus* and, furthermore, suggest that the only phalanx preserved in *Ligabueino* pertains to the manus (Carrano *et al.* 2004).

Subsequent analyses (Sampson *et al.* 2001; Carrano *et al.* 2002) suggested that *Masiakasaurus* and *Laevisuchus* were also noasaurids, but could not demonstrate this with convincing character evidence. Although additional studies later confirmed the noasaurid relationships of *Masiakasaurus* (Wilson *et al.* 2003; Sereno *et al.* 2004; Fig. 3), *Laevisuchus* remained in abelisauroid limbo. *Velocisaurus* has also been linked to *Masiakasaurus* and *Noasaurus*, but not through formal phylogenetic analysis (Agnolín *et al.* 2003; Carrano *et al.* 2004). The present study confirms that all three taxa are noasaurids, for the first time along with *Genusaurus*. Character support is weak, but this reflects the large amount of missing data; it is worth noting that there is little conflicting

character information that would suggest alternative placements for these taxa.

Abelisauridae

There has been little controversy surrounding the constituency of Abelisauridae. However, *Ilokelesia* has been considered either a basal abelisaurian (Coria & Salgado 2000; Fig. 2), an indeterminate abelisauroid (Carrano *et al.* 2002; Fig. 3), or a stem-abelisaurid (Wilson *et al.* 2003; Sereno *et al.* 2004; Tykoski & Rowe 2004; Fig. 3). It is placed firmly within Abelisauridae in our analysis. The primitive positions of this form in previous analyses were largely due to its incomplete nature.

Other abelisaurids have been confidently placed and only their interrelationships have been disputed. Most studies reporting any ingroup resolution have favoured a sister-taxon relationship between *Carnotaurus* and *Majungasaurus* (*Majungatholus*), with *Abelisaurus* as the outgroup to this pair (Sereno 1999; Sampson *et al.* 2001, Wilson *et al.* 2003; Sereno *et al.* 2004; Tykoski & Rowe 2004; Figs 2, 3). Numerous characters have been used to support such an arrangement, engendering a perception that *Abelisaurus* is more 'primitive' than the ornate and 'derived' carnotaurines.

However, our results contradict this topology, instead supporting a clade comprising *Majungasaurus* and the Indian abelisaurids. *Carnotaurus* is grouped with *Ilokelesia* in a separate clade (Carnotaurinae *sensu* Sereno 1999). Furthermore, *Abelisaurus* does not occupy a basal position with respect to other 'higher' abelisaurids. These results (see also Carrano & Sampson 2004) rely on the inclusion of several new characters (altering the balance of character support) and more abelisaurid taxa (increasing the chance for homoplasy of any one character) to overturn support for the more 'traditional' results. Previous studies have also achieved results consistent with the amount of character data preserved: the incomplete *Abelisaurus* was the outgroup to a clade composed of the nearly completely known *Majungasaurus* and *Carnotaurus*. Although our hypothesis is relatively weakly supported, it is based on positive character combinations. A caveat must be noted here: *Carnotaurus* and *Majungasaurus* share a number of derived features (e.g. character 105, bifurcate cervical ribs) that might feasibly unite these taxa in a clade within Abelisauridae; however, the elements in question are not preserved on other abelisaurids and thus their distribution within the group cannot be assessed at this time.

Fragmentary taxa

Despite our attempts at comprehensiveness, we did not include every potential ceratosaur taxon in this analysis. Several presumed ceratosaurs were excluded because they were deemed too fragmentary, or provided no unique character combinations (Wilkinson 1995). The phylogenetic determinations discussed below are made to the most specific level possible. Although many of these forms cannot be identified beyond a rather general level (i.e. Abelisauridae), they nevertheless add important temporal and geographical data to the story of ceratosaur evolution (Figs 5, 6). Other reports of 'neoceratosaurs' and related forms could not be confirmed and are not discussed here further. A comprehensive listing is presented in Table 2.

Betasuchus bredai (Seeley, 1883) Huene, 1932

This small theropod is known from a single proximal femur from the Maastricht Tuff in the Netherlands. It is strikingly primitive for a Late Cretaceous theropod, exhibiting an anteromedially orientated head that is slightly ventrally directed in anterior view. The lesser trochanter is projected proximally but does not reach the level of the femoral head. There is no evidence for a trochanteric shelf, but instead the femur exhibits a rounded bulge for insertion of M. iliofemoralis. These conditions characterise ceratosaurs but are more derived than the condition in coelophysoids and other primitive forms. Supposed resemblances to the femur of *Dryptosaurus aquilunguis* (ANSP 9995; Carpenter *et al.* 1997) are superficial theropod features; *Betasuchus* is far too primitive to be a coelurosaur, but instead represents the latest surviving European ceratosaur.

Coeluroides largus Huene & Matley, 1933

Coeluroides is one of several fragmentary theropods from the Maastrichtian Lameta Formation of Bara Simla, India, all of which were recently restudied by Novas *et al.* (2004); we offer only brief comments here. *Coeluroides* is known from four dorsal vertebrae and a single caudal, which are from an animal similar in size to *Indosaurus* or *Indosuchus*. They resemble comparable elements from *Majungasaurus* and *Carnotaurus*, but do not preserve much morphology that would permit a specific assignment. The base of the neural spine on GSI K27/562 is relatively long anteroposteriorly, the transverse processes are roughly triangular in dorsal view and the anterior interspinous fossa is wide and deep. Based on their large size and the flattened centrum proportions of the caudal vertebra (GSI K27/574), we tentatively identify *Coeluroides* as an abelisaurid.

Compsosuchus solus Huene & Matley, 1933

Other representatives from the Lameta fauna can be similarly broadly placed, largely in agreement with recent observations (Novas & Bandyopadhyay 1999; Novas *et al.* 2004). The type and only specimen of *Compsosuchus* is a fused axis, odontoid and intercentrum. The specimen is of moderate size, larger than *Masiakasaurus* and *Noasaurus*. The axial centrum bears a single large pleurocoel, the intercentrum is slightly upturned and the ventral surface lacks a keel. The specimen appears to pertain to an abelisauroid, perhaps a noasaurid due to its small size.

Dryptosauroides grandis Huene & Matley, 1933

One cervical and six dorsal vertebrae, along with four dorsal ribs, were described as the type of *Dryptosauroides grandis*. These resemble the same elements in abelisaurids, although most are incomplete. The dorsals are primarily from the posterior portion of the trunk, as they lack both pleurocoels and parapophyses on the centrum.

Genyodectes serus Woodward, 1901

Genyodectes was one of the first South American dinosaur genera to be described (Woodward 1901). Its provenance has long been questioned, but recent work (Rauhut 2004) indicates that it derives from the Aptian–Albian Cerro Barcino Formation of Chubut, Argentina. This incomplete specimen preserves the anterior portion of a snout, including both premaxillae and the anterior parts of both maxillae
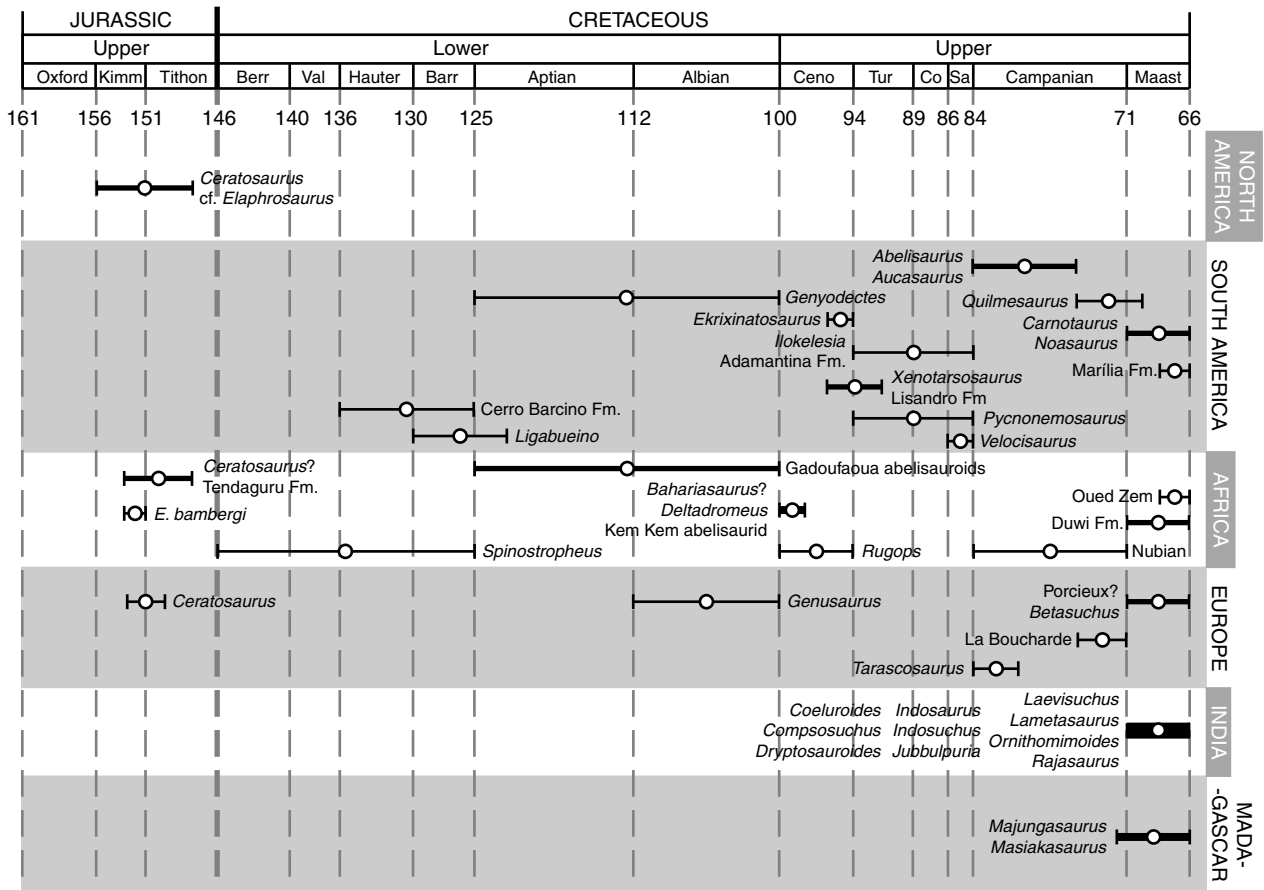
Figure 5 Temporal and geographical distribution of Ceratosauria, arranged stratigraphically and by continent. Most taxa are known from single samples, so the 'error bars' reflect uncertainty in age, not true range durations. The line thickness reflects the number of named (and, where indicated, unnamed) taxa. No ingroup relationships are implied by the arrangement of taxa. Timescale from Gradstein *et al.* (2004). Abbreviations: **Barr**, Barremian; **Berr**, Berriasian; **Ceno**, Cenomanian; **Co**, Coniacian; **Fm.**, Formation; **Hauter**, Hauterivian; **Kimm**, Kimmeridgian; **Maast**, Maastrichtian; **Oxford**, Oxfordian; **Sa**, Santonian; **Tithon**, Tithonian; **Tur**, Turonian; **Val**, Valanginian.
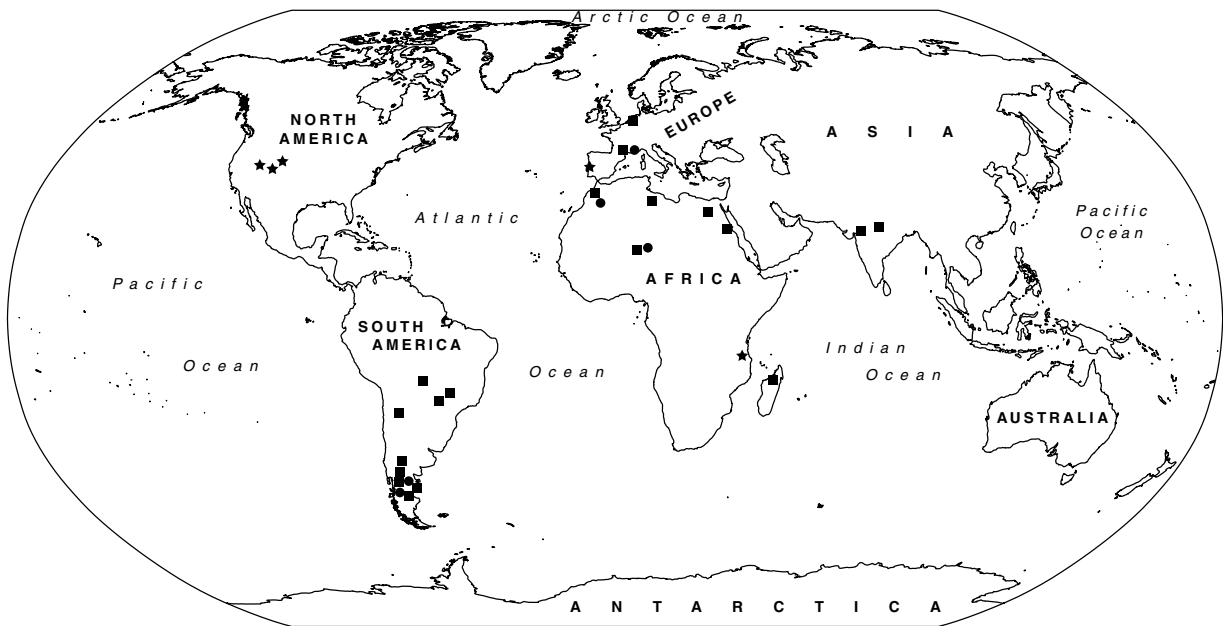
Figure 6 Geographical distribution of Ceratosauria. Robinson projection of modern continental arrangement, showing Late Jurassic (stars), Early Cretaceous (circles) and Late Cretaceous (squares) ceratosaur localities.

Table 2 Fragmentary ceratosaurs.

Original taxonomic assignment	Hypodigm	Horizon and age	Localities	Current taxonomic assignment
A. Formally named ceratosaur taxa				
Betasuchus bredai Seeley, 1883 (Huene, 1932)	BMNH 32997	Maastricht Formation; Maastrichtian, Late Cretaceous	Near Maastricht, Limburg, Netherlands	Ceratosauria
Ceratosaurus (?) *roechlingi* Janensch, 1925	HMN MB.R.1926, 1934, 1935, 1938, 2160, 2166; possibly HMN 37, 68, 69	Middle and Upper Saurian Beds, Tendaguru Formation; late Kimmeridgian–late Tithonian, Late Jurassic	Quarries St and Mw, Tendaguru Hill, Mtwara, Tanzania	Ceratosauria (Ceratosauridae?)
Coeluroides largus Huene & Matley, 1933	GSI IM K27/562, 574, 587, 595, 695	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Compsosuchus solus Huene & Matley, 1933	GSI IM K27/578	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauroidea (Noasauridae?)
Dryptosauroides grandis Huene & Matley, 1933	GSI IM K20/334, 609, 615, 623–625, K27/549, 555, 601, 602, 626	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Genyodectes serus Woodward, 1901	MLP 26–39	Cerro Castaño Member, Cerro Barcino Formation; Aptian-Albian, Early Cretaceous	Cañadon Grande, Chubut Province, Argentina	Ceratosauria (Ceratosauridae?)
Indosuchus raptorius Huene & Matley, 1933	GSI IM K20/350, K27/685	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Jubbulpuria tenuis Huene & Matley, 1933	GSI IM K20/612, K27/614	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauroidea (Noasauridae?)
Lametasaurus indicus Matley, 1924	GSI IM uncatalogued (lost?)	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Ligabueino andesi Bonaparte, 1996	MACN-N 42	lower part of La Amarga Formation; Barremian-early Aptian, Early Cretaceous	La Amarga, 70 km south of Zapala, Neuquén, Argentina	Abelisauroidea
Ornithomimoides? *barasimlensis* Huene & Matley, 1933	GSI IM K27/531, 541, 604, 682	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauroidea (Noasauridae?)
Ornithomimoides mobilis Huene & Matley, 1933	GSI IM K20/610, 614B, K27/586, 597, 599, 600	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Pycnonemosaurus nevesi Kellner & Campos, 2002	DGM 859-R	Adamantina Formation; Turonian–Santonian, Late Cretaceous	Fazenda Roncador, near Paulo Creek, Mato Grosso, Brazil	Abelisauridae
Quilmesaurus curriei Coria, 2001	MPCA PV-100	Allen Formation; late Campanian–early Maastrichtian, Late Cretaceous	Salitral Ojo de Agua, Río Negro Province, Argentina	Abelisauridae
Tarascosaurus salluvicus Le Loeuff & Buffetaut, 1991	FSL 330201–3	Unnamed Fuvélien beds; early Campanian, Late Cretaceous	Lambeau de Beausset, Provence, Bouches-du-Rhône, France	Abelisauroidea
Xenotarsosaurus bonapartei Martínez *et al.*, 1986	UNPSJB-PV 184, PV 612	Bajo Barreal Formation; late Cenomanian–early Turonian, Late Cretaceous	Estancia 'Ocho Hermanos', Chubut Province, Argentina	Abelisauridae
B. Referred ceratosaur taxa				
Ceratosaurus sp./ cf. *Ceratosaurus* sp./*Ceratosaurus dentisulcatus* (Mateus & Antunes 2000; Antunes & Mateus 2003; Mateus *et al.* 2006)	Teeth, femur, tibia	Camadas de Alcobaça Formation, Praia de Amoreira–Porto Novo Member; late Kimmeridgian-early Tithonian, Late Jurassic	Rodela do Valmitão, Louriñha and Guimarota, Leiria, Portugal	*Ceratosaurus* sp.

Table 2 Continued.

Original taxonomic assignment	Hypodigm	Horizon and age	Localities	Current taxonomic assignment
Elaphrosaurus sp. (Galton 1982; Carpenter 1998)	DMNH 36284, USNM 8415	Brushy Basin Member, Morrison Formation; Kimmeridgian–Tithonian, Late Jurassic	March-Felch and Small's Quarries, Garden Park, Colorado, USA	Ceratosauria
Majungasaurus crenatissimus (Mathur & Srivastava 1987)	Tooth	Lameta Formation; Maastrichtian, Late Cretaceous	Temple Hill, 1 km west of Rahioli, Gujarat, India	Abelisauridae
cf. *Majungasaurus* sp. (Russell 1996)	NMC 41861	Kem Kem Beds; early Cenomanian, Late Cretaceous	Kem Kem region, Tafilalt, Morocco	Abelisauridae
Megalosaurus crenatissimus (Gemmellaro 1921; Smith & Lamanna 2006)	MGUP MEGA002	Duwi Formation; Maastrichtian, Late Cretaceous	Sciarauna-el-Ghibli, Kosseir-el-Khadim and Gebel Duwi, Egypt	Abelisauridae
C. Unnamed Ceratosaur Taxa				
'Coelurosaurier B' (Janensch 1925; Rauhut 2005)	HMN MB.R.1750	Middle Saurian Bed, Tendaguru Formation; late Kimmeridgian, Late Jurassic	Quarry St, Tendaguru Hill, Mtwara, Tanzania	Abelisauroidea
'Coelurosaurier C' (Janensch 1925; Rauhut 2005)	HMN MB.R.1751	Upper Transitional Sands, Tendaguru Formation; late Kimmeridgian–Tithonian, Late Jurassic	Quarry H, Tendaguru Hill, Mtwara, Tanzania	Abelisauroidea
Abelisauria indet. (Rauhut *et al.* 2003)	MPEF PV 1699, 1699/1, 1699/2	La Paloma Member, Cerro Barcino Formation; Hauterivian–Barremian, Early Cretaceous	El Jujeño, Cerro Chivo, Chubut Province, Argentina	Abelisauria or Abelisauroidea
Abelisauridae indet. (Smith & Dalla Vecchia 2006)	MPCM 13693	Chicla Formation; Aptian–Albian, Early Cretaceous	Nalut, Jabal Nafusah, Libya	Abelisauroidea indet.
Abelisauridae indet. (Russell 1996)	NMC 41859, 41861, 41869, 50807, 50808, 50382	Kem Kem Beds; early Cenomanian, Late Cretaceous	Kem Kem region, Tafilalt, Morocco	Abelisauridae
Theropoda indet. (Russell 1996)	NMC 50807, 50808	Kem Kem Beds; early Cenomanian, Late Cretaceous	Kem Kem region, Tafilalt, Morocco	Abelisauridae
Theropoda indet. (Russell 1996)	NMC 41869, 50382	Kem Kem Beds; early Cenomanian, Late Cretaceous	Kem Kem region, Tafilalt, Morocco	Abelisauroidea
Abelisauridae indet. (Sereno *et al.* 2004; Mahler 2005)	UCPC 10	Kem Kem Beds; early Cenomanian, Late Cretaceous	Erfoud region, Tafilalt, Morocco	Abelisauridae or Carcharodonto-sauridae
Abelisauroidea indet. (Novas *et al.* 2005)	MPCM 13573	Kem Kem Beds; early Cenomanian, Late Cretaceous	Erfoud region, Tafilalt, Morocco	Abelisauroidea
Abelisauria indet./Abelisauridae indet. (Lamanna *et al.* 2002)	UNPSJB-PV 247	Lower member, Bajo Barreal Formation; late Cenomanian–early Turonian, Late Cretaceous	Estancia 'Ocho Hermanos', Sierra de San Bernardo, Chubut Province, Argentina	Abelisauridae
Abelisauridae indet. (Martínez *et al.* 2004)	MPM-99	Bajo Barreal Formation; Turonian, Late Cretaceous	Cañadón de los Corrales, Estancia María Femina, Santa Cruz Province, Argentina	Abelisauridae
Abelisauria? indet. (Canudo *et al.* 2004)	ENDEMAS PV 3, 4, 5	Lisandro Formation; late Cenomanian–early Turonian, Late Cretaceous	Anfiteatro, Río Negro Province, Argentina	Abelisauria or Abelisauroidea
Abelisauria indet./Abelisauroidea indet. (Coria *et al.* 2006)	MCF-PVPH 237	Lisandro Formation; Turonian, Late Cretaceous	Cerro Bayo Mesa, 30 km south of Plaza Huincul, Neuquén Province, Argentina	Abelisauridae
Abelisauridae indet. (Candeiro *et al.* 2004, 2006)	MMR/UFU-PV 0006, URC 44-R, UFRJ-DG 371-Rd, 374-Rd, 378-Rd	Adamantina Formation; Turonian–Santonian, Late Cretaceous	Santo Anastácio, Alfredo Marcondes & Florida Paulista, São Paolo and Sierra de Boa Vista & Alfredo Marcondes, Minas Gerais, Brazil	Abelisauridae

Table 2 Continued.

Original taxonomic assignment	Hypodigm	Horizon and age	Localities	Current taxonomic assignment
Theropoda gen. et sp. indet. (Stromer & Weiler 1930)	BSP uncatalogued (lost?)	Nubian Sandstone; Campanian, Late Cretaceous	Mahamîd, Egypt	Abelisauroidea
Neoceratosauria indet. (Allain & Pereda Suberbiola 2003)	Tibia	Unnamed Begudien beds; late Campanian, Late Cretaceous	La Boucharde, 2 km southeast of Trets, Bouches-du-Rhône, France	Abelisauridae
Abelisauridae indet. (Buffetaut *et al.* 1988)	Maxilla, Méchin Collection	Unnamed upper Rognacien beds; Maastrichtian, Late Cretaceous	Near Porcieux, Provence, Bouches-du-Rhône, France	Abelisauridae or Carcharodonto-sauridae
Allosauridae indet., Carnosauria indet. (Huene & Matley 1933)	GSI IM K20/336, 396, 619, K27/527, 529, 530, 532, 533, 536, 538–540, 543, 546, 548, 550, 551, 554, 557, 558, 560, 563, 564, 567–570, 572, 573, 575–577, 579–581, 583–585, 590, 591, 593, 594, 596, 598, 603, 617, 618, 620, 627, 628, 633, 636, 651, 652, 654, 656, 658–660, 664, 667, 671, 684, 686, 687, 688, 690, 691, 693, 698, 700, 705, 708–710	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauridae
Coelurosauria indet. (Huene & Matley 1933)	GSI IM K20/337, K27/524, 534, 579, 625, 629–632, 640, 641, 643, 644, 646–650, 655, 665, 667, 694, 697, 681	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Noasauridae
Allosauridae indet., Carnosauria indet., Coelurosauria indet. (Huene & Matley 1933)	GSI K20/362, 626, K27/524, 526, 542, 561, 566, 574, 587, 589, 599, 605–612, 616, 621, 632, 661, 666, 672–674, 676, 677, 680, 712	'Carnosaur Bed', Lameta Formation; Maastrichtian, Late Cretaceous	Bara Simla Hill, Jabalpur, Madhya Pradesh, India	Abelisauroidea
cf. Abelisauridae indet. (Buffetaut *et al.* 2005)	WDC-CCPM-005	Unnamed phosphatic beds; late Maastrichtian, Late Cretaceous	near Oued Zem, Khouribga, Morocco	Abelisauridae
Abelisauridae indet. (Candeiro *et al.* 2006)	CPP 002, 020–021, 121, 123, 129b,c, 131–132, 134–136, 144, 150, 154, 158, 161/1, 198, 205–207, 211, 242, 372, 375/2, 446, 451/1, 452/1, 463, 476–478	Sierra de Galga Member, Marília Formation; late Maastrichtian, Late Cretaceous	Peirópolis, Minas Gerais, Brazil	Abelisauridae
D. Unconfirmed ceratosaur occurrences				
cf. Abelisauridae indet. (Maganuco *et al.* 2005)	MSNM V5778–V5784, V5788, V5790, V5794, V5798, V5799, V5806, V5821, V5957, V5962	Isalo IIIb Subunit; Bathonian, Middle Jurassic	Ambondromamy to Port Bergé region, Mahajanga Basin, Madagascar	
Ceratosauria indet. (Martin *et al.* 2006)	Not indicated	Qigu Formation; Oxfordian, Late Jurassic	Luihuanggou gorge, 40 km southwest of Urumqi, Xinjiang, China	

Table 2 Continued.

Original taxonomic assignment	Hypodigm	Horizon and age	Localities	Current taxonomic assignment
Ceratosauria? indet. (Canudo & Ruiz-Omeñaca 2003)	Caudal vertebra	Vega Formation; late Oxfordian–early Kimmeridgian, Late Jurassic	Playa de la Vega, Ribadesella, Asturias, Spain	
Ceratosauria indet. (Bonaparte 1996)	Metatarsal	Rayoso Formation; Aptian, Early Cretaceous	Quilil Malal, Neuquén Province, Argentina	
Abelisauridae indet. and Noasauridae indet. (Sereno *et al.* 2004)	UCPC uncatalogued	Elrhaz Formation (GAD 5); Aptian–Albian, Early Cretaceous	Gadoufaoua, Niger	
Abelisauridae? indet./Neoceratosauria indet. (Astibia *et al.* 1990; Pereda-Suberbiola *et al.* 2000)	Not indicated	S2U1 and S1U3 beds, Vitoria Formation; late Campanian, Late Cretaceous	Laño Quarry, Burgos, Castilla y Léon, Spain	
Abelisauridae indet. (Buffetaut *et al.* 1999)	Teeth	'Grès à Reptiles'; late Campanian–early Maastrichtian, Late Cretaceous	Massecaps, near Cruzy, Hérault, Aude, France	
Neoceratosauria indet. (Canudo *et al.* 1999)	MPZ 98/67, 2004/3, 4, 5, 8	Conques Formation; late Maastrichtian, Late Cretaceous	Blasi 1, 2 and 3, near Arén, Huesca, Aragón, Spain	
Vitakridrinda sulaimani (Malkani 2006)	MSM-59-19, 60-19, 61-19, 62-19, 53-2, 54-2, 55-2, 56-1, 57-3, 58-15, 155-19	Vitakri Member, Pab Formation; Maastrichtian, Late Cretaceous	Vitakri, Mari Bohri and Alam Kali Kakor, Sulaiman Range, Balochistan, Pakistan	

The taxa listed in this table were not included in the phylogenetic analysis due to their incompleteness, but are identified here to the most inclusive group possible. The occurrences are divided into four groups: (A) taxa that have been given formal names, (B) specimens that have been referred to existing ceratosaurian taxa, (C) unnamed ceratosaurs; and (D) unconfirmed reports of ceratosaurs. The latter may represent genuine ceratosaur occurrences, but we have not examined these specimens directly and cannot confirm these identifications based on the published reports.

Institutional Abbreviations:

CPP = Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis; **ENDEMAS PV** = El Ente para el Desarrollo de la Margen Sur, Cipoletti; **MMR/UFU** = Museu de Minerais e Rochas 'Heinz Ebert', Rio Claro; **MSM** = Museum of the Geological survey of Pakistan, Quetta; **MPZ** = Museo Paleontológico de la Universidad de Zaragoza, Zaragoza; **MSNM** = Museo Civico di Storia Naturale di Milano, Milano. Additional institutional abbreviations are listed in the text under 'Operational Taxonomic Units'.

and dentaries. Recently reprepared and redescribed (Rauhut 2004), MLP 26-39 displays one ceratosaur synapomorphy, the presence of numerous small neurovascular foramina on the dentigerous elements. Rauhut (2004) proposed that *Genyodectes* is the sister taxon to *Ceratosaurus*, based on the presence of extraordinarily long maxillary tooth crowns. Here we assign *Genyodectes* to Ceratosauria, making it the oldest representative of this clade in South America.

Indosuchus raptorius Huene & Matley, 1933

Indosuchus is the third large theropod taxon named from the original Lameta 'Carnosaur Bed' at Bara Simla. Based on two partial braincases, now lost, *Indosuchus* was characterised by a comparatively thin skull roof, apparently quite unlike that of *Indosaurus* (Huene & Matley 1933). The loss of these specimens is particularly frustrating because they provided some of the only supposed evidence for two distinct large theropods at Bara Simla.

Subsequently, Chatterjee (1978) described several skull elements (AMNH 1955, 1960, 1753) that had been recovered by Barnum Brown in 1922 along with two caudal vertebrae (AMNH 1957, 1958). He suggested that the gracile nature of the maxilla allowed its reference to the thin-skulled *Indosuchus*. However, this specimen was, in fact, recovered from the same locality as the original Bara Simla materials (Matley 1931) and, thus, there is no reason to suppose that these elements can be associated any more reliably than those described by Huene & Matley (1933). Furthermore, the original braincases of *Indosaurus* and *Indosuchus* were not well preserved, such that even their distinctiveness has been doubted (Novas *et al.* 2004).

A comparatively complete skeleton from a large abelisaurid was found more recently at Rahioli, in Gujarat, including new cranial materials (ISI R163; Chatterjee & Rudra 1996). Unfortunately, the skull and postcranial elements are of uncertain association and cannot bear directly on the *Indosuchus*/*Indosaurus* problem. The postcranium also represents a chimera of at least two theropod individuals and one sauropod (S.D.S., pers. obs.), complicating efforts to use it as a key for future identifications. The cranial materials have yet to be described. Without sustained effort to retrieve more complete theropod materials from the infratrappean beds of the Lameta Formation, this complex taxonomic problem is likely to remain unsolved.

Although described as an allosaurid (Huene & Matley 1933) and a tyrannosaurid (Walker 1964; Chatterjee 1978), *Indosuchus* is indeed an abelisaurid (Bonaparte & Novas 1985).

Jubbulpuria tenuis Huene & Matley, 1933
This small theropod is represented by two vertebrae from the Bara Simla collection, both described as dorsals (Huene & Matley 1933). GSI K27/614 appears to derive from a noasaurid, based on its small size and elongated amphicoelous centrum. GSI K20/612, however, resembles the middle caudal vertebrae of *Masiakasaurus*, which are similarly proportioned and retain both a neural spine and transverse process.

Lametasaurus indicus Matley, 1924
The first theropod named from the Lameta Formation was originally identified as a theropod (Matley 1921) and later as a stegosaur, due to its unusual morphology and association with a number of dermal scutes (Matley 1924). Finally Chakravarti (1934, 1935) correctly re-identified most of these materials as belonging to a theropod, an opinion supported and detailed by Walker (1964). The holotype materials were damaged and incomplete and are now lost. However, they apparently came from the same area in the quarry (Matley 1924) and so may represent associated parts of an individual, although this cannot now be ascertained; the presence of at least two individuals and hundreds of individual bones at the site (Matley 1921) argues against such as association. The morphology of the sacrum, ilium and tibia conform to those of Abelisauridae. The scutes are probably titanosaurian in origin, although it would be enlightening to compare them with the dermal ossifications of *Ceratosaurus*.

It is interesting to speculate that if *Indosaurus* and *Rajasaurus* are indeed closely related (or identical; see earlier discussions of these taxa), then the robust theropod limb materials from Bara Simla may pertain to *Indosaurus*. The resulting taxon might then be considered a junior synonym of *Lametasaurus*. Based on comparisons with other Late Cretaceous ecosystems, it is difficult to imagine the Lameta Formation including more than two co-existing abelisaurid taxa, particularly given the relatively small size of the Indian subcontinent, which was probably either isolated during the Maastrichtian or connected only to Madagascar (Scotese 2001; but see Briggs 2003). Indeed, given the fragmentary nature of the preserved materials, it is conceivable that the formation contained only a single abelisaurid, paralleling the situation in the Maastrichtian of Madagascar. Thus, we regard it as likely that *Coeluroides*, *Dryptosauroides*, *Indosuchus*, *Indosaurus*, *Lametasaurus*, *Ornithomimoides mobilis* (see below) and *Rajasaurus* represent only one or two distinct taxa within Abelisauridae.

Ligabueino andesi Bonaparte, 1996
Ligabueino was based on a very incomplete, tiny postcranial skeleton from the Barremian–early Aptian La Amarga Formation of Neuquén, Argentina (Bonaparte 1996; Leanza *et al.* 2004). The specimen is not well preserved, but the isolated cervical and dorsal neural arches are very similar to those of abelisauroids. Specifically, the neural spines are anteroposteriorly short, the cervical arch bears a lamina connecting the prezygapophysis and epipophysis and the dorsal arch

shows evidence of a connecting web between the parapophysis and diapophysis. Other, plesiomorphic, features are also apparent: the femoral head is anteromedially directed and the brevis fossa of the ilium is wide. The ilium also exhibits the more derived character of a pubic peduncle that is longer than the ischial peduncle. Two features resemble noasaurids: the fibular condyle of the femur is bulbous in distal view (similar to that of *Masiakasaurus*) and the dorsal vertebral centrum is anteroposteriorly long. *Ligabueino* is an abelisauroid and, possibly, the earliest known noasaurid, but it does not display any unambiguous synapomorphies of the latter clade.

Ornithomimoides mobilis Huene & Matley, 1933
The type of *O. mobilis* includes six middle and posterior dorsal vertebrae from the Late Cretaceous Bara Simla collection (Huene & Matley 1933). They are moderate-sized specimens, approximately the size of a subadult *Majungasaurus* and most are rather incomplete. GSI K20/614B and K20/610 both retain clear neurocentral sutures, suggesting that this animal reached larger adult sizes. The centra are amphicoelous, lack pleurocoels and are relatively long anteroposteriorly. *Ornithomimoides mobilis* is referred to Abelisauridae.

Ornithomimoides? barasimlensis Huene & Matley, 1933
Four dorsal vertebrae form the type of this taxon, also from Bara Simla hill (Huene & Matley 1933). These are markedly smaller than those of *O. mobilis*, but like them lack centrum pleurocoels and are relatively long antero-posteriorly. The broken centrum of GSI K27/541 reveals significant neural arch pneumaticity, although it could be either camerate or camellate in nature. The ventral surface of the centrum is rounded, a hypantrum is evident and the posterior spinal chonos is relatively large. We refer *O.? barasimlensis* to Noasauridae. If the Lameta Formation resembles the Maevarano Formation in paleoecological structure as well as taxonomic composition, then *Laevisuchus*, *Compsosuchus*, *O.? barasimlensis* and, perhaps, *Jubbulpuria* may all represent the remains of a single species of noasaurid.

Pycnonemosaurus nevesi Kellner & Campos, 2002
This theropod is based on a very fragmentary postcranial skeleton from the Turonian–Santonian Adamantina Formation of Brazil (Bertini 1996; Kellner & Campos 2002). Several elements exhibit abelisaurid features: the caudal vertebrae have distally expanded transverse processes and proportionally wide neural arch bases; the pubic boot delineates a distinctive dorsally placed anteroposterior channel and the tibia has a distally expanded cnemial crest. Unfortunately, the incomplete condition of the specimen makes it impossible to diagnose it more specifically than to Abelisauridae. Other abelisaurid materials from the Baurú Group (Bertini 1996; Bittencourt & Kellner 2002) may pertain to this or another similar taxon.

Quilmesaurus curriei Coria, 2001
Originally described as a 'very peculiar' theropod of uncertain relationships (Coria 2001), *Quilmesaurus* shows several features that reveal its abelisauroid affinities (Kellner & Campos 2002; Juárez Valieri *et al.* 2004). Among them, the distally expanded cnemial crest, hypertrophied flange along

the medial edge of the distal femoral shaft and profile of the proximal end of the tibia match these same features in *Carnotaurus*, *Aucasaurus*, *Majungasaurus*, *Masiakasaurus* and other abelisauroids. As noted elsewhere in this paper (and in Carrano *et al.* 2002), lack of fusion between the distal tibia and tarsals does not preclude membership in Ceratosauria. Indeed, the morphology of the distal end of the tibia is comparable to the condition in *Majungasaurus* (Carrano 2007). We consider *Quilmesaurus* to be an abelisauroid and probably an abelisaurid based on its large size.

Tarascosaurus salluvicus Le Loeuff & Buffetaut, 1991

This is an even more fragmentary taxon represented by two partial dorsal vertebrae and a proximal left femur from the Campanian of Provence, France. Like that of *Betasuchus*, the proximal femur of *Tarascosaurus* has a large lesser trochanter with a prominent foramen at its proximal end. Although the distal femur is missing, the femoral head appears to have been anteromedially directed. The dorsal vertebrae resemble those of abelisauroids in having highly pneumatised neural arches but comparatively poorly pneumatised centra. The anteroposteriorly short neural arch is very similar to that of *Majungasaurus* and the parapophysis is situated at the end of a distinct pedicle. This species is probably an abelisauroid.

Xenotarsosaurus bonapartei Martínez *et al.*, 1986

The unusual structure of the tarsus of *Xenotarsosaurus*, which includes extensive fusion and a rectangular astragalar ascending process, was used to differentiate it from other known theropods in the original description (Martínez *et al.* 1986) and later led to its inclusion in Ceratosauria (Rowe 1989*b*). The incompleteness of the only known specimen has made assignment difficult, with some workers questioning its phylogenetic status (Coria & Rodriguez 1993). However, several features support a position within Abelisauroidea, and probably Abelisauridae: (1) flat anterior and concave posterior faces of anterior dorsal vertebra, (2) anteromedially directed femoral head, (3) marked ridge along anteromedial edge of distal femur, (4) large cnemial crest, (5) distal tibia expanded mediolaterally to back fibula, (6) fibula with a large, posteriorly open medial fossa, (7) anteroventrally directed astragalar condyles with a horizontal vascular groove across the anterior surface and (8) tall, rectangular, laminar ascending process.

More recently, an abelisaurid maxilla (UNPSJB-PV 247; Lamanna *et al.* 2002) and a fragmentary abelisaurid postcranial skeleton (MPM-99; Martínez *et al.* 2004) were also discovered in the Bajo Barreal Formation. Neither specimen provides sufficient overlap to permit definitive referral to *Xenotarsosaurus*, but neither preserves information that would refute such an association. Lamanna *et al.* (2002) suggested that size differences might preclude such a referral for UNPSJB-PV 247, noting that the vertebral sutures are closed on UNPSJB-PV 184/PV 612, implying that it was from a smaller sized adult. Unfortunately, sutural closure is not necessarily an indicator of individual maximum size in dinosaurs, although it can identify the relative stage of skeletal maturity. Indeed, dinosaur species may have exhibited a wide range of sizes as adults, similar to pterosaurs (Unwin 2001), in which case the maximum size of any one specimen would be of little aid in determining the maximum size of the species. Thus it is possible that all these materials belong to a single abelisaurid taxon, although MPM-99 derives from slightly younger beds in the formation (M. C. Lamanna, pers. comm.).

South American, Cretaceous abelisauroids

Fragmentary remains of abelisauroids are known from elsewhere in South America, documenting the broad temporal and geographical distribution of the group on this continent. The Early Cretaceous Cerro Barcino Formation (Chubut Group) of Chubut, Argentina has yielded teeth referred to Abelisauria indet. (Rauhut *et al.* 2003). Coria *et al.* (2006) described the partial postcranial skeleton of a large abelisauroid (MCF-PVPH 237) from the Lisandro Formation of Neuquén, Argentina. Although incomplete, the size and morphology is congruent with Abelisauridae and it is here referred to that group. Teeth questionably assigned to Abelisauria indet. have been identified from outcrops of this formation in Río Negro as well (Canudo *et al.* 2004).

The Adamantina Formation of southern Brazil has produced other remains of abelisauroids in addition to the holotype of *Pycnonemosaurus nevesi* (see above). Among them, a premaxilla (URC 44-R) and numerous teeth have been referred to Abelisauridae (Candeiro *et al.* 2004, 2006). Abelisaurid teeth have also been reported from the Maastrichtian Marília Formation near Peirópolis (Santucci & Bertini 2006; Candeiro *et al.* 2006).

Tendaguru ceratosaurs

Janensch (1925) based the type of *Ceratosaurus* (?) *roechlingi* on the following elements: (1) a ventrally grooved middle caudal vertebra that retains its neural spine and one transverse process, (2) an anterior caudal, (3) the condylar part of a left quadrate, (4) a fused left astragalocalcaneum, (5) a second middle caudal and (6) a left fibula with a large, posteriorly facing medial fossa. Three other middle caudals from another quarry were also referred to this species. In addition, two tibiae (HMN 37 and 69) and a right femur (HMN 68) are very similar to these same elements in *Ceratosaurus* and Janensch suggested that they might belong to *C.* (?) *roechlingi*. None of these elements were found in association (and indeed, one was found at a separate stratigraphical level), but several may indeed derive from a single large bodied ceratosaur taxon in the Tendaguru. Although there are no apparent synapomorphies to support referral of this taxon to *Ceratosaurus*, the general morphology of the preserved elements does indicate an animal of similar phylogenetic status (i.e. a basal ceratosaur).

Recently Rauhut (2005) re-identified several smaller theropod specimens from Tendaguru as abelisauroids. These included two tibiae previously referred to as 'Coelurosaurier B' and 'Coelurosaurier C'. He noted similarities between these tibiae and those of small abelisauroids such as *Masiakasaurus*, particularly in possessing a subdivided astragalar facet on the anterior tibial surface. We concur with the identification of these specimens as small members of Abelisauroidea, the oldest known members of the clade, but we have not found sufficient data to assign them to the Noasauridae. Rauhut (2005) also identified the holotype of *Ozraptor subotaii* Long & Molnar, 1998 as belonging to a Middle Jurassic abelisauroid, but we consider this fragmentary distal tibia to be too incomplete for assignment.

European abelisauroids

Buffetaut *et al.* (1988) described a right maxilla from the Maastrichtian ('Rognacien') of southeastern France. These authors felt that the specimen had 'Gondwanan affinities', citing the reduced ventral antorbital fossa and lack of a maxillary fenestra. The maxilla does indeed resemble those of abelisauroids, although the poor preservation makes it difficult to determine whether its external surface was sculptured. However, it is also similar to carcharodontosaurids in these features and has the more strongly sloping ascending ramus characteristic of such taxa. Unfortunately, the medial side of the maxilla is still embedded in matrix, so salient features that might distinguish between these two groups (such as the presence of striations on the paradental plates, or a maxillary antrum that expands widely into the anterior ramus) cannot be observed. We agree with Novas (1992*a*) that this specimen cannot yet be confidently assigned to either clade, although its size is more in agreement with known European abelisauroid materials.

A large (approximately 40 cm long) tibia was discovered in the late Campanian beds at La Boucharde, Bouches-du-Rhône, France and assigned to Neoceratosauria (Allain & Pereda Suberbiola 2003). This tibia bears several abelisauroid synapomorphies, especially the presence of a large, pendant and expanded cnemial crest. Moreover, its large size and stocky proportions suggest that it belongs to Abelisauridae, although the material is insufficient for formal referral. Regardless, it is probably distinct from the materials assigned to *Tarascosaurus* and *Betasuchus* and, therefore, indicates the presence of multiple ceratosaur lineages in Europe through the end of the Cretaceous.

North African, medial Cretaceous abelisauroids

Russell (1996) described two right dentaries from the early Cenomanian Kem Kem red sandstones of the Tafilalt, Morocco as pertaining to abelisaurids. One (NMC 41861), referred to as cf. *Majungasaurus* sp., shows a marked mediolateral curvature along its length and bears at least nine rectangular alveoli. It may belong to an abelisaurid, but shows only more broadly distributed abelisaurid features and is therefore probably not referable to *Majungasaurus*. The second (NMC 41859), described as Abelisauridae gen. et sp. indet., preserves only four alveoli along with a dorsally placed lateral nutrient furrow and a narrow splenial groove. Russell (1996: 374) compared this specimen explicitly to *Majungasaurus*, *Carnotaurus* and the Lameta theropods.

Russell (1996) also described several indeterminate theropod specimens, some of which may pertain to abelisauroids. In particular, NMC 41869 (a proximal right femur assigned to 'bone "taxon" M') has a distally situated lesser trochanter and robust fourth trochanter that resemble the condition in abelisauroids and other primitive theropods. Similar features can be observed in a smaller femur, NMC 50382, which additionally has an anteromedially orientated femoral head. Two skull roof fragments (NMC 50807, 50808) display a sagittal crest between the supratemporal fenestrae and a sloping, striated contact for the nasals on the anterior frontals; both are characteristics of abelisaurids.

Additional Moroccan materials include a small, incomplete maxilla that could belong to either an abelisaurid (UCPC 10; Sereno *et al.* 2004; Mahler 2005) or a carcharodontosaurid. Although described as Abelisauridae indet.

based on the presence of rectangular alveoli (Mahler 2005), this character is homoplastic (it occurs within tetanurans as well) and the medial maxilla lacks the characteristic striations seen on the paradental plates of all other abelisaurid dentigerous bones. Finally, at least one abelisauroid pedal ungual has also been described from these deposits (Novas *et al.* 2005).

Taken in aggregate, these fragmentary materials appear sufficient to demonstrate the presence of abelisauroids, and probably abelisaurids, in the Moroccan Kem Kem. It is possible that some of these materials may pertain to the basal ceratosaur *Deltadromeus*, but this cannot yet be determined.

Furthermore, recent work in the Early Cretaceous deposits of Niger have produced several putative abelisauroid specimens in addition to *Rugops*. These include the partial skeleton of a noasaurid and the fragmentary remains of an abelisaurid. Both are from the Elrhaz Formation (GAD 5 beds) at Gadoufaoua, which have been assigned an Aptian–Albian age; their study is in progress (Sereno *et al.* 2004; Brusatte & Sereno 2006).

North African, Late Cretaceous abelisauroids

Several fragmentary discoveries point to the presence of abelisauroids in the North African Late Cretaceous, roughly contemporaneous with those in other areas of Gondwana. Unfortunately, all are currently too poorly known to place into a well resolved phylogeny.

Among these remains, a small proximal tibia from the Campanian Nubian Sandstone of Mahamîd, Egypt (Stromer & Weiler 1930: pl. III, 47a,b) bears a prominent, upturned cnemial crest resembling those of abelisauroids (Carrano *et al.* 2002). Stromer & Weiler (1930: 8–9) compared it to *Ceratosaurus* and *Elaphrosaurus*, noting these and other features that are now known to typify abelisauroids. We assign this specimen to Abelisauroidea.

Several isolated teeth also appear to derive from abelisauroids, perhaps even abelisaurids. One tooth (MGUP MEGA002) derives from the Maastrichtian Duwi Formation of Egypt, originally discovered by Italian workers before 1912 (Gemmellaro 1921) and referred to Abelisauridae (Smith & Lamanna 2006). A second tooth (WDC-CCPM-005) from the Maastrichtian phosphatic deposits of northwestern Morocco may also belong to an abelisaurid (Buffetaut *et al.* 2005). These teeth probably represent some of the latest known members of the clade in Africa.

Evolutionary Implications

Morphology

Some of the most dramatic morphological specialisations of ceratosaurs occur in the skull. Although primitive ceratosaurs (e.g. *Ceratosaurus*) retain the long, low skull of other theropods, several proportional changes are evident within Abelisauridae. All abelisaurids exhibit some increase in skull height, even when the overall length does not appear to be diminished (either relative to postcranial elements, or as evidenced by the proportions of the mandible). Certain abelisaurids also shorten the skull, resulting in a blunt, tall profile that is extremely unusual among theropods. *Aucasaurus* and *Carnotaurus* represent the extremes of both conditions (Fig. 7). The noasaurid skull remains poorly understood, but new materials of *Masiakasaurus* indicate that it was
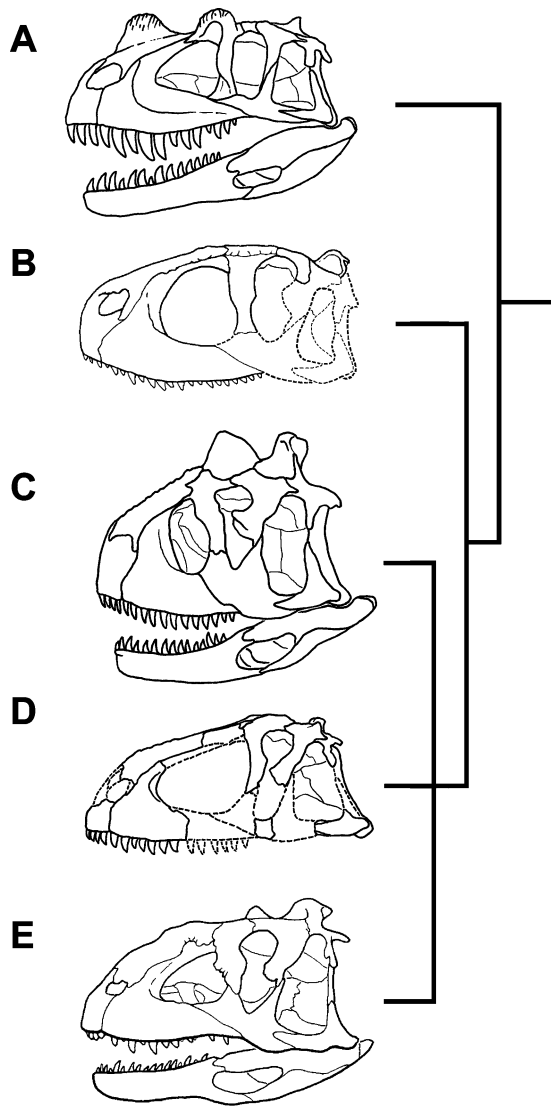
Figure 7 Skull evolution in Ceratosauria. (**A**) *Ceratosaurus nasicornis*, based on USNM 4735, MWC 1.1 and UMNH VP 5728 (modified from Sampson & Wittmer 2007). (**B**) *Rugops primus*, based on MNN IGU1 (modified from Sereno *et al.* 2004). (**C**) *Carnotaurus sastrei*, based on MACN-CH 894 (modified from Bonaparte *et al.* 1990). (**D**) *Abelisaurus comahensis*, based on MPCA 11098 (modified from Bonaparte & Novas 1985). (**E**) *Majungasaurus crenatissimus*, based on FMNH PR 2100 (modified from Sampson & Wittmer 2007).

the notable regularity of these patterns across taxa implies that they record consistent (i.e. homologous) arrangements of related neurovascular and other soft tissue structures throughout Abelisauridae.

Skull roof thickening and elaboration (often into horns or knobs) has long been cited as an abelisaurid characteristic. These features are quite variable in degree within Abelisauridae, with some taxa (*Abelisaurus*, *Indosuchus*, *Rugops*) lacking much ornamentation or thickening. When present, the specific morphology of cranial elaborations appear to be species-specific. Indeed, the observed variability is so great that few phylogenetically meaningful patterns can be observed, strengthening the argument for low level taxonomic relevance. This suggestion is bolstered by the observation that cranial ornamentation probably underwent significant ontogenetic modifications as well (Sampson *et al.* 1998).

In spite of these significant and easily recognisable changes, ceratosaurs display few fundamental alterations to the basic theropod skull plan. Some fusion has occurred in the skull roof, but there has been no obvious element loss (although the two patterns can be hard to distinguish; cf. *Abelisaurus*) and most sutural contacts are consistent with their arrangement in other basal members of Theropoda. The most significant changes appear to be in the nature of the contacts themselves, with a tendency toward the development of more intricate articulations, occasionally including peg-and-socket joints.

The lower jaw is highly specialised in Noasauridae (as observed in *Masiakasaurus*), but only anteriorly and there appear to be few modifications specific to Abelisauridae. Both groups display an enlarged external mandibular fenestra associated with rearrangement of the positions of the contact between the dentary and postdentary elements and hypertrophy of the dentary–surangular socket. This implies at least some functional change at the intramandibular joint at the base of Abelisauroidea, perhaps associated with increased overall mobility or a change towards greater mediolateral flexibility instead of flexion–extension sliding. Certain of these changes are already evident in *Ceratosaurus*.

Forelimb shortening is also characteristic of Abelisauridae, although the fragmentary available materials of more primitive ceratosaurs suggest that this trend may have begun earlier. The forelimb elements of *Elaphrosaurus* and *Ceratosaurus*, while short relative to those of the hindlimb, are not significantly proportionally shorter than those of basal tetanurans such as *Torvosaurus* and *Acrocanthosaurus*. Certainly the distal forelimb elements are highly shortened in Abelisauridae and most extremely so in *Carnotaurus*, but even in these forms most phalanges (including unguals) seem to have been retained. There is little evidence for digit or even element loss in the abelisaurid forelimb.

Other, more functionally important, changes also occurred at the forelimb articulations. The humeral head is nearly globular, rather than elongate and subrectangular as in most other theropods. The elbow joint is flattened on the humerus and strongly concave on the radius and ulna, while the distal ends of these bones are markedly convex. The carpus is absent or unknown, but was probably quite mobile (at least one endpoint of wrist movement can be seen in the articulated manus of *Aucasaurus*, which appears to be hyperextended). Increased shoulder-joint mobility is perhaps also reflected in the expanded muscle origins on the scapulocoracoid of most ceratosaurs.

proportionally long and low, unlike the condition in abelisaurids (Carrano *et al.* 2004).

Pronounced texturing characterises numerous abelisaurid dermatocranial elements, but fewer in noasaurids and none in *Ceratosaurus*. The similarities in this texturing on the maxillae of *Rugops* and the Argentine specimen UNPSJB-PV 247 led Sereno *et al.* (2004) to suggest that these two taxa were particularly closely related. This 'clade' was later extended to include a maxilla from Morocco (Mahler 2005). However, the patterns on these maxillae are extremely similar to those of *Majungasaurus*, *Carnotaurus*, several Indian specimens and *Abelisaurus* (Sampson & Witmer 2007) and probably represent an abelisaurid feature. We cannot confirm any specific similarities between the African forms and UNPSJB-PV 247 that are not found in other taxa. Instead,

Body size evolution cannot be detailed within clades, but the presence of a derived small-bodied group (Noasauridae) and larger basal taxa indicates at least one instance of size reduction during ceratosaur evolution. Primitive forms seem to have been moderate to large in size (approaching or slightly exceeding 1 metric ton), with the largest abelisaurid descendants approaching twice this size. No ceratosaurs appear to have been true 'giants' (in excess of 5 metric tons).

Biogeography

Initially, abelisauroids were noted for their near dominance as Gondwanan terrestrial predators during the Cretaceous and were one of several groups whose presence distinguished so-called Gondwanan faunas from those of Laurasia (e.g. Bonaparte & Kielan-Jaworowska 1987). Abelisauroids still appear to have been the dominant predators (both ecologically and in terms of diversity) across most Gondwanan landmasses in the post-Cenomanian Cretaceous and they certainly represent the most common theropod fossils in South America, India and Madagascar during this time. They are less common but were present in both Europe and Africa as well, but remain unknown from Cretaceous North America. No ceratosaurs have been described from Asia, Antarctica and (probably) Australia.

Given the global range of Late Jurassic ceratosaurs, the group was probably only later restricted to Gondwana, implying a regional extinction of the group in at least North America and Asia. European ceratosaurs may have been relictual, or re-entered from Africa via dispersal. By the Late Cretaceous, the faunal abundances of ceratosaurs varied widely and were generally contrapuntal to those of coelurosaurs. Ceratosaurs were absent from coelurosaur dominated faunas (North America, Asia), rare in faunas where basal tetanurans were common (Africa) and dominated faunas where coelurosaurs were rare or restricted to smaller body sizes (South America, India, Madagascar) (Carrano & Sampson 2002).

The biogeographical history of ceratosaurians has received renewed attention recently, primarily associated with efforts to clarify the patterns of vicariance and dispersal in vertebrate evolution that may have accompanied the breakup of Gondwana (e.g. Krause et al. 1998; Sampson et al. 1998). These studies have used finer scale phylogenetic hypotheses of mammals, sauropods and theropods to support close connections between South America, India and Madagascar (but not Africa) well into the Late Cretaceous.

More recent works have criticised this hypothesis, citing the presence of abelisaurids that predate Gondwanan fragmentation (Lamanna et al. 2002; Sereno et al. 2004), the potential for distinct small and large-bodied abelisauroid lineages since the Bajocian (Rauhut 2005), or occurrences of abelisaurids in the early Late Cretaceous of Africa (Wilson et al. 2003; Sereno et al. 2004; Mahler 2005). Indeed, abelisauroids seem to have persisted in Africa through to the Campanian and Maastrichtian (Stromer & Weiler 1930; Carrano et al. 2002; Buffetaut et al. 2005; Smith & Lamanna 2006).

Unfortunately, many of these studies fail to employ any formal analyses, relying instead on assertions of both relationship and biogeographical history. Crucially, the specific interrelationships of abelisaurids (and noasaurids) are frequently ignored. It is insufficient merely to note the presence of a taxon from a particular clade in some place at some time. Even given the presence of such a taxon, its contribution to any biogeographical scenario is negligible if it cannot be placed into a specific phylogenetic context. Furthermore, even given a robust cladogram, subsequent biogeographical analyses need to be performed in order to reject from among the several proffered scenarios. It is not enough to qualitatively link taxa (such as Rugops, UNPSJB-PV 247 and the Moroccan maxilla) and use this relationship as evidence against other biogeographical scenarios (Sereno et al. 2004; Mahler 2005), especially when those inferred relationships do not bear directly on the problem because the taxa are supposed to be basal members of their clade.

Attempts to clarify the biogeographical history of ceratosaurs (or any group) must employ: (1) a quantitatively supported phylogenetic hypothesis, (2) constraints provided by geophysical evidence of continental fragmentation (3) one or more specific, testable biogeographical hypotheses and (4) an analytic means of testing the latter.

Although our analyses are imperfect, they do provide certain predictions and implications. Within Abelisauridae, South America appears to have hosted the primary radiation and the Indian and Madagascan abelisaurids are sister taxa, nested within this larger group. The simplest explanation for this pattern is that the Indo–Madagascan forms dispersed from South America into these two regions, although this could have occurred prior to tectonic separation (direct terrestrial dispersal) or after (vicariance). Nevertheless, the majority of known abelisaurids are South American; only a phylogenetic hypothesis that places all South American forms into a single clade would *not* imply dispersal from South America. Therefore we must consider that current sampling patterns may be biasing these data toward such a result.

If (accepting the report of Sereno et al. 2004) the undescribed African noasaurid is inserted into an unresolved polytomy with other noasaurids, the predominance of African forms at the base of Ceratosauria leads to the inference that this continent was home to the primary initial radiation of the clade. The presence of Rugops in Africa raises the possibility of an African origin for Abelisauridae as well. However, the African component of this radiation is composed entirely of basal members of these clades, with no African taxa nested among more derived abelisaurids (noasaurids are too poorly resolved). Thus the current presence of basal abelisauroids (Rauhut 2005), an indeterminate noasaurid (Sereno et al. 2004) and basal abelisaurids (Sereno et al. 2004; Mahler 2005) in Africa have no impact on existing biogeographical scenarios.

The minimum divergence times implied by our phylogeny suggest that noasaurid and abelisaurid dispersals to Indo–Madagascar could have occurred after the separation of Africa from South America and other Gondwanan continents (Fig. 8). Unfortunately, the fossil record of both groups is still quite poor, especially prior to the Campanian outside of South America (Fig. 9). It is currently impossible to determine whether abelisauroids even existed in India or Madagascar prior to the Campanian, so we cannot identify dispersal or vicariance as their process of origin. If they were absent prior to this interval, vicariance would be the favoured process. But if these minimum divergence estimates are highly inaccurate (as they may well be), then most or all of these clades could have originated far earlier than the fossil record shows. Dispersal might then be more likely.
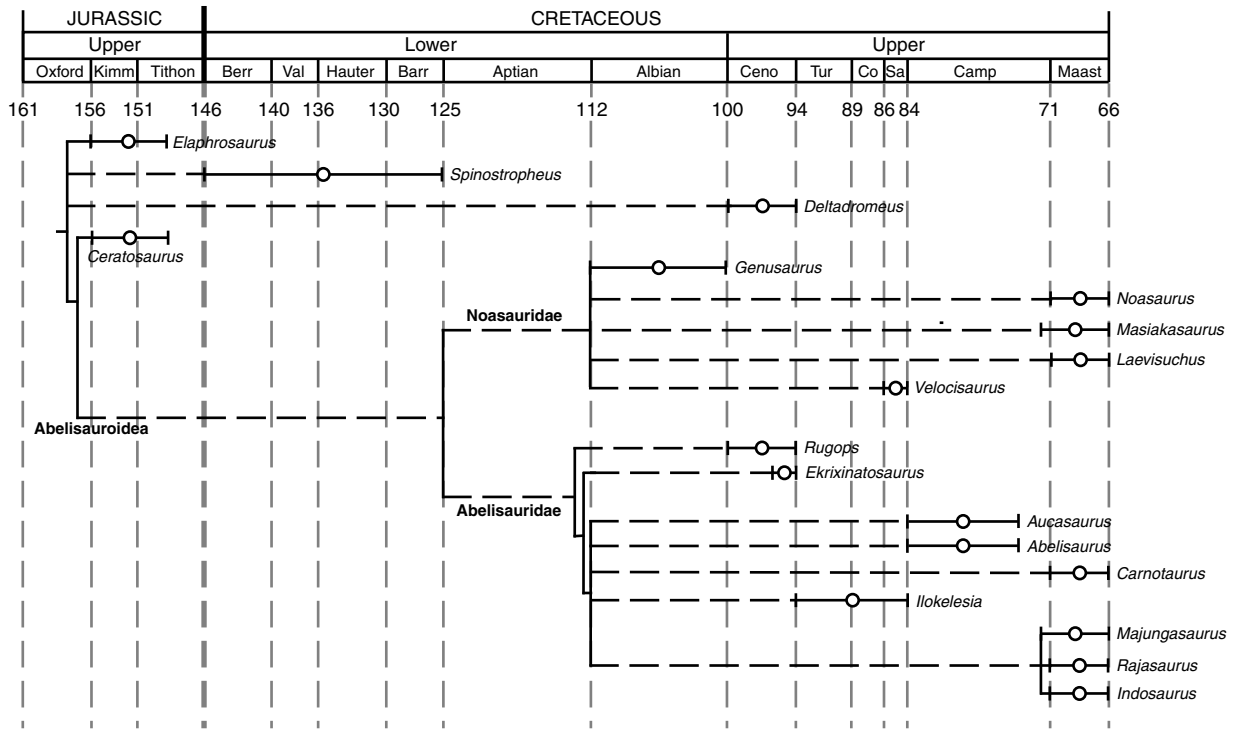
Figure 8 Stratigraphically calibrated phylogeny of Ceratosauria, based on present results (strict consensus). Minimum estimated divergence times are shown, based only on the taxa included in the phylogenetic analysis. Timescale from Gradstein *et al.* (2004). Abbreviations as listed in legend to Fig. 5.

Associated with the process of 'arrival' is an ongoing debate centred on the timing and sequence of the Gondwanan breakup. This debate centres on whether Africa was an early departure from the Gondwanan landmass (and whether Indo–Madagascar remained connected to Antarctica; Krause *et al.* 1998; Sampson *et al.* 1998), or instead maintained lingering connections into the Late Cretaceous (Wilson *et al.* 2003; Sereno *et al.* 2004). Apparent patterns of dinosaur dispersal and vicariance can be used to support either of these proposals or, alternatively, can be supported by either proposal. Without a more detailed record of contemporaneous terrestrial faunas on most of these continents, we remain unable to reject any
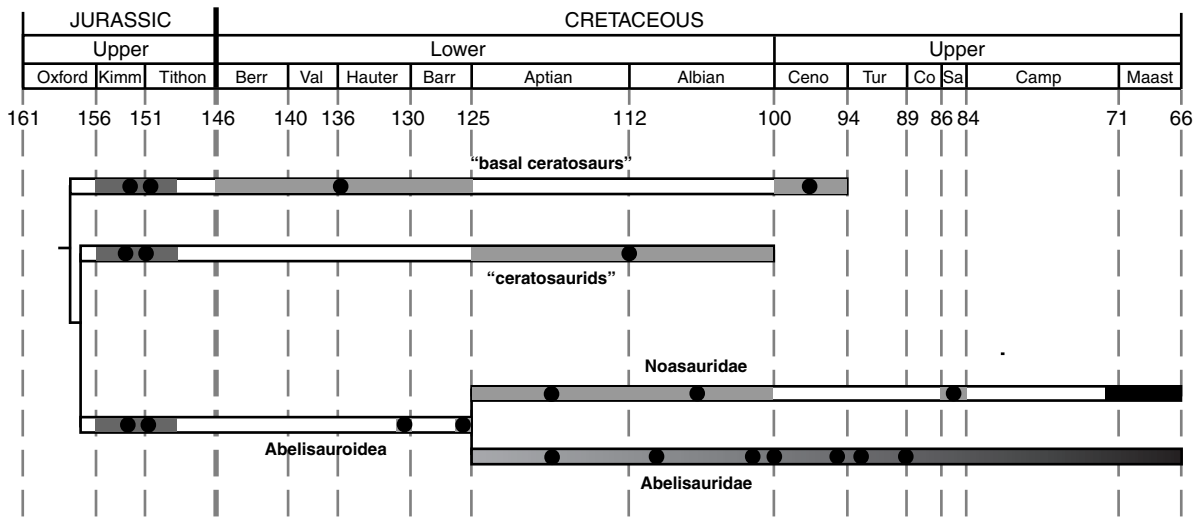
Figure 9 Stratigraphically calibrated phylogeny of Ceratosauria, combining present results and incomplete taxa. Minimum estimated divergence times are based on the earliest known occurrence of a member of each clade, even if that particular specimen was not included in the phylogenetic analysis. Black circles indicate individual samples and black bars indicate particularly dense temporal sampling. The grey bars represent 'error bars' for poorly dated taxa, while white bars represent unsampled intervals. Timescale from Gradstein *et al.* (2004). Abbreviations as listed in legend to Fig. 5.

of these possibilities. Relative likelihoods of dispersal and vicariance have been suggested but not explored empirically for dinosaurs, but such testing would be welcome given the complicated nature of these processes in other groups (e.g. Zink *et al.* 2000).

Stratigraphical fit

The phylogenetic hypothesis presented here shows significant congruence with the known stratigraphic record of ceratosaurs, with a Stratigraphic Consistency Index (SCI) of 0.667 (Huelsenbeck 1994). A Spearman rank correlation of age rank and clade rank is highly significant (rho = 0.84, $p < 0.0001$: Fig. 10). The Relative Completeness Index (RCI; Hitchin & Benton 1997) is difficult to calculate, because missing lineages are overestimated when only phylogenetically resolved taxa are assessed. But even when stem abelisauroids and stem abelisaurids are taken into account, the RCI is very low, 63.63%, indicating that the amount of missing record exceeds that preserved. This is perhaps overly low, influenced by the presence of the Albian *Genusaurus* amongst an unresolved clade of otherwise Late Cretaceous forms.

Nevertheless, although the ceratosaur record is very incomplete and includes several lengthy missing lineages, there are comparatively few instances of related clades exhibiting an inverted stratigraphical relationship (only *Rugops*, which appears slightly after the more derived *Ilokelesia*). *Deltadromeus* is a late surviving member of the most primitive ceratosaur clade and its 55 My missing lineage is the longest within Ceratosauria. *Genyodectes* may also reside at the end of a long (at least 35 My) missing lineage (Rauhut 2004).

The most obvious gaps in the ceratosaur fossil record occur in the Early Cretaceous (Fig. 9), where the fossiliferous horizons of North America, England, Antarctica, Asia and Australia have thus far yielded no definitive remains from this group. The significant African and South American deposits of this age have produced abundant remains of other theropods but few abelisauroids, suggesting that the latter were present but not yet dominant in these regions. How-

ever, enough fragmentary remains have been discovered to demonstrate that both Noasauridae and Abelisauridae were present at least by the Aptian. The origins of Abelisauroidea must, therefore, predate this stage and may extend to the Kimmeridgian (Rauhut 2005) or earlier. The stem abelisauroid lineage includes only a few incomplete forms, scattered along a 20–21 My interval of ceratosaur evolution (Fig. 9).

The origins of Ceratosauria are also poorly documented because no ceratosaur remains are known from deposits prior to the Late Jurassic. Late Jurassic forms include taxa from at least three lineages (e.g. *Ceratosaurus*, *Elaphrosaurus* and the small Tendaguru forms), demonstrating that some diversification had already occurred. The presence of coelurosaurs (e.g. *Proceratosaurus*) in the Middle Jurassic, along with the oldest confirmed tetanuran (*Cryolophosaurus*) in the Early Jurassic, implies a considerable missing lineage between the origin of Ceratosauria and its first appearance in the fossil record. Specifically, based on current understanding of ceratosaur relationships to other theropods (Carrano *et al.* 2002; Rauhut 2003; Wilson *et al.* 2003), Ceratosauria must have diverged no later than the Early Jurassic (based on the ?Pliensbachian age of *Cryolophosaurus*), resulting in a missing lineage of at least 35 My.

Persistent problems

Despite extensive taxon sampling, examination of original specimens and inclusion of many additional taxa, these analyses achieved a limited amount of resolution within Ceratosauria. Several factors seem to have contributed to this result.

Certainly much of the poor phylogenetic resolution is due to the nature of this analysis. Our goal was to sample both taxa and morphologies very thoroughly. As a result, we included characters that could only be scored for a few taxa and taxa for which only a few characters could be scored. Analyses that seek to test for patterns of congruence inherently include more homoplasy than those seeking only to illustrate particular topologies (see discussion in Rauhut 2003 for a more detailed commentary on this topic) and, consequently, cannot hope to produce the same degree of resolution.

A complementary problem involves the current nature of the ceratosaur fossil record. Certainly this group is not particularly well sampled through time, with especially large gaps evident in the Early Cretaceous and no taxa known from prior to the Late Jurassic. To further complicate matters, those taxa that are known are often highly incomplete. Although it might be possible to score many characters for any single taxon, very few can be scored across multiple taxa. Furthermore, because there are few skeletal elements that can be compared among many ceratosaurs, it is difficult even to identify characters that might discriminate between different ingroup clades. This problem is especially apparent within Abelisauridae, where several variable characters (e.g. 15, 19, 25, 28, 40) imply contradictory sister taxon relationships for individual taxa.

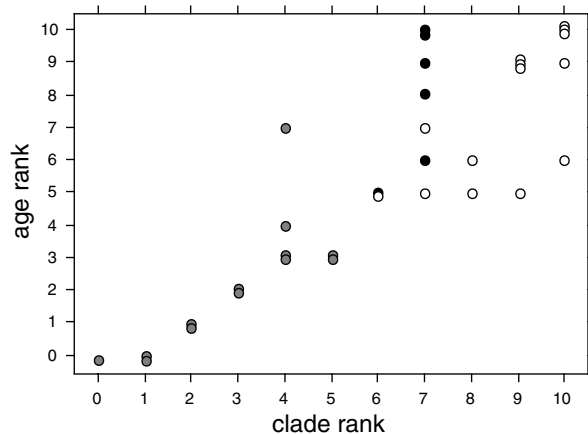**Figure 10** Age rank–clade rank correlations for Ceratosauria, based on present results. Note that the phylogeny was not reduced to a comb prior to calculation of the Spearman-Rank correlation. Grey circles, non-ceratosaurs and basal ceratosaurs; open circles, abelisaurids; filled circles, noasaurids.

CONCLUSIONS

New discoveries and ongoing studies emphasise that Ceratosauria is a diverse group of theropods, more derived than

coelophysoids, that originated early in dinosaur history and enjoyed a global distribution. Unfortunately, the fragmentary nature of many ceratosaur taxa has led to poorly resolved phylogenies, or phylogenies that focus only on well-known forms. The result has been a comparatively poor understanding of the evolutionary relationships of ceratosaur taxa, with a concomitant loss in our ability to decipher the temporal, morphological and biogeographical components of their history.

Here we provide the most thorough phylogenetic analysis of ceratosaur relationships to date, utilising 18 ingroup taxa and 151 characters. Our results indicate that *Elaphrosaurus*, *Deltadromeus* and *Spinostropheus* are the most primitive ceratosaurs, followed by *Ceratosaurus* and Abelisauroidea. The latter is composed of two diverse clades, Noasauridae and Abelisauridae. Although many noasaurids are poorly known, we resolve five taxa as members of this clade: *Genusaurus*, *Laevisuchus*, *Masiakasaurus*, *Noasaurus* and *Velocisaurus*. The better known Abelisauridae includes the basal forms *Rugops* and *Ekrixinatosaurus* along with numerous more derived forms. Interestingly, we do not find strong support for a close relationships between *Carnotaurus* and *Majungasaurus*; instead, the latter taxon is grouped with two Indian forms to the exclusion of any South American taxa.

In addition to these 18 taxa, we can identify many other fragmentary ceratosaurs from numerous sites ranging in age from Late Jurassic through Late Cretaceous. Although we could not include these in our formal analysis, their presence significantly enhances our understanding of the temporal and geographical history of Ceratosauria. The sister-taxon relationship between Ceratosauria and Tetanurae indicates an Early Jurassic divergence at the latest, so the fossil record remains poor through the Late Jurassic. Abelisauroids seem to have diverged by this time, suggesting that its component clades (Noasauridae and Abelisauridae) may have histories that extend deep into the Cretaceous (or even the Jurassic). Even so, high ceratosaur diversities have still only been recovered from Late Cretaceous formations of Gondwana.

Morphologically, basal ceratosaurs retain many primitive theropod features and share other derived features with tetanurans. Some skull, pectoral and forelimb modifications are already present in *Elaphrosaurus* and *Ceratosaurus*, but only abelisaurids exhibited the most derived conditions in these anatomical regions. The abelisaurid forelimb, in particular, probably retained significant mobility in spite of being shortened and may have developed novel functionalities. The noasaurid skull was apparently little modified aside from the unusual anterior jaws and dentition. The pattern of ceratosaur evolution indicates an origin at moderately large body sizes, with larger sizes achieved in some basal forms (*Deltadromeus* and *Ceratosaurus*) as well as certain abelisaurids (e.g. *Carnotaurus*). In contrast, noasaurids are one of the few dinosaur groups to exhibit a marked size decrease.

Finally, the biogeographical history of Ceratosauria remains nearly impossible to decipher with confidence thanks to poor phylogenetic resolution within both Abelisauridae and Noasauridae. The basal (or unresolved) positions of all known African forms prevent these taxa from refuting the theory that South America, Madagascar and India shared a common biogeographical history into the Late Cretaceous. However, the significantly poorer fossil record of Late Cretaceous Africa (as well as Antarctica and Australia) underscores the low confidence we should have in any particular biogeographical scenario. Significantly better resolution will only come with additional, and more complete, discoveries.

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APPENDIX 1. LIST OF CHARACTERS

The list of characters used in the present analyses has been grouped by major anatomical region. Characters are described briefly and the first time they were reported is given in bold, with subsequent uses to date in roman type. The references are listed by number; for reference details see Supplementary Data Table 1, available online at: Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477201907002246. Original character number and/or associated groupings follow each reference in parentheses (including asterisks and other original notations). Note that not all previous references describe or utilise the character in the same manner; they are grouped here to indicate similar general content and/or intent.

Skull

1. External surface of maxilla and nasal: smooth (0), sculptured (1). The facial dermatoskeletal elements are generally smooth or lightly textured in theropods, with neurovascular foramina but few (or faint) vessel traces. In abelisaurids (and carcharodontosaurids), the maxilla and nasal bear conspicuous sculpturing and texturing, resulting in a topography that often reveals traces of vessel pathways across one or more elements. These pathway patterns appear very similar in many of these taxa (Sereno *et al.* 2004) and are probably homologous across a wider group, reflecting similar distributions of suprajacent soft-tissues. The extensive sculpturing of these skull bones in abelisaurs may, therefore, represent ossification of the connective tissues underlying and surrounding the neurovascular soft tissues.

13 (Abelisauridae); 14 (Abelisauridae); 15 (Abelisauridae, Carcharodontosauridae); 32 (Abelisauridae, Carcharodontosauridae); 35 (11); 36*b* (19); 41 (6); 42 (Abelisauridae); 43 (1); 44 (1); 45*a, b* (18); 47*a, b* (2, 14); 48 (1); 49(4)

2. External surface of postorbital, lacrimal and jugal: smooth (0), sculptured (1). Although most previous workers have combined this with the previous character, we have observed variation in whether most of the facial bones are sculptured, or only the maxilla and nasal. Specifically, noasaurids appear to possess only circumorbital sculpturing, although most of the skull is sculptured in all known abelisaurids.

32 (Abelisauridae, Carcharodontosauridae); 36*b* (19); 42 (Abelisauridae); 43 (1); 44 (1); 45*b* (18); 47*a, b* (2); 48 (1); 49 (4)

3. Maxillary process of premaxilla: well-developed (0), reduced to a short triangle (1). The maxillary process of the premaxilla extends posteromedially from the bone's medial surface at a point just posterodorsal to the symphysis. It usually projects slightly beyond the posterior extent of the premaxillary body to contact both the maxilla and palatine. Primitively (e.g. *Syntarsus*, *Allosaurus*, *Dilophosaurus*) it is

a large flange that can be twice as long as wide at its base. However, in abelisaurids (e.g. *Majungasaurus*, 'Indosuchus'; Sampson *et al.* 1996, 1998) it is reduced to a blunt triangle that is no longer than its basal width. The condition is unknown in noasaurids.

26; 32; 44 (4); 47*a*, *b*; 48 (10)

4. Subnarial foramen: enclosed (0), reduced/open dorsally (1). A marked subnarial foramen (located at the premaxillary–maxillary juncture) is a synapomorphy of Saurischia (Gauthier 1986) that is retained in most theropods. It probably represents an enlarged neurovascular foramen. Its reduction in abelisaurids (often appearing to be absent; Coria & Salgado 2000) appears to be in agreement with the general reduction in size of most facial neurovascular foramina in these taxa. In fact the foramen has probably opened dorsally with the loss of the bony separation between it and the narial opening (Sampson & Witmer 2007). Although the premaxilla of *Noasaurus* is unknown (and that of *Masiakasaurus* is poorly preserved), the anterior border of the maxilla in these taxa shows no evidence of a subnarial foramen, which we interpret as the derived condition in these forms.

43 (11); 48 (11); 50

5. Height/length ratio of premaxilla ventral to external naris: 0.5–2.0 (0), > 2.0 (1). Primitively, theropod premaxillae are approximately as long as tall beneath the external naris. Certain theropod clades elongate (coelophysoids, spinosaurids) or abbreviate (abelisauroids; Bonaparte 1991a) the rostrum, resulting in premaxillary height : length ratios that lie in the tails of this distribution. In most ceratosaurs, the premaxilla is particularly shortened, usually twice as tall dorsoventrally as it is long anteroposteriorly.

6 (Ornitholestinae); 17 (3); 21 (13); 26 (Neoceratosauria); 28 (Abelisauridae); 30 (12); 36*c* (14); 38 (5); 39 (30); 43 (10); 44 (5); 45*a*, *b* (1); 47*a*, *b* (4); 48 (5)

6. Proportions/presence of the anterior ramus of the maxilla: absent (0), anteroposteriorly long (1), or tall and blunt (2). The anterior maxillary ramus extends anteriorly from its junction with the ascending ramus toward the premaxillary–maxillary suture; it represents the horizontal extension of the maxilla ventral to the external naris. Primitively (in *Herrerasaurus*, *Eoraptor* and ornithischians) the anterior ramus is effectively absent and the anterior maxillary border is continuous from the ascending ramus down to the alveolar border. In most neotheropods the ramus is long, extending far beneath the naris; it can be thin and finger-like (coelophysids) or quite deep dorsoventrally (most tetanurans; Sereno *et al.* 1994, 1998). In most ceratosaurs, the anterior ramus is tall but abbreviate, typically reaching only to the posterior edge of the naris.

17 (1); 22 (Torvosauridae); 27 (32); 33 (1); 36*c* (119); 38 (14); 44 (6); 45*a*, *b* (11); 48 (14)

7. Facet for nasal articulation on maxilla: shallow, anterolateral (0), socket, lateral (1). In most theropods, the nasal articulation on the maxilla is a groove or facet that faces anteriorly or anterolaterally. It is typically shallow and lacks a distinct rim. This contact is more robust in *Ceratosaurus* and abelisauroids, forming a distinct 'pit' at the ventralmost corner of the external naris. It also appears to be more laterally placed, although this may simply be a consequence of its overall enlargement.

**47*a*, *b* (15, 16); 50

8. Palatal process of maxilla: long and ridged (0), short and rectangular (1). The palatal process of the maxilla projects medially from the anteromedial portion of the bone. In noasaurids, this process is a very simple, rectangular flange that bears only faint marks of its contacts with other bones. This contrasts with the condition in abelisaurids, *Ceratosaurus* and most other theropods, where it is larger, more anteriorly and medially projecting and bears particularly distinct furrows for contact with the vomer, pterygoid and opposing maxilla.

44 (11); 48 (20)

9. Anteroventral border of antorbital fenestra: graded or stepped (0), demarcated by raised ridge (1). An 'alveolar ridge' characterises coelophysids (*Syntarsus, Coelophysis, Liliensternus*) as well as noasaurids (*Masiakasaurus, Noasaurus*) and *Eoraptor*, but is absent in *Dilophosaurus* and most other theropods. Most neotheropods have either a weakly graded or shelf-like ventral edge of the antorbital fossa. This feature is discussed in detail by Tykoski (2005).

8 (17); 10 (Coelophysidae); 17 (2); 29 (3); 36*b* (44); 39 (15); 40 (2); 44 (12); 45*a*, *b* (15); 47*a*, *b* (37); 48 (17)

10. Ventral portion of antorbital fossa: present on maxilla (0), absent (1). Most theropods exhibit a substantial antorbital fossa below the ventral margin of the antorbital fenestra on the lateral surface of the maxilla (Witmer 1997). In many abelisaurids (*Rugops, Carnotaurus, Majungasaurus*) and carcharodontosaurids, this fossa is reduced or essentially absent and, therefore, the internal and external antorbital fenestrae exist at the same dorsoventral level. This is also the condition in the primitive theropods *Eoraptor* and *Herrerasaurus*, but not in coelophysoids, *Ceratosaurus* or noasaurids.

17 (2); 33 (40); 39 (35); 44 (13); 45*a*, *b* (12); Lamanna *et al.* 2002 (11); 48 (18); 50

11. Anteroposterior length of maxillary–jugal contact relative to total maxilla length: less than 40% (0), more than 40% (1). In the majority of theropods, the jugal–maxillary suture typically represents less than 40% of the total anteroposterior length of the maxilla. In abelisaurids, however, shortening of the maxilla is associated with proportional lengthening of this suture, which reaches 40–50% of the total length of the maxilla.

32 (Abelisauridae); 36*b* (27); 42 (Abelisauridae); 43 (6); 44 (32); 49 (6)

12. Nasal–nasal contact in adults: separate (0), partly or fully fused (1). The nasals remain separate at maturity in most theropods, but are fused in *Baryonyx*, adult tyrannosaurids and some abelisaurids (*Abelisaurus* and *Majungasaurus*, but not *Carnotaurus*). *Rugops* displays a condition in which the nasals are fused anteriorly but remain separate posteriorly (Sereno *et al.* 2004). This could be viewed as a phylogenetically intermediate state, but given the small size of *Rugops* it might also be a sign of immaturity in the holotype individual.

36*b* (21); 35 (16); 38 (28); 41 (8); 43 (2); 44 (14); 47*a*, *b* (29); 48 (21)

13. Row of foramina on dorsal nasal surface: absent (0), present (1). In most theropods, the dorsal (external) surface of the nasal does not bear any pronounced foramina. However, in *Rugops*, this bone is perforated by a series of foramina that

run along a roughly anteroposterior line. Although described as an autapomorphy of this taxon (Sereno *et al.* 2004), similar foramina are also present in the abelisaurid *Carnotaurus*. There is no evidence for them in other abelisauroids for which nasals are known (i.e. *Abelisaurus, Majungasaurus*).

14. Posterior narial margin: fossa (0), laterally splayed hood (1). Typically, the posterior margin of the external naris is adjacent to a variably sized fossa, which presumably was related to the soft-tissue structures associated with the naris itself. This fossa may be faint or nearly absent, but is present primitively in theropods. Accordingly, the mediolateral width of the naris along its posterior edge is equal to or less than the width along its anterior edge. In ceratosaurs, the posterior narial border is flared laterally to form a 'hood' that extends out mediolaterally farther than the anterior edge of the naris.

45*a, b* (7); 44 (16); 48 (23)

15. Location of nasal–frontal contact relative to highest point of orbit: anterior (0), directly above (1). The nasal and frontal contact via an overlapping joint in theropods, which is located anterior to the highest point of the orbit. This condition is observed in several abelisaurids as well (e.g. *Carnotaurus, Indosuchus, Rugops*). In some abelisaurids, however, this contact is placed just above the highest point of the orbit, as is seen in *Abelisaurus, Indosaurus* and *Majungasaurus*.

16. Condition of prefrontal in adults: separate (0), partly or completely fused (1). Plesiomorphically, theropods have a separate prefrontal ossification well into maturity. The bone typically is exposed only briefly on the skull surface, but extends down ventrally along the medial side of the lacrimal. In most abelisaurids and carcharodontosaurids, the prefrontal is fused to the lacrimal. Often fusion is so complete that the two bones cannot be separated and, indeed, Sereno *et al.* (1996) claimed that there was no prefrontal in *Carcharodontosaurus*. (In fact, the prefrontal is of typical size and shape in that taxon and vestiges of its sutural contact are visible on specimen SGM Din-1.) Here again, *Rugops* shows partial fusion, which may be a phylogenetically intermediate condition or a sign of skeletal immaturity.

17. Frontal–parietal contact in adults: separate (0), fused (1). The frontals and parietals fuse at maturity in at least two theropod clades: abelisaurids (*Abelisaurus, Carnotaurus, Majungasaurus*) and carcharodontosaurids (*Carcharodontosaurus, Acrocanthosaurus*). In other theropods, a suture is retained between these two bones.

36*b* (23); 35 (38); 38 (39); 43 (4); 44 (18); 47*a, b* (46); 48 (31); 49 (5)

18. Skull roof dorsoventral thickness: thin, relatively flat (0), thickened (1). The theropod skull roof is primitively relatively thin, with thickenings ventrally that mark the attachments of the braincase elements, as seen in *Herrerasaurus* and *Ceratosaurus*. The external (dorsal) surface tends to be flat, showing little topography anterior to the parietal component of the nuchal crest. In some – but not all – abelisaurids, the frontoparietal region is thickened to more than twice its typical condition. Although further elaborations are also commonly present (such as the paired frontal 'horns' in *Carnotaurus*), they appear to be autapomorphic for each species.

28 (Abelisauridae); 43 (16); 47*a, b* (3); 48 (33)

19. Skull roof ornamentation: none (0), midline (1), lateral (2). When present, skull roof ornamentation is variable in position within Abelisauridae. The primary knob or horns may be positioned on the midline (as a single structure) or laterally (as paired structures).

43 (17); 48 (22, 33)

20. Arrangement of bones along dorsal margin of orbit: postorbital and lacrimal separated by frontal, which forms part of orbital rim (0), contact between postorbital and lacrimal that excludes frontal from orbital rim (1). The lacrimal and postorbital are usually separated by the frontal in basal theropods, resulting in a significant frontal component to the dorsal orbital rim. This frontal exposure is reduced in several theropods and is entirely absent in abelisaurids, tyrannosaurids and carcharodontosaurids. In abelisaurids, this is achieved by the lacrimal and postorbital meeting lateral (external) to the frontal, with the prefrontal probably attached to the medial lacrimal (and thus contacting the postorbital along an unknown extent).

4 (Tyrannosauridae); 15 (Neoceratosauria); 16 (Abelisauridae); 27 (48); 28 (Abelisauridae, Carcharodontosauridae); 31 (8); 32 (Abelisauridae, Carcharodontosauridae); 35 (27); 36*b* (222); 38 (50); 39 (36); 40 (90); 41 (11); 43 (3); 44 (24); 45*a, b* (39); 47*a, b* (24); 48 (27)

21. Knob-like dorsal projection of parietals and supraoccipital: absent (0), present (1). In nearly all theropods, the parietals extend up dorsally to meet the rising supraoccipital portion of the low nuchal crest. In abelisaurids, a taller projection is formed from the parietals and supraoccipital, capped by an expanded, knob-like structure.

21 (14); 30 (13); 32 (*Majungatholus + Carnotaurus*); 44 (20); 45*a, b* (42); 47*a, b* (49)

22. Development of median parietal skull table: flat, broad (0), narrow, with sagittal crest (1). The approximation of the upper temporal fenestrae produces a narrow frontoparietal bridge in most theropods. This is typically flat and about half as wide as each fenestra, producing a characteristic 'hourglass' shape. In contrast, a distinct sagittal crest is present in abelisaurids, due to the exceptional proximity of the upper temporal fenestrae. The highly compressed interfenestral region forms a bar or stalk rather than a gently curving saddle.

13 (Abelisauridae); 11; 19 (8); 25; 35 (34); 36*b* (24); 38 (43); 39 (43); 45*a, b* (43); 47*a, b* (47); 48 (34)

23. Size and elevation of nuchal wedge and parietal alae: moderate (0), tall and expanded (1). The nuchal crest is present but low in most theropods, with its height dictated by the development of the dorsal projection of the parietals. The crest is enlarged and expanded in abelisaurids, although not in other ceratosaurs. In these forms the nuchal crest may be twice as tall as in other basal theropods, associated with an increase in the height of the parietal projection. A large nuchal crest also occurs in tyrannosaurids, although it differs in several morphological details from that in abelisaurids.

5 (advanced neotheropods, Tyrannosauridae, advanced tyrannosauroids); 21 (63, 103); 30 (3*, 97); 35 (35, 40); 36*b* (25); 39 (31); 43 (5); 44 (21); 47*a, b* (56, 57); 48 (35)

24. Postorbital suborbital flange: absent (0), present (1). The theropod orbit varies in shape from rounded to dorsoventrally elongate (Chure 2000). This pattern is related to

increases in body size and the negative scaling properties of vertebrate eyes (Carrano 2001); thus many large theropods (e.g. tyrannosaurids) have dorsoventrally elongate, 'keyhole-shaped' orbits. Among non-coelurosaurs this characteristic shape is present in some basal allosauroids, carcharodontosaurids and abelisaurids. In the latter two groups it is formed by suborbital flanges that project from the anterior edge of the postorbital and the posterior edge of the lacrimal (see below).

3 (Carnosauria); 4 (Carnosauria, Tyrannosauridae); 13 (Abelisauridae); 14 (Abelisauridae); 16 (Abelisauridae); 21 (28); 27 (49); 28 (Abelisauridae, Carcharodontosauridae); 30 (27); 31 (9); 32 (Abelisauridae, Carcharodontosauridae); 35 (22); 38 (42, 53); 39 (41); 41 (12); 43 (14); 44 (23); 45*a*, *b* (40); 47*a*, *b* (40); 48 (37); 49 (8)

25. Anteroposterior length of postorbital relative to height: markedly less (0), equal to or greater (1). In most theropods, the anteroposterior length of the postorbital along the dorsal margin is markedly less than its dorsoventral height (i.e. less than the length of the ventral process). Despite the relatively short overall proportions of the skull, the postorbital in many abelisaurids (e.g. *Carnotaurus*, *Majungasaurus*) is as long or longer anteroposteriorly than it is tall.

32 (*Majungatholus + Carnotaurus*).

26. Orientation of posterior edge of postorbital: vertical (0), sloped anteroventrally (1). The postorbital is primitively vertically orientated in theropods, as approximated by the orientation of its posterior edge. Although the postorbital appears to be anteroventrally orientated in *Herrerasaurus*, the posterior edge still descends perpendicularly relative to the anterior and posterior rami. In abelisaurids, however, this edge slopes distinctly anteroventrally.

32 (Abelisauridae); 39 (40); 43 (18); 44 (25); 48 (40); 49 (7)

27. Morphology of anteroventral portion of ventral process of the postorbital: confluent with remainder of process (0), step and fossa present (1). The ventrolateral postorbital of *Ilokelesia* and *Carnotaurus* is 'stepped' medially, forming a broadly open fossa. This feature is absent in other basal theropods, including other abelisaurids. Although the ventrolateral flange is similarly shaped in *Abelisaurus* and *Majungasaurus*, no step or fossa is present.

32 (*Majungatholus + Carnotaurus*); 35 (14); 36*b* (28); 44 (26); 47*a*, *b* (41); 48 (39)

28. Morphology of dorsalmost postorbital–squamosal contact: smooth (0), knob (1). In most theropods, including most ceratosaurs, the dorsal skull roof is relatively flat and unornamented along the posterolateral margin, where the postorbital and squamosal articulate. Abelisaurids exhibit a series of rugosities along this edge, which in some taxa (*Carnotaurus*, *Abelisaurus*) are enlarged into a distinct, larger knob formed by portions of the postorbital and squamosal.

29. Appearance of postorbital–squamosal contact in lateral view: contact edges visible (0), edges covered by dermal expansions (1). Along the lateral skull surface, the postorbital and squamosal typically articulate via a tongue-in-groove joint in most theropods. This joint is visible along its entire lateral extent. In abelisaurids, however, the postorbital has developed significant dermal expansions that cover the

majority of this joint in lateral view (Sampson & Witmer 2007).

30. Anterior process of lacrimal: includes antorbital fossa and rim (0), antorbital fossa only (1). Whereas in most theropods the anterior process includes both a component of the dorsal antorbital fossa and a thicker portion forming its dorsal rim, in abelisaurids the process includes only the fossa. The lacrimal anterior process is thus reduced to a dorsoventrally narrow flange in abelisaurids. The apparent lack of contact between this process and the ascending ramus of the maxilla (e.g. Coria *et al.* 2002) is generally an artifact of poor preservation.

16 (Abelisauridae); 22 (Torvosauroidea); 27 (33); 32 (Abelisauridae); 38 (35); 39 (37); 43 (12); 44 (27); 47*a*, *b* (17); 48 (26)

31. Lacrimal fossa: exposed laterally (0), covered by dermal ossifications (1). Pneumatisation of the lacrimal is evident from the presence of a lacrimal fossa situated at the junction of the anterior and ventral rami, which in turn connects to the interior of the bone via a foramen. This foramen is present in nearly all theropods more derived than coelophysids, including *Ceratosaurus*, where it is expanded in conjunction with the development of a lacrimal 'horn'. In abelisaurids, however, the fossa is covered by a well-developed sheet of dermal bone, obscuring it from lateral view.

11; 17 (4); 16 (Abelisauridae); 18 (Allosauroidea); 21 (27); 22 (Tetanurae); 27 (2); 30 (26); 31 (10); 35 (19); 36*a* (113), 36*c* (1); 38 (33); 39 (38); 41 (13); 40 (67); 43 (13); 44 (30); 45*a*, *b* (32); 47*a*, *b* (22, 23); 48 (28); 50

32. Suborbital process of lacrimal: absent (0), present (1). As with the postorbital, the lacrimal of carcharodontosaurids (small in *Carcharodontosaurus*), abelisaurids and certain tyrannosaurids has a projection that extends posteriorly into the orbital fenestra. These two flanges delineate the orbital portion of this fenestra. This flange is present in all abelisaurids where this bone is known, although it is quite small in *Carnotaurus*.

3 (Carnosauria); 13 (Abelisauridae); 16 (Abelisauridae); 28 (Abelisauridae, Carcharodontosauridae); 32 (Abelisauridae); 36*a* (114); 38 (36); 41 (19); 44 (31); 48 (29)

33. Morphology of lacrimal along dorsal orbit rim: flat (0), raised brow or shelf (1). The lacrimal is relatively flat and lacks expansion above the dorsal part of the orbit in most basal theropods. In abelisaurids, this portion of the lacrimal is expanded to form a 'brow', which varies in form from a sloping eave (e.g. *Abelisaurus*, *Rugops*) to a more distinct shelf (e.g. *Carnotaurus*).

47*a*, *b* (25)

34. Morphology of jugal–maxilla contact: slot or groove (0), lateral shelf (1). The contact between the maxilla and jugal forms a shallow slot in most theropods, with the jugal sitting dorsally (and occasionally slightly medially) atop the maxilla. The lacrimal buttresses this articulation on the medial side. In abelisaurids, the dorsal maxillary articulation for the jugal forms a laterally facing shelf, against which the medial side of the ventral jugal abuts. The lacrimal–jugal contact is also specialised (see character 35).

32; 42 (Abelisauridae); 47*a*, *b* (18)

35. Morphology of jugal–lacrimal articulation: simple butt joint (0), overlapping and pocketed (1). A distinct, flat facet is present on the lacrimal for a butt-joint articulation with the jugal in most tetanurans. It is absent in more primitive theropods, in which the anterior ramus of the jugal is slender and dorsoventrally narrow. In abelisaurids, the jugal–lacrimal articulation is highly modified, with the expanded anterior jugal articulating within a distinct pocket on the lateral lacrimal.

22 (Tetanurae); 27 (3); 36*c* (2); 38 (34); 44 (34); 45*a*, *b* (23); 47*a*, *b* (26, 27)

36. Relative lengths of posterior jugal prongs: upper prong much shorter than lower (0), both prongs subequal in length (1). In most theropods, the upper of the two posterior jugal prongs is markedly shorter than the lower prong. In abelisaurids, however, the two are subequal in length.

18 (Allosauroidea); 31 (15); 38 (60); 41 (18); 48 (44)

37. Squamosal contribution to nuchal crest: absent or minimal (0), present and broad (1). A wide nuchal crest is present in most theropods, but primitively it is formed from the supraoccipital and parietal, with little or no contribution from the squamosal. Abelisaurids are unusual in having a dorsoventrally deep squamosal contribution to this crest.

32 (Abelisauridae); 35 (36); 39 (44); 44 (38)

38. Quadrate flange of squamosal: wraps around quadrate head (0), ends posterior to quadrate head (1). In nearly all basal theropods, including basal tetanurans and *Ceratosaurus*, the quadrate flange (postquadratic process) of the squamosal curves ventrally to wrap around the head of the quadrate. In abelisaurids, this flange extends more posteriorly to terminate posterior to the quadrate head. The condition cannot yet be observed in any noasaurid.

39. Dorsoventral proportions of quadratojugal prongs for jugal: narrow (0), deep (1). These two prongs tend to be dorsoventrally narrow in most theropods, roughly equal in dimension to the jugal prongs with which they articulate. In abelisaurids, the quadratojugal prongs are dorsoventrally deeper than the jugal prongs, exaggerating the depth of the entire jugal–quadratojugal articulation.

40. Overlap of quadratojugal onto quadrate posteriorly: absent (0), present (1). In most basal theropods, the ventralmost portion of the quadrate–quadratojugal articulation is unfused and the suture follows a ventrally-directed line toward the quadrate condyle. Most ceratosaurs share this morphology, but complete fusion (i.e. obliteration of the suture) at this joint is rare, present only in *Ceratosaurus*. However, a few abelisaurids (*Abelisaurus, Majungasaurus*) exhibit an additional quadratojugal process that overlaps the ventral quadrate posteriorly.

41. Quadrate foramen: present (0), absent (1). The quadrate foramen is variably present and positioned within members of Theropoda. In most taxa, it is large or moderate in size and located at the lateral edge of the quadrate. The medial surface of the quadratojugal forms its lateral wall. In abelisauroids, however, the foramen appears to have been lost altogether, although it is not clear whether the associated soft tissues have been lost or relocated.

17 (96); 18 (Allosauroidea); 22 (Torvosauroidea); 24 (12); 27 (36); 31 (17); 33 (28); 38 (67); 39 (42); 41 (21); 43 (15); 44 (39); 45*a*, *b* (49); 48 (49)

42. Ossification of interorbital region: weak or absent (0), extensive (1). In the majority of theropods, the interorbital septum remains almost entirely unossified into adulthood. Specimens of these taxa show little bony material ventral to the canal for cranial nerve I. In abelisauroids and carcharodontosaurids, however, this region is well ossified, forming a median bony lamina that separates the left and right orbital cavities.

6 (Allosaurinae); 5 (Allosauridae); 19 (9); 32 (Abelisauridae/Carcharodontosauridae); 35 (42); 38 (85); 44 (40)

43. Morphology of trigeminal foramen: single (0), partly or fully split (1). Primitively, there is a single foramen for the exit of the trigeminal nerve (cranial nerve V) from the endocranial cavity, located anterodorsal to the prootic pendant. In allosauroids, there is some separation of the trigeminal branches within the endocranial cavity, so that two nerves exit instead of one, V_1 (ophthalmic) and V_{2-3} (maxillo–mandibular). An incipient separation is evident in *Ceratosaurus* and most abelisauroids.

18 (Allosauroidea); 31 (26); 35 (44); 40 (16); 41 (28); 44 (41); 48 (55)

44. Vagal canal opening: through otoccipital (0), onto occiput (1). The opening for the vagal canal (for passage of cranial nerve X) passes through the otoccipital in coelophysoids and other basal theropods, including *Herrerasaurus*. Thus the opening occurs anterior to the occiput. In tetanurans and ceratosaurs, however, the canal opens onto the occiput itself (Sampson & Witmer 2007).

45. Depth of basisphenoid recess: shallow (0), deep (1). Shallow in primitive theropods, the basisphenoid recess (or basisphenoid fontanelle) is quite deep in most tetanurans and ceratosaurs. It is at least as deep as it is wide and eventually penetrates dorsally well behind the ventral portion of the basioccipital.

20; 18 (Allosauroidea); 27 (52); 31 (21); 36*a* (199), 36*b* (55); 45*a*, *b* (57)

46. Shape of opening for basisphenoid recess: ovoid (0), teardrop-shaped (1). The opening of the basisphenoid recess is ovoid in most theropods, including primitive forms where the recess is shallow, as well as more derived tetanurans (e.g. *Allosaurus*) in which it can be quite deep. Ceratosaurs have a distinctly teardrop-shaped opening.

47. Depth of indentation between basal tubera and basisphenoid processes: deep notch (0), shallow embayment (1). Primitive theropods (including *Ceratosaurus*) have a deep, curving notch between the basal tubera and the base of the basisphenoid processes in lateral view. This same region is much more shallowly embayed in tetanurans and most other ceratosaurs.

48. Medial fossa ventral to occipital condyle: absent (0), present (1). The posterior surface of the basioccipital ventral to the occipital condyle is relatively flat in *Herrerasaurus* and ceratosaurs. This region shows little morphological development in most of these taxa, with neither ridges nor a fossa present. In coelophysoids and tetanurans, a distinct central fossa is usually developed ventral to the condyle, which can become quite deeply excavated in derived tetanurans.

28 (Abelisauridae)

49. Size of dorsal groove on occipital condyle: wide (0), narrow (1). In most theropods, the exoccipitals are relatively closely appressed on the dorsal surface of the basioccipital, leaving only a narrow groove to floor the neural canal as it exits the foramen magnum. Some abelisaurids, however, (e.g. *Indosaurus, Majungasaurus*, but not *Indosuchus*) have a particularly wide groove, formed because the exoccipitals are spaced farther apart on the basioccipital.

5 (*Eustreptospondylus*); 11; 31 (19)

50. Orientation of basioccipital–basisphenoid suture: oblique (0), horizontal (1). The suture between the basioccipital and basisphenoid is obliquely orientated in most theropods, with the highest point at the lateral edge and the lowest point near the midline. In contrast, the suture runs almost horizontally in abelisauroids.

51. Depth of median ridge on supraoccipital: less than width (0), greater than width (1). A strong median ridge appears to characterise abelisaurids, as well as *Ceratosaurus*. In these taxa, the anteroposterior depth of the ridge is equal to or greater than its mediolateral width. In contrast, a weaker ridge is present in most tetanurans and only a faint ridge is apparent in more primitive theropods.

14 (Abelisauridae); 38 (84); 44 (44); 48 (51)

52. Morphology of jugal process of palatine: tapered process, triradiate palatine (0), expanded process, tetraradiate palatine (1). Primitively in theropods, the jugal process of the palatine is tapered distally. The palatine in these forms has a triradiate appearance. In tetanurans and ceratosaurs, it develops a 'lacrimal flange' that gives the palatine a tetraradiate appearance.

22 (Allosauroidea); 27 (43); 31 (32); 36*a* (116), 36*c* (125); 38 (77); 41 (34); 44 (45); 45*a, b* (65); 47*a, b* (54)

53. Pocket on ectopterygoid flange of the pterygoid: absent (0), present (1). A deeply excavated pocket on the ectopterygoid flange of the pterygoid supposedly characterises coelurosaurs (e.g. Gauthier 1986), but this feature appears to be more widely distributed. A pocket is present in most tetanurans, as well as many ceratosaurs, although it is absent in coelophysoids and other more basal theropods.

3 (Coelurosauria); 4 (54); 21 (88); 29 (7); 30 (82)

54. Shape of pterygoid articulation with basipterygoid process: tab-like (0), acuminate (1). The pterygoid articulation with the basipterygoid process is tab-like in most theropods, with a blunt process for contact with the basipterygoid processes. In contrast, the process is acuminate in *Majungasaurus* and *Carnotaurus*.

55. Arrangement of jugal and pterygoid processes of ectopterygoid: oblique (0), parallel (1). The jugal and pterygoid processes of the ectopterygoid are orientated obliquely to one another in most primitive theropods in dorsal view. In contrast, these processes are nearly parallel in tetanurans and those ceratosaurs in which the ectopterygoid can be observed (i.e. *Ceratosaurus, Majungasaurus*).

56. Proportions of ectopterygoid: gracile (0), robust (1). The ectopterygoid is a relatively slender bone in most basal theropods, including tetanurans, but is unusually robust in ceratosaurs, independent of any other changes in morphology.

57. Ventral excavation into ectopterygoid: absent (0), fossa (1), groove (2). A fossa is present on the ventral surface of the ectopterygoid in most theropods, situated slightly medially. It appears to be lacking in *Herrerasaurus*, but is present in *Syntarsus*, abelisaurids and allosauroids. The fossa is deeper and broad in most tetanurans, whereas in abelisaurids it forms a distinct groove.

3 (Carnosauria + Coelurosauria); 4 (15); 12 (Theropoda, Coelurosauria); 34 (10); 35 (31); 36*a* (87); 38 (81); 45*a, b* (67)

58. Size of external mandibular fenestra: small to moderate (0), large (1). The primitive archosaur mandible has an external mandibular fenestra, bounded by the dentary (anteriorly), surangular (dorsally) and angular (ventrally). In primitive theropods it is similar in size to those of other archosaurs. In abelisauroids, however, the fenestra is substantially enlarged, with a concomitant reduction in overlap between the dentary and postdentary bones. Allosauroids are characterised by a reduced external mandibular fenestra, achieved largely by dorsoventral expansion of the surangular (rather than the angular below the fenestra); this also occurs in *Dilophosaurus*. In most other theropods, the fenestra is of moderate size, such that the surangular is less than twice the depth of the angular.

2 (26); 11; 14 (Abelisauridae); 21 (105); 22 (Allosauridae); 27 (47); 28 (Abelisauridae); 30 (98); 31 (37, 38); 32 (Abelisauridae); 35 (6, 8); 38 (110, 115, 118); 40 (68, 101); 41 (37, 38); 42 (Abelisauroidea); 45*a, b* (75); 48 (58)

59. Position of anterior end of external mandibular fenestra relative to last dentary tooth: posterior (0), ventral (1). The anterior end of the external mandibular fenestra tends to be situated well posterior to the last dentary tooth in most theropods. However, in abelisauroids the anterior end of the fenestra sits nearly directly vertically beneath the last dentary tooth, as is apparent in *Majungasaurus, Carnotaurus* and *Masiakasaurus*.

36b (29); 42 (7); 47*a, b* (61)

60. Horizontal ridge on lateral surface of surangular below mandibular joint: weak or moderate (0), strong (1). Primitively, the lateral surangular is planar and lacks any prominent ridge or shelf below the mandibular joint. However, a marked ridge is present in abelisaurids, allosauroids and most coelurosaurs.

4 (Carnosauria); 21 (26); 30 (25); 38 (116); 48 (60)

61. Contour of posterior edge of splenial: straight (0), curved or notched (1). The anterior margin of the internal mandibular fenestra, formed primarily by the posterior edge of the splenial, is straight in primitive theropods (*Eoraptor, Herrerasaurus*, coelophysoids). In contrast, this margin is curved in abelisauroids and basal tetanurans and strongly notched in advanced tetanurans.

22 (Neotetanurae); 27 (26); 31 (40); 32 (*Majungatholus + Carnotaurus*); 36*c* (23); 38 (120); 41 (39); 45*a, b* (79)

62. Prongs at anterior end of splenial: one (0), two (1). The anterior end of the splenial tapers to a single point in most theropods, including coelophysoids and tetanurans. In many ceratosaurs, however, it develops a second small prong, subequal in size to the first.

63. Morphology of dentary–surangular articulation just above external mandibular fenestra: small notch (0), large socket (1). Most theropods have a small surangular prong that

fits into a small, narrow notch on the posterior dorsal dentary, just ventral to the dentary prong that inserts into a groove on the surangular. Ceratosaurs (including *Ceratosaurus*) show a substantially modified condition, with an enlarged socket that accepts a broad, rounded surangular prong.

42 (Abelisauroidea); 44 (54); 47*a, b* (63); 48 (57)

64. Shape of articulated dentary rami in dorsal view: V-*shaped (0),* U-*shaped (1).* Most theropods have fairly straight dentary rami in dorsal view, with an obliquely orientated symphysis (relative to the long axis) and, thus, diverge linearly and gradually from one another when articulated. This gives the articulated rami a V-shape in dorsal view. In abelisaurids, however, the dentary rami are curved, such that the symphysis is more nearly perpendicular to the long axis of the bone anteriorly. When articulated, these dentaries form a U-shape in dorsal view.

19 (14); 29 (15); 34 (28); 36*b* (18); 38 (107); 40 (31); 45*a, b* (76); 47*a, b* (70)

65. Position of lateral dentary groove: at or above mid-depth (0), in ventral half (1). All theropods have a longitudinal groove along the lateral surface of the dentary, which contains exit foramina for neurovascular structures associated with the buccal region. This groove also marks a transition from a surface texture more like that of other external skull bones (ventrally) to one more like that of internal skull bones (dorsally). The groove is usually positioned at or above the mid-depth of the dentary, but in certain abelisaurids (*Majungasaurus, Carnotaurus*) it is located ventral to mid-depth (Sampson & Witmer 2007).

66. Position of posterior end of posteroventral process of dentary relative to posterior end of posterodorsal process: far posterior (0), directly ventral (1). The posteroventral process of the dentary, located ventral to the external mandibular fenestra, usually extends far posterior to the posterodorsal process and forms most of the ventral border of the fenestra. In abelisaurids and *Masiakasaurus*, the posteroventral process is shorter, ending approximately below the posterodorsal process.

36b (30); 42 (8); 44 (55); 47*a, b* (65)

67. Arrangement of premaxillary tooth carinae: nearly symmetrical, on opposite sides (0), more asymmetrical, both on lingual side (1). Premaxillary teeth in primitive theropods are nearly symmetrical, changing only slightly in orientation relative to the anterior maxillary teeth. In basal tetanurans and abelisaurids, the two carinae begin to migrate towards the lingual face, creating a slight asymmetry in tooth cross-section. This is accentuated in coelurosaurs, in which the premaxillary teeth become markedly asymmetrical, and reaches its most extreme in the D-shaped teeth of tyrannosaurids.

5 (Neotheropoda); 21 (126); 30 (118); 31 (46); 38 (132); 41 (41); 44 (56)

68. Number of maxillary teeth: more than 12 (0), 12 or fewer (1). In most theropods, there are more than 12 maxillary teeth, although there are often fewer than 15 in tetanurans, abelisauroids and *Dilophosaurus*. Noasaurids (*Noasaurus, Masiakasaurus*) have fewer than 11 maxillary teeth.

44 (58); 48 (16)

69. Surface texture of paradental plates: smooth (0), vertically striated or ridged (1). The paradental (usually termed 'interdental' despite being situated medial to the teeth) plates are generally smooth in theropods, although in certain basal tetanurans (*Megalosaurus, Torvosaurus*) they have a slightly roughened texture. Abelisauroids are unique in displaying strong vertical ridges on the paradental plates, which distinguishes them from carcharodontosaurids.

26 (*Majungatholus + Indosuchus*); 32 (Abelisauridae); 42 (Abelisauridae); 44 (61); 48 (68)

70. Visibility of paradental plates in medial view: widely exposed (0), obscured (1). The paradental plates are very widely visible in most ceratosaurs and allosaurids and somewhat less so in other primitive theropods (although still clearly visible). In these taxa, the dorsoventral exposure of the paradental plates is at least equal to the length of one alveolus. However, in noasaurids (as well as spinosaurids and *Dilophosaurus*) the plates are almost entirely hidden by the medial wall of the bone.

44 (60); 48 (66)

71. Medial groove in paradental plates exposing replacement teeth: present (0), absent (1). This character has a complicated history. Paradental and interdental plates together form the medial and anteroposterior walls of each alveolus. 'Fused' paradental plates occur in all theropods, because the plates form a continuous medial wall along the medial portion of the dentigerous bone. Teeth form as germs at the base of the alveolus along its medial side and are often visible through the 'special foramina' (*sensu* Edmund 1957). As the germs grow and begin to enter the alveolus beneath the existing tooth, they move more laterally. Eventually they push the existing tooth out, resorbing its root in the process. This lateral shift occurs at different points and in doing so creates the distinction seen between 'fused' and 'separate' paradental plates. If the tooth remains medially positioned for a longer period of time (as in spinosauroids), it creates a long groove in the medial surface of the paradental plate. If it moves laterally sooner, then the plates appear fused, as in most ceratosaurs and carcharodontosaurids.

24 (6); 25; 26 (*Majungatholus + Indosuchus*); 32 (Abelisauridae); 34 (29); 35 (3); 38 (135); 40 (62); 48 (67)

Axial Skeleton

72. Neural arch pneumaticity: moderate (0), extreme (1). All theropods exhibit some degree of neural arch pneumaticity. However, it is typically moderate in basal theropods, involving the formation of laminae and fossae but few extensive foramina or instances of multiple foramina within a fossa (but see *Sinraptor* for a counter-example). In more extreme cases, such as many abelisauroids, neural arch pneumaticity creates multiple foramina within the basic arch fossae, as well as foramina in the peduncles/pedicles and occasionally above the dorsoventral plane of the transverse process.

44 (Abelisauroidea); 46 (65); 48 (85)

73. Internal structure of presacral vertebrae: solid (0), camerate (1), camellate (2). Novas (1992*b*) and Britt (1993) noted that most theropod vertebrae display characteristic internal pneumatic structures. Primitive theropods have relatively solid or densely spongy internal structure, often termed 'non-pneumatic'. More derived, 'pneumatic' taxa have either large internal chambers (camerae), or numerous, pervasive smaller chambers (camellae). Camerae are present in coelophysoids and many basal tetanurans, whereas camellae are found in

Ceratosaurus, Torvosaurus, carcharodontosaurids and some coelurosaurs.

14 (Abelisauridae); 16 (Theropoda); 31 (62); 35 (53); 38 (181); 40 (25); 41 (53); 44 (66); 45*a*, *b* (96)

74. Length of axial epipophyses: moderate (0), long (1). Epipophyses are present on the axis of all theropods, but vary in length and morphology. Primitive forms have relatively short epipophyses, approximately equal to the anteroposterior length of the postzygapophyseal facet. In tetanurans and ceratosaurs, the epipophyses are long, extending far beyond the posterior edge of the postzygapophysis.

4 (69); 31 (52); 34 (30); 38 (144); 39 (32); 41 (46); 44 (67); 45*a*, *b* (92)

75. Morphology of axial spinopostzygapophyseal lamina: weakly concave (0), deeply invaginated (1). The morphology of the axial neural spine has been frequently discussed with regard to theropod systematics, but in fact the primary observations actually concern the morphology of the axial spinopostzygapophyseal lamina (Wilson *et al.* 2003), which runs between the neural spine and the postzygapophysis (and/or epipophysis). In primitive theropods, this lamina is weakly concave and, as a result, the neural spine appears broad in anterior view. In ceratosaurs and tetanurans, the lamina is deeply invaginated, giving the spine narrower appearance.

4 (39); 11; 18 (Allosauroidea); 20; 21 (112); 27 (7); 31 (53); 34 (31); 35 (48); 36*c* (4), 38 (139); 41 (47); 44 (68); 45*a*, *b* (93); 47*a*, *b* (75); 48 (75, 76)

76. Development of axial diapophyses: weak, nubbin (0), prominent, pendant (1). Axial diapophyses are present in all theropods, forming the articulation between the second cervical rib and the axial centrum. In most theropods, the diapophyses are prominent and slightly ventrally pendant. However, they are present only as weak nubbins in coelophysoids (*Dilophosaurus, Coelophysis, Syntarsus*) and *Herrerasaurus*.

8 (14); 10 (Coelophysoidea); 21 (10); 30 (9); 35 (51); 36*a* (124), 38 (143); 44 (70); 48 (72)

77. Axial pleurocoels: absent (0), present (1). Axial centrum pleurocoels are absent in coelophysoids, as well as in herrerasaurids and *Eoraptor*. They appear to be present in nearly all other theropods, including ceratosaurs and most tetanurans. These pleurocoels appear to represent the serial homologues of the anteriorly placed pleurocoels in the postaxial presacral vertebrae and are located between the diapophysis and parapophysis.

8 (16); 10 (Coelophysoidea); 21 (11); 30 (10); 35 (50); 36*b* (39); 38 (145); 39 (14); 42 (Neoceratosauria); 44 (71); 45*a*, *b* (91); 48 (77)

78. Posterior pleurocoel in postaxial presacral vertebrae: absent (0), fossa only (1), fossa with pneumatic foramen (2). Considerable variation is associated with the posterior pleurocoel in theropods. Primitively the fossa is lacking, as in *Herrerasaurus*, but all other theropods show some development of this feature. In coelophysoids and *Elaphrosaurus*, an extensive fossa is developed that is bounded posteriorly by a distinctive rim; an associated foramen is also present in *Dilophosaurus*. Most ceratosaurs have a distinctive foramen that sits within a small, restricted pneumatic fossa, which itself lacks the marked posterior rim seen in coelophysoids. Other theropods have neither a fossa nor a foramen.

8 (1); 10 (1); 14 (Abelisauridae); 16 (Ceratosauria); 21 (4, 90); 22 (Ceratosauria); 25; 29 (23); 30 (1*, 84); 31 (58); 34 (36); 36*b* (1); 38 (148); 39 (2); 41 (52); 44 (65); 45*a*, *b* (88, 89, 90); 47*a*, *b* (81, 82); 48 (78, 79, 94)

79. Demarcation of dorsal surface of neural arch from diapophyseal surface in anterior cervical vertebrae: gently sloping (0), ridge (1). In most theropods, the epipophysis and prezygapophysis are connected by a sloping or gently convex surface. In these taxa there is no clear demarcation between the dorsal surface of the neural arch and the lateral, or diapophyseal, surface. Most abelisaurids and noasaurids, however, exhibit a marked ridge between the epipophysis and prezygapophysis that creates a 'corner' and partitions these two regions of the neural arch.

13 (Abelisauridae + Noasauridae); 14 (Noasauridae); 37 (7); 39 (23); 43 (26 [incorrectly listed as 27]); 44 (72); 47*a*, *b* (83); 48 (71); 49 (12)

80. Anteroposterior position of cervical neural spines: posterior half of centrum (0), anterior half of centrum (1). In most theropods, the neural spines of all postaxial cervical vertebrae are placed over the centre of the centrum or posterior to this point. In many taxa the neural spines are inclined past the posterior border of the centrum itself. However, noasaurids (*Masiakasaurus, Laevisuchus, Noasaurus*) are unusual in that the neural spines of at least some cervicals are located anterior to the midpoint of the centrum.

44 (74); 48 (87)

81. Ventral keel on anterior cervicals: present (0), faint or absent (1). The ventral surface of the centrum bears a prominent keel in most primitive theropods, including coelophysoids and *Herrerasaurus*. It is reduced to a faint ridge, or is entirely absent, in tetanurans and ceratosaurs.

45*a*, *b* (97)

82. Anterior prongs on postaxial cervical epipophyses: absent (0), present (1). A narrow, acuminate process extends anteriorly from the cervical epipophyses in *Noasaurus, Carnotaurus* and *Ilokelesia*. This process is absent in all other theropods, including *Masiakasaurus* and *Majungasaurus*. However, it may represent a late-stage ontogenetic development in abelisauroids and, therefore, may assume a wider distribution once the cervicals of fully mature individuals of *Masiakasaurus* and *Majungasaurus* are found.

13 (Abelisauridae + Noasauridae); 14 (Noasauridae); 16; 36*b* (31); 37 (6); 39 (29); 43 (19); 44 (75); 48 (81); 49 (9)

83. Development of pre- and postspinal fossae in postaxial cervical vertebrae: narrow (0), broad (1). The pre- and postspinal laminae each bound a fossa at the base of the neural spine. In most theropods, this fossa varies in depth but is relatively narrow, only slightly wider than the neural spine. The fossa is typically deep in abelisauroids and *Ceratosaurus* and much broader than the width of the neural spine.

39 (26); 44 (73)

84. Position of cervical zygapophyses: close to midline (0), placed far laterally (1). The cervical zygapophyses are placed close to the midline in primitive theropods such as coelophysoids, but also *Spinostropheus* and *Elaphrosaurus*. They are more laterally placed in tetanurans and most other ceratosaurs.

34 (35); 38 (155); 44 (76); 45*a*, *b* (99)

85. Morphology of anterior cervical epipophyses: low, blunt (0), long, thin (1), long, robust (2). In most theropods the postaxial epipophyses are moderately developed, extending posteriorly approximately as far as the postzygapophyses are long. They tend to increase in size towards C5/6 and then decrease again towards the dorsal series. The epipophyses are low in primitive theropods and basal tetanurans and nearly absent in many coelurosaurs. In contrast, they are long and thin in noasaurids and many coelophysoids and even more pronounced (long and robust) in abelisaurids and *Ceratosaurus*.

2 (*Yangchuanosaurus* + allosaurs + coelurosaurs); 14 (Abelisauridae); 16 (Abelisauria); 19 (22); 20; 23 (34); 28 (Abelisauria); 32 (Abelisauridae); 35 (55); 36*a* (89); 38 (149, 152); 40 (24); 44 (77); 45*a, b* (102); 48 (80); 49 (10)

86. Length/height ratio of mid-cervical centra: less than 3 (0), more than 3 (1). The extremely elongate centra of coelophysoid mid-cervicals are unusual among theropods, found elsewhere only in *Spinostropheus* and *Elaphrosaurus*. In nearly all other theropods, the cervical centra are less than three times as long as they are tall.

19 (23); 39 (45); 44 (79); 47*a, b* (78); 48 (86)

87. Height of postaxial cervical neural spines: moderate or tall (0), short (1). Most theropods exhibit relatively tall cervical neural spines, approximately equal in height to the height of the centrum face. Abelisauroids, *Elaphrosaurus* and coelophysoids exhibit markedly shorter cervical neural spines, often less than half the height of the centrum face.

6; 13 (Abelisauridae + Noasauridae); 14 (Abelisauridae); 16 (Abelisauria); 28 (Abelisauria); 29 (21); 34 (39); 37 (3); 38 (154); 39 (28); 44 (78); 48 (82); 49 (11)

88. Accessory fossa on dorsal surface of postaxial cervical transverse processes: present (0), absent (1). The dorsal surface of the transverse processes in the postaxial cervical vertebrae is typically flat in most theropods. However, a shallow fossa is evident on this surface in *Elaphrosaurus* and *Spinostropheus*.

89. Shape of dorsal transverse processes in dorsal view: rectangular (0), triangular (1). Most theropods, including many primitive taxa, have dorsal transverse processes that project nearly directly laterally and are rectangular in dorsal view. In coelophysoids, however, the transverse processes of the dorsals are triangular and appear backturned, largely due to the strong posterior sweep of the anterior edge.

8 (2); 10 (2); 35 (57); 36*b* (56); 38 (170); 39 (3); 44 (80); 48 (92)

90. Height of dorsal parapophyses: slightly elevated from centrum (0), project far laterally (1). In coelophysoids and basal tetanurans, the dorsal parapophyses extend laterally from the arch, but this is reduced in allosauroids so that it is nearly flush with the arch. In abelisauroids the parapophyses extend nearly twice as far laterally.

15 (Neoceratosauria); 18 (Allosauroidea); 31 (67); 42 (Abelisauridae); 44 (81); 47*a, b* (89); 48 (93)

91. Paradiapophyseal lamina: absent, weak (0), pronounced (1). In many abelisauroids, especially abelisaurids, a prominent 'web' connects the parapophysis and transverse process in the dorsal vertebrae. This 'web', the paradiapophyseal lamina, is typically absent in theropods, or else exists only as a very low ridge.

44 (82)

92. Dorsal vertebral centrum length ratio relative to height: more than 2 (0), less than 2 (1). Relatively long dorsal centra are primitive for theropods, occurring in *Eoraptor* and coelophysoids. They appear to shorten progressively in basal tetanurans, allosauroids and coelurosaurs, resulting in a general shortening of the trunk. However, relatively long dorsal centra are also present in *Elaphrosaurus*, whereas herrerasaurids have relatively short posterior dorsal centra. Body size may exhibit some influence on these proportions, although this has not been investigated.

36*b* (48); 45*a, b* (112); 47*a, b* (88); 48 (91)

93. Number of sacral vertebrae: 2 [primordial sacrals only] (0), 5 [1 dorsosacral, 2 caudosacrals] (1), 6 [2 dorsosacrals, 2 caudosacrals] (2). The primitive condition for Dinosauria (and Dinosauromorpha) is to have two sacral vertebrae permanently connected to the ilium via modified transverse processes and sacral ribs. *Eoraptor* and herrerasaurids have these original two sacrals; the transverse process of the last dorsal contacts the ilium in *Herrerasaurus* but is otherwise unmodified and is here considered a dorsal. All theropods more derived than Herrerasauridae incorporate at least one dorsal and two caudals into the sacral series. Ceratosaurs add an additional dorsal; successive 'sacrals' are typically unmodified dorsals or caudals that contact the iliac blades via a transverse process only.

4 (19, Troodontidae); 12 (Theropoda); 13 (Abelisauridae); 14 (Abelisauridae); 15 (Neoceratosauria); 16 (14); 16 (Theropoda, Neoceratosauria); 21 (121); 22 (Coelurosauria); 29 (25); 30 (113); 34 (49); 35 (59); 36*a* (6), 36*b* (127), 36*c* (39); 38 (185); 39 (18); 42 (Abelisauroidea); 44 (84); 45*a, b* (113); 46 (68, 69); 47*a, b* (91); 48 (95)

94. Transverse dimensions of mid-sacral centra relative to other sacrals: equivalent (0), constricted (1). The co-ossified theropod sacral centra are typically parallel-sided in dorsal view, with each centrum having approximately equivalent mediolateral dimensions. In certain abelisaurids, however, the mid-sacral centra are constricted mediolaterally relative to those more anterior and posterior.

13 (Abelisauridae); 14 (Abelisauridae); 36*b* (32); 38 (186); 44 (85); 47*a, b* (94)

95. Orientation of ventral margin of mid-sacral centra: horizontal (0), arched (1). A dorsally arched ventral margin of the sacrum characterises many, but not all, ceratosaurs. In other theropods, the ventral margin of the co-ossified sacrum is nearly horizontal.

36*b* (16); 44 (86); 47*a, b* (93); 48 (97)

96. Dorsal edge of sacral neural spines: as thin as remainder of spine (0), thickened (1). In most theropods, the sacral neural spines taper, or retain an even thickness, as they reach their dorsal apex. The spines are thickened transversely at the dorsal apex in most ceratosaurs, often to twice their mid-height thickness.

97. Condition of sacral neural spines in adults: separate (0), fused (1). Fused sacral neural spines occur in some coelophysoids (*Coelophysis, Syntarsus*) and certain abelisauroids (*Masiakasaurus, Majungasaurus, Carnotaurus*).

Fusion is apparently absent in tetanurans and more primitive theropods, as well as *Dilophosaurus* (although ontogenetic stage may be a factor for specimens of the latter).

8 (5); 10 (4); 38 (188); 39 (5); 40 (100); 44 (87); 47*a*, *b* (96); 48 (99)

98. Pneumaticity of sacral neural spines: weak or absent (0), well developed (1). The sacral neural spines are highly pneumatised in ceratosaurs, showing extensive development of fossae and foramina along the lateral sides of the spines. Many taxa show a characteristic set of paired fossae alongside the main supporting lateral ridge of the spine. In other theropods, however, there is little or no evidence of any pneumaticity.

99. Morphology of anterior caudal neural spines: sheet-like (0), rod-like (1). 'Sheet-like' neural spines are present in the anterior caudal vertebrae of primitive theropods, as well as most tetanurans and coelophysoids. These spines retain a significant anteroposterior length, similar to (but shorter than) the posterior dorsals. In abelisaurids the anterior caudals have 'rod-like' neural spines, due to their short anteroposterior length.

**45*a*, *b* (124); 44 (88)

100. Proportions of anterior caudal neural arch base relative to centrum proportions: smaller (0), equal or greater (1). In anterior view, the base of the neural arch is typically narrower mediolaterally than the centrum in the anterior caudal vertebrae of theropods. In most abelisauroids, however, the neural arch base is 'swollen' and equals or exceeds the mediolateral width of the centrum.

101. Distal morphology of anterior to mid-caudal transverse processes: tapering (0), anteroposteriorly expanded (1). The distal ends of the transverse processes usually taper to a thin edge throughout the tail in theropods. In some abelisaurids, the distal transverse processes of the caudals in the anterior half of the tail are highly modified. Instead of tapering, the processes expand anteriorly and posteriorly to form a T-shape in dorsal view. In *Aucasaurus*, at least, the presence of a linear scar just proximal to this expansion suggests that the more distal region might represent caudal ribs that have ossified and fused to the transverse processes. Because these expansions may appear later in ontogeny, their absence in some taxa known primarily from immature specimens (e.g. *Majungasaurus*) is equivocal.

14 (Abelisauridae); 39 (25); 42 (Abelisauridae); 43 (24, 25 [incorrectly listed as 25, 26]); 44 (89); 48 (102); 49 (13)

102. Contact between cervical vertebrae and cervical ribs in adults: separate (0), fused (1). Most theropod adults retain a visible suture between the cervical vertebral parapophyses and the capitular facet of the cervical ribs, although it is not known whether any mobility occurred at this joint. In many coelophysoids and ceratosaurs (including *Elaphrosaurus*), however, this joint is fused and the external suture is obliterated.

3 (Coelurosauria); 4 (55); 12 (Coelurosauria); 31 (79); 38 (165); 44 (90); 48 (88)

103. Wing-like process at the base of the anterior cervical rib shafts: absent (0), present (1). The long rib shafts of cervicals 4–8 are expanded perpendicular to their long axis near the junction of the capitulum and tuberculum. This cre-

ates an 'aliform' process, as observed in ceratosaurs such as *Carnotaurus*, *Ilokelesia* and *Majungasaurus*. Such an expansion is lacking in *Coelophysis*, *Herrerasaurus* and *Allosaurus*, as well as other theropods.

31 (82); 39 (24); 40 (23); 41 (67); 43 (27 [incorrectly listed as 28]); 44 (92); 47*a*, *b* (103, 104)

104. Bifurcate cervical rib shafts: absent (0), present (1). First observed in *Majungasaurus* (*Majungatholus*; Sampson *et al.* 1998), the cervical rib shaft is bifurcate in *Carnotaurus* as well. In these forms, a short secondary shaft extends parallel to the main shaft for up to 25% of the total rib length. This has not been observed in other ceratosaurs or other theropods.

32 (*Majungatholus*)

Appendicular skeleton

105. Relative width of scapular blade: broad, more than twice glenoid depth (0), narrow, less than twice glenoid depth (1). The scapular blade is relatively broad in primitive dinosaurs and basal theropods (*Eoraptor*, coelophysoids), with its breadth exceeding twice the dorsoventral depth of the glenoid. This condition is also present in *Ceratosaurus* and abelisaurids, although not in *Herrerasaurus*. In tetanurans, the scapular blade becomes anteroposteriorly narrow and strap-like, particularly so in allosauroids and coelurosaurs.

2 (34); 3 (Coelurosauria); 4 (41, 42*); 5 (advanced neotheropods); 11; 12 (Tetanurae); 21 (113); 31 (86); 34 (59); 36*a* (98); 38 (211); 44 (97); 45*a*, *b* (132); 48 (105)

106. Development of posteroventral process on coracoid: moderate (0), pronounced (1). The posteroventral process of the coracoid varies in size and development among theropods. It is relatively small in coelophysoids, *Ceratosaurus* and basal tetanurans, extending a distance approximately equivalent to the depth of the glenoid. In many ceratosaurs (*Carnotaurus*, *Majungasaurus*, *Deltadromeus*) the process is more pronounced and extends farther from the body of the coracoid, whereas in more derived coelurosaurs it is relatively elongate and can appear 'crescentic'.

3 (Coelurosauria); 4 (42); 21 (102); 22 (Neotetanurae); 27 (28, 59); 30 (96); 31 (89); 33 (29); 34 (61); 35 (66); 36*c* (28, 55); 38 (217, 218); 40 (29); 44 (98); 45*a*, *b* (136); 47*a*, *b* (109); 48 (109)

107. Spacing between glenoid and posteroventral process of coracoid: moderate (0), close (1). The glenoid and posteroventral process of the coracoid are widely separated in many theropods, including spinosaurs, *Herrerasaurus*, *Allosaurus* and most ceratosaurs. However, these two structures lie in very close proximity in most coelophysoids and *Elaphrosaurus*.

108. Size of coracoid: shallow (0), very deep (1). The coracoid is primitively shallow, with its anteroventral length equal to approximately twice its dorsoventral depth. The bone is strikingly deep dorsoventrally in *Elaphrosaurus*, *Masiakasaurus* and *Deltadromeus*, as well as most abelisaurids. In these forms, the depth of the coracoid is considerably more than half its length.

14 (Abelisauridae); 42 (Abelisauroidea); 43 (21 [incorrectly listed as 22])

109. Shape of humeral head: elongate (0), globular (1). In the majority of theropods, the humeral head has a distinctly elongate profile in proximal view, with the long axis orientated mediolaterally (externo-internally). In contrast, abelisauroids (but not *Ceratosaurus*) are characterised by a more rounded humeral head that is enlarged, globular and correspondingly more distinct from the internal and external tuberosities.

45a, *b* (140); 42 (Abelisauroidea); 43 (22 [incorrectly listed as 23]); 44 (100); 47*a*, *b* (110); 48 (112)

110. Shape of distal humeral condyles: rounded (0), flattened (1). The distal end of the humerus bears two confluent, but distinct, rounded condyles for articulation with the proximal radius and ulna in most theropods. These condyles are flattened in ceratosaurs, although not otherwise reduced.

44 (101); 47*a*, *b* (114); 48 (113)

111. Placement of humeral greater tubercle relative to internal tuberosity: proximal (0), distal (1). The greater (lateral) tubercle of the humerus is located proximal to the internal tuberosity (medial tubercle) in most theropods and nearly at the same level as the humeral head. In ceratosaurs, the greater tubercle is more distally placed relative to the internal tuberosity, reversing these relationships.

47a, *b* (111)

112. Longitudinal torsion of humeral shaft: absent (0), present (1). In primitive theropods, the long axes of the proximal and distal humeral articular surfaces are nearly parallel. They become increasingly rotationally offset from one another in more derived forms (e.g. tetanurans, ceratosaurs, *Segisaurus*) as the intervening shaft undergoes varying degrees of longitudinal twisting (torsion).

38 (234); 44 (102)

113. Size of deltopectoral crest: prominent (0), low (1). Although a prominent (long) deltopectoral crest is synapomorphic for Dinosauria (e.g. Sereno 1999), its size and development varies within different groups. Most theropods have a well-developed crest that is distinct from the shaft, exceptionally so in spinosaurs. The reverse is true of ceratosaurs, which exhibit a very low deltopectoral crest that, while still long, may be no more than a raised ridge.

2 (37); 4 (Ornithomimidae); 34 (64); 38 (241); 40 (55); 44 (103); 45*a*, *b* (142); 47*a*, *b* (112)

114. Length of humerus relative to femur length, more than one-third (0), less than one-third (1). Forelimb shortening has been noted in several theropod groups, particularly tyrannosauroids. This may occur due to overall size reduction throughout the limb, or due to preferential shortening of certain elements. The abelisaurid *Carnotaurus* has a humerus reduced to less than one-third femur length, and more recent discoveries have confirmed similar proportions in *Aucasaurus* and *Majungasaurus*.

16 (Neoceratosauria); 23 (35); 38 (229, 230); 40 (58); 42 (Abelisauridae); 44 (99); 45*a*, *b* (139)

115. Relative length of longest manual phalanges: more than twice width (0), less than twice width (1). Manus length is known to increase generally during theropod evolution, from primitively short (*Eoraptor*) toward very elongate (Maniraptora). Intermediate theropods (coelophysoids and basal tetanurans) have a moderately long manus in which the longest manual phalanges are more than twice as long as wide. However, some ceratosaurs show a secondary reduction in manus length, accomplished primarily through extensive shortening of all phalanges (as well as the metacarpals).

3 (Carnosauria + Coelurosauria); 4 (7, 43); 31 (95); 38 (233); 40 (77); 41 (74); 45*a*, *b* (147, 161); 46 (92)

116. Contacts between pelvic elements in adults: separate (0), fused (1). This feature is difficult to observe in some taxa, because the relative maturity of particular specimens is not always evident (Tykoski & Rowe 2004). Pelvic element fusion is generally absent in (presumably) mature individuals of most theropod taxa, although it has been observed in some coelophysoids and most ceratosaurs. The indistinct iliac–pubic contact in *Carnotaurus* may represent partial fusion of these elements, but the iliac–ischial contact remains patent. The only described ilium of *Majungasaurus* is from a subadult.

4 (Ceratosauria); 8 (6); 10 (5); 16 (Ceratosauria); 21 (118); 22 (Ceratosauria); 30 (110); 31 (120); 35 (83); 36*b* (2); 38 (285); 39 (6); 44 (109); 47*a*, *b* (120); 48 (120)

117. Posterior width of iliac brevis fossa: subequal to anterior width (0), twice anterior width (1). The brevis fossa is present primitively in Dinosauria. Most theropods have a brevis fossa whose medial and lateral edges are parallel in ventral view; thus the mediolateral width posteriorly is subequal to that anteriorly. However, most coelophysoids and ceratosaurs (as well as *Torvosaurus* and *Megalosaurus*) have a brevis fossa in which the medial and lateral edges diverge posteriorly, so that the fossa widens to approximately twice its anterior width.

11; 20; 22 (Ceratosauria); 34 (76); 36*b* (4); 38 (291); 44 (110); 45*a*, *b*(176); 48 (127)

118. Morphology of lateral ilium between supra-acetabular crest and brevis shelf: gap (0), continuous (1) (Fig. 11). In most ceratosaurs (although not in *Rajasaurus*), the supra-acetabular crest is continuous posteriorly with a distinct ridge that connects with the prominent lateral margin of the brevis fossa. This is in contrast to the condition in most theropods, in which the lateral expansion of the supra-acetabular crest gradually declines posteriorly until it essentially disappears just beyond the edge of the acetabulum. As a result, there is a gap between the crest and the lateral brevis fossa margin in these forms.

119. Shape of posterior margin of iliac postacetabular process: convex (0), undulating (1) (Fig. 11). Like the preacetabular process (character 122), the iliac postacetabular process is generally convex along its (posterior) margin in most theropods. In some ceratosaurs, the process has an undulating margin. This is caused primarily by the expansion of the ilium along its dorsal margin to form an enlarged attachment surface for the caudosacral vertebrae.

22 (Ceratosauria); 36*b* (5); 38 (298); 42 (Neoceratosauria); 44 (119); 46 (120); 47*a*, *b* (124); 48 (128)

120. Shape of dorsal margin of iliac postacetabular process: convex (0), straight (1). The dorsal margin of the ilium is convex in most theropods, especially tetanurans but also certain coelophysoids (e.g. *Dilophosaurus*). In coelophysids and many ceratosaurs (but not *Ceratosaurus*), this margin is nearly straight.

19 (47); 35 (73); 36*c* (86); 38 (297); 44 (117); 48 (122)
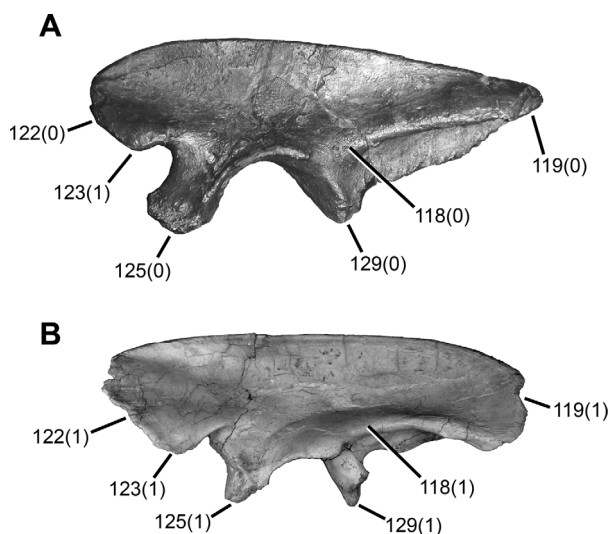
Figure 11 Ilia of (**A**) *Eustreptospondylus oxoniensis* (OUM J.13558; right ilium, reversed) and (**B**) *Majungasaurus crenatissimus* (UA 8676; left ilium) in lateral view, showing character states. Not to scale.

Figure 12 Distal pubes of *Carnotaurus sastrei* (MACN-CH 894) in anterior view, showing the derived condition for character 126. Scale bar = 5 cm.

121. Relative sizes of iliac–pubic and iliac–ischial articulations: subequal (0), iliac–pubic articulation larger (1). In basal theropods, the pubic and ischial peduncles of the ilium are nearly equal in size, with the ischial peduncle being only slightly the smaller of the two. In tetanurans and abelisaurs, the pubic peduncle is markedly larger than the ischial, especially in its anteroposterior dimension.

   22 (Tetanurae); 27 (11); 31 (107); 35 (71); 36*c* (7); 38 (304); 44 (114); 45*a, b* (177); 47*a, b* (130); 48 (131)

122. Shape of anterior margin of iliac preacetabular process: rounded (0), undulating (1) (Fig. 11). In most theropods with an anteriorly expanded ilium, the preacetabular blade has a rounded or generally convex outline between the anteroventral corner and the dorsal margin. In ceratosaurs, this margin is 'notched' to create a concavity. As a result, the anterior margin has an undulating shape overall.

   22 (Neotetanurae); 36*c* (31); 38 (294); 45*a, b* (173); 47*a, b* (123)

123. Anteroventral lobe of iliac preacetabular process: absent (0), present (1) (Fig. 11). Most ceratosaurs and tetanurans exhibit a distinct anteroventral lobe on the iliac preacetabular process. This lobe descends ventrally beneath the level of the preacetabular process where it meets the pubic peduncle, and is absent in coelophysoids and other primitive theropods. The lobe is distinct from character 122, because it is present in many tetanurans that lack that more dorsally placed feature.

   31 (102); 41 (81); 45*a, b* (168); 48 (125)

124. Contact between pubic apices: separate (0), contacting (1). The pubic apron runs continuously down the pubic shaft in all theropods in which it is present. Primitively, the apron terminates before the distal end of the bone and the two pubic apices are separate. When fusion occurs between the distal pubes (as in tetanurans and abelisauroids), the apron may either be confluent with this fusion or terminate above it. In the latter case, a 'foramen' remains between the distal apron and the proximal boot.

   25; 38 (311, 314); 41 (87); 44, (120) 45*a, b* (182); 48 (139)

125. Morphology of contact between pubis and ilium: planar (0), peg-and-socket (1) (Fig. 11). The iliac–pubic contact is planar or gently undulating in primitive theropods and this morphology is retained in most derived taxa. However, in *Ceratosaurus* and abelisauroids (*Majungasaurus, Masiakasaurus, Rajasaurus* and possibly *Carnotaurus*) the ilium has a peg that articulates into a deep socket in the proximal pubis. This unusual morphology is mirrored in the iliac–ischial articulation (see 130, below).

   42 (Neoceratosauria); 44 (123); 47*a, b* (128); 48 (133)

126. Morphology of dorsal surface of pubic boot on midline: convex (0), concave (1) (Fig. 12). In tetanurans and other theropods in which the pubes contact distally, the conjoined bones often form an expanded 'boot', which may be fused. Along the midline, the contact between the two pubes is typically convex, often with a midline ridge and the presence of a foramen between the pubes above this point does not affect this morphology. In ceratosaurs, the conjoined pubes have a distinctly concave dorsal surface, forming a channel that itself is the ventral border of the foramen between the pubes.

127. Notch ventral to obturator process on ischium: absent (0), present (1). Numerous early theropod studies noted the presence of an obturator 'notch' or foramen in the proximal ischium. Rauhut (2000, 2003) correctly noted that this notch was usually an artifact of the presence or absence of a distinct notch at the distal end of the obturator flange/process. This notch is variably present in basal theropods; when absent, the obturator process grades smoothly into the distal ischial shaft.

   25; 45*a, b* (190)

128. Morphology of distal ischium: rounded, separate (0), expanded, triangular, fused (1). The distal ischium bears a small, rounded expansion in primitive theropods. This is retained in tetanurans and reduced in coelurosaurs. In ceratosaurs (*Carnotaurus, Elaphrosaurus* and *Deltadromeus*), the

distal ischium develops an anteroposteriorly elongate and triangular foot, formed by the fused left and right elements. Similar fusion is also seen in *Neovenator*.

13 (Abelisauridae + Ceratosauridae); **14** (Abelisauridae); **19** (52); **21** (43); **23** (50); **30** (42); **31** (119); **35** (79); **36***a* (134), **36***b* (8), **36***c* (68); **38** (327); **40** (63); **41** (96); **44** (127); **45***a, b* (193); **46** (123); **47***a, b* (141); **48** (143)

129. Morphology of contact between ischium and ilium: planar (0), peg-and-socket (1) (Fig. 11). Like the pubis, the contact between the ilium and ischium develops a peg-and-socket morphology in abelisauroids (as well as in *Giganotosaurus*). In other theropods, the contact between these elements is relatively flat or slightly convexo-concave.

47*a, b* (129)

130. Proportions of limb bones: moderate to gracile (0), robust (1). Distinct differences are apparent in the limb bone proportions of theropods. Although most theropods scale similarly at similar body sizes (Carrano 2001), certain abelisaurids show unusually robust hind limb elements (Carrano 2007). These include *Quilmesaurus*, *Pycnonemosaurus*, *Majungasaurus*, *Rajasaurus* and some of the unassigned Lameta theropod materials.

131. Dimorphism in hind limb morphology: absent (0), present (1). Dimorphism in the morphology of the femur (Colbert 1990; Raath 1990; Rowe & Gauthier 1990) and tibia (Carrano *et al.* 2002) has been noted among 'ceratosaurs', but in fact most theropods are not known from large enough sample sizes for this to be accurately determined. Nevertheless, such dimorphism – including the morphology of the lesser trochanter, robustness of limb proportions and development of muscle attachment scars – appears to be absent from *Herrerasaurus*, *Allosaurus* and many tetanurans. It cannot be assessed for any abelisaurid at this time.

8; **10**; **36***b* (10); **44** (131); **47***a, b* (143)

132. Morphology of anterolateral muscle attachments on proximal femur: continuous trochanteric shelf (0), distinct lesser trochanter and attachment bulge (1). Primitive theropods and dinosauromorphs have a single trochanteric shelf that wraps around the anterolateral proximal femur (Hutchinson 2001). In coelophysoids the anterior portion becomes slightly extended as a small, spike-like lesser trochanter while the remainder is retained as a shelf. In ceratosaurs and tetanurans, the lesser trochanter becomes elevated while the lateral shelf is reduced to a discrete rugosity, the insertion for M. iliofemoralis. An additional accessory trochanter appears in more derived tetanurans.

4 (Ceratosauria); **8** (7); **10** (6); **16** (2, 17); **22** (Ceratosauria); **23** (33); **35** (85); **36***b* (11); **39** (7); **38** (338); **40** (51); **44** (134); **48** (148, 149, 151)

133. Development of medial epicondyle of femur: rounded (0), ridge (1), long flange (2). The medial epicondylar edge of the femoral shaft, which separates the anterior origin of the M. femorotibialis from the medial shaft, is rounded in primitive theropods. In most ceratosaurs, the medial epicondyle becomes a pronounced, sharp ridge, with associated striations along the medial edge. A moderate ridge is also present in *Syntarsus* and *Segisaurus*. Noasaurids (especially *Masiakasaurus*) present a hypertrophied flange along the medial epicondyle.
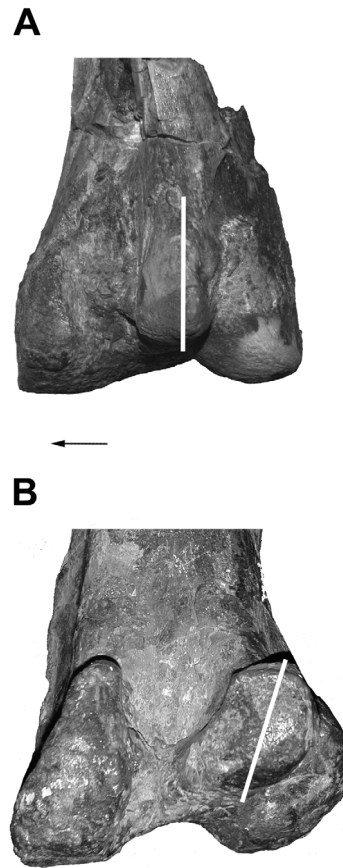
Figure 13 Distal femora of (**A**) *Coelophysis* sp. (UCMP 129618, reversed from left) and (**B**) *Carnotaurus sastrei* (MACN-CH 894, right) in posterior view, showing states for character 134. The white line indicates the long axis of the tibiofibularis crest. The long axis of the femur is approximately vertical and the arrow points medially. Not to scale.

35 (87); **38** (340); **40** (49); **41** (105); **42** (Abelisauroidea); **44** (135); **45***a, b* (202); **48** (152)

134. Morphology and orientation of femoral tibiofibularis crest: narrow, longitudinal (0), broad, oblique (1) (Fig. 13). The tibiofibularis crest is located proximal to the fibular condyle on the posterior distal femoral shaft. When viewed posteriorly, this crest is relatively narrow mediolaterally and its long axis is orientated longitudinally. In ceratosaurs, however, the crest is broader and its long axis is orientated obliquely with respect to the long axis of the femoral shaft.

135. Distal expansion of tibial cnemial process: absent (0), present (1). In mediolateral view, the cnemial crest is not elevated above the proximal articular surface of the tibia (or only slightly so) in primitive taxa and tetanurans and its ventral edge slopes evenly toward the tibial shaft. However, in abelisauroids, *Ceratosaurus* and *Deltadromeus*, the cnemial crest is expanded proximally at its distal end. In mediolateral view, the crest appears to have a lobular distal end that projects considerably above the articular surface, as well as a marked ventral projection.

13 (Abelisauridae); 35 (89); 42 (Abelisauroidea); 44 (138); 47*a, b* (144); 48 (156)

136. Shape of distal tibia in distal view: rounded (0), mediolaterally elongate (1). The shape of the distal tibia appears to be correlated with development of the tibial malleoli and astragalar buttress. Primitively subcircular in distal view, the distal tibia becomes rectangular and eventually more triangular, as it widens transversely. Primitively, the tibial lateral malleolus is lobate and thickened, as in *Herrerasaurus* and coelophysoids. In more derived theropods, as the tibia comes to partly back the fibula, the lateral malleolus assumes a more flattened, tabular shape.

3 (Dinosauria); 4 (47*); 7 (3); 22 (Tetanurae); 27 (14); 31 (132); 35 (88); 36*c* (10); 38 (352); 44 (139); 45*a, b* (208, 219); 47*a, b* (150); 48 (158, 160)

137. Development of fibular fossa on medial aspect of proximal fibula: posterior groove (0), posteriorly open fossa (1), medially open fossa (2). The fibular fossa has a complex morphology within Theropoda. Primitively, it is present only as a small, shallow groove along the posterior edge of the medial proximal fibula (although this is deepened slightly in *Syntarsus* and *Liliensternus*). In ceratosaurs, this fossa still faces posteriorly, but is much deeper and greatly expanded across the medial face. In spinosauroids, the medial fibula bears little or no evidence of any fossa or groove. Allosauroids have a deep fossa that is entirely contained on the medial face and no longer opens posteriorly. A similar fossa is present in most coelurosaurs, although it varies widely in depth.

4 (Ceratosauria); 8 (9); 27 (63); 34 (88); 35 (92); 36*c* (46); 38 (355, 356); 42 (Neoceratosauria); 44 (140); 45*a, b* (209, 210); 47*a, b* (151, 152); 48 (161)

138. Size of iliofibularis tubercle on fibula: moderate (0), large (1). All dinosaurs possess a tubercle for insertion of the M. iliofibularis and it can be observed in both *Eoraptor* and *Herrerasaurus*. It persists in all tetanurans and most coelurosaurs, but is especially pronounced in ceratosaurs (*Xenotarsosaurus, Majungasaurus, Deltadromeus, Elaphrosaurus*), where it often becomes a ridge or flange.

9; 21 (57); 30 (55); 38 (357); 42 (Neoceratosauria); 44 (141); 45*a, b* (211); 48 (163)

139. Contact between fibula and ascending process of astragalus in adults: separate (0), fused (1). Fusion between these elements occurs in the adults of most abelisauroids, including noasaurids and abelisaurids. It is absent in *Ceratosaurus*, probably *Elaphrosaurus* and most other theropods (including coelophysoids).

44 (142)

140. Morphology of astragalar ascending process: blocky (0), laminar (1). Primitively, the astragalar ascending process is low and triangular, wedged between the anterolateral tibia and the anteromedial fibula. This morphology is present in *Eoraptor*, Herrerasauridae and coelophysoids and is somewhat similar in *Ceratosaurus*. In abelisauroids, the ascending process is a rectangular, laminar flange, and it is laminar in tetanurans although more triangular in shape.

2 (40, 41); 4 (48*); 7 (9); 16 (7); 19 (56); 22 (Tetanurae); 27 (16); 36*a* (71), 36*c* (12); 38 (362); 40 (8); 44 (145); 45*a, b* (214); 47*a, b* (155); 48 (166)

141. Orientation of astragalar distal condyles: ventral (0), 10–30° anterior (1), 30–45° anterior (2). Theropods show a general shift in the orientation of the astragalar distal condyles. In basal forms, the condyles are fully ventral, sitting directly beneath the distal tibia and with an angle of 0° to the long axis of that bone in lateral view. The condyles become progressively more anterior, lying 10–30° anterior to this axis in ceratosaurs and nearly 45° anterior to it in more derived tetanurans.

22 (Tetanurae); 27 (18); 31 (136); 36*c* (14, 59); 35 (93); 38 (364); 41 (110); 44 (143); 45*a, b* (217); 47*a, b* (158)

142. Horizontal groove across the anterior face of the astragalar condyles: absent or weak (0), pronounced (1). There is evidence that a vascular structure traverses the anterior astragalar condyles in all theropods: the medial and lateral edges usually each bear a horizontal groove. These grooves disappear in the central portion of the anterior condyles in primitive theropods. However, in abelisauroids and tetanurans, these two grooves are continuous across the anterior face, forming a single, pronounced horizontal groove.

1; 21 (23); 27 (19); 30 (22); 31 (137); 34 (91); 35 (95); 36*c* (60); 38 (365); 40 (6); 44 (147); 45*a, b* (218); 48 (169)

143. Contact between astragalus and calcaneum in adults: separate (0), fused (1). The astragalus and calcaneum are fused to each other and to the tibia/fibula in several basal theropods, including coelophysoids, *Ceratosaurus, Deltadromeus* and abelisauroids (*Xenotarsosaurus, Masiakasaurus, Majungasaurus*). In other theropods, including tetanurans, *Herrerasaurus* and *Eoraptor*, these two bones remain separate even in adults. However, in ceratosaurs the tibia and fibula are not fused together directly except via the ascending process.

1; 8 (10); 10 (8); 14 (Abelisauridae); 16 (Ceratosauria); 22 (Ceratosauria); 31 (133); 35 (94); 36*b* (13); 38 (366, 368); 39 (9); 41 (107); 44 (149); 48 (168)

144. Development of astragalar articular surface for distal end of fibula: large, dorsal (0), reduced, lateral (1). Primitively, the distal fibula articulates with both the astragalus and calcaneum. The fibular cup on the astragalus is large and faces dorsally in (e.g.) *Herrerasaurus* and coelophysoids. Some reduction is evident in *Majungasaurus* and tetanurans (*Allosaurus, Torvosaurus, Eustreptospondylus, Sinraptor*), resulting in a cup that opens laterally as well as dorsally. This change is due to reduction in size of the distal fibula, as well as a positional shift in the articulation. In many coelurosaurs, the articular cup is entirely on the (reduced) calcaneum.

22 (Tetanurae); 27 (17); 36*c* (13); 38 (360); 44 (148) 45*a, b* (213)

145. Height of the ascending process of the astragalus relative to depth of astragalar body: less or equal (0), greater (1). There has been much discussion regarding the specifics of this character, but it has been observed for decades that increasingly derived theropods show a general increase in the height of the astragalar ascending process (e.g. Welles & Long 1974). In basal theropods, there appears to be a basic increase in the process height, so that it is taller than the depth of the astragalar body. Further increases are relevant only to coelurosaur phylogeny and are not discussed here.

1; 2; 3 (Carnosauria + Coelurosauria, Coelurosauria); 4 (65, 50, Tyrannosauridae); 5; 12 (Tetanurae);

15 (Coelurosauria); 21 (81, 99); 30 (75); 31 (135); 34 (89); 35 (96); 40 (5); 41 (109); 44 (146); 45*a, b* (215); 47*a, b* (155); 48 (167)

146. Width of metatarsal II relative to widths of metatarsals III and IV: subequal (0), reduced (1). Metatarsal II is strongly reduced in shaft diameter relative to III and IV in *Noasaurus*, *Velocisaurus* and *Masiakasaurus* and slightly so in *Elaphrosaurus* and, perhaps, *Deltadromeus*. The condition occurs homoplastically in troodontids as well. In other theropods, II is subequal in size to III and IV.

    14 (Noasauridae); 44 (151); 47*a, b* (163); 48 (172)

147. Proportions of distal end of metatarsal IV: broader than tall (0), taller than broad (1). The distal end of metatarsal IV is relatively broad in primitive theropods and other dinosaurs, exceeding its height (or dorsoventral depth). In most neotheropods, the reverse proportions are evident: the distal end is taller (deeper) than broad. It has also been noted that *Masiakasaurus* and *Deltadromeus* appear to share an unusually narrow distal metatarsal IV (Wilson *et al.* 2003; Sereno *et al.* 2004), but the high degree of variation and lack of associated materials of *Masiakasaurus* make this difficult to assess.

    36*a* (144), 47*a, b* (166, 167)

148. Antarctometatarsus: absent (0), present (1). It has long been noted that several groups of coelurosaurs exhibit a derived metatarsus morphology in which metatarsal III is reduced proximally and 'pinched' between metatarsals II and IV. Most theropods retain a metatarsus in which III has the largest proximal area of the central three metatarsals. However, in most abelisauroids, the 'opposite' condition prevails, where II and IV are further reduced relative to III. The proximal surface of metatarsal III is considerably larger in both anteroposterior and mediolateral dimensions, a condition originally termed an 'antarctometatarsus' by Holtz (see Carrano *et al.* 2002).

    16 (Ceratosauria); 44 (155)

149. Morphology of lateral and medial grooves on pedal unguals: single (0), double (1). So-called 'blood' grooves are present on all theropod pedal ungual phalanges. Primitively, one groove is present on each side (lateral and medial) of the ungual, running approximately parallel with the dorsal surface. Abelisauroids (but not *Ceratosaurus*) are unique in possessing two widely separate grooves on each side of the ungual, which converge at the tip of the bone (Sampson *et al.* 2001; Novas & Bandyopadhyay 2001). The proximal ends of these grooves are often connected by a third, dorsoventrally-directed groove that runs parallel to the proximal surface. Other theropods may show evidence of two grooves, but these are invariably restricted to the most proximal part of the ungual only.

    42 (Abelisauroidea); 44 (156); 48 (175)

150. Mediolateral symmetry of pedal digit II ungual: symmetrical (0), asymmetrical (1). In most theropods, including primitive forms, pedal digit II has a roughly symmetrical, triangular ungual in cross-section. In abelisauroids, this ungual is triangular but strongly asymmetrical mediolaterally.

    44 (157)

151. Length of pedal digit phalanges I-1 + I-2 relative to III-1: greater (0), less than or equal (1). Pedal digit I undergoes progressive reduction throughout non-avian theropods,

although it always retains two phalanges (one an ungual). It does not undergo retroversion until well within Aves and maintains its primitive articulation near the tarsus along the posteromedial shaft of metatarsal II. In most tetanurans, pedal digit I reduction begins by shortening of the phalanges. The result is that digit I is held well off the ground in tetanurans. Primitively (*Eoraptor*, *Herrerasaurus*, coelophysids and *Segisaurus*), the combined length of these phalanges is longer than the first phalanx of digit III, but in tetanurans (*Afrovenator*, *Allosaurus*, *Sinraptor*) they are subequal to it.

    22 (Neotetanurae); 27 (31); 31 (145); 35 (99); 36*c* (34); 38 (382); 40 (87); 44 (158)

Appendix 2. Taxon-by-character matrix for the 21 taxa used in this study

The three outgroup taxa are listed first, followed by the 18 ingroup taxa. Characters are scored from 0 to 1 or 0 to 2. Polymorphisms were assumed to represent uncertainties.

Herrerasaurus   00000 00001 00000 00000 00000 00000 00000 00?00 00000 00000 00000 00100 00000 00000 00000 00000 00000 00000 01000 00000 00001 00000 00000 00000 00000 00000 00000 00000 00000 00000 0

Syntarsus   00000 10010 00000 00000 00000 00000 00000 00000 00100 00000 01000 00000 00000 00100 00100 00001 11010 00100 01000 01000 01000 00000 11011 00000 00000 10110 00000 00100 00100 0

Allosaurus   00000 10000 00000 00001 00000 00000 00000 00000 00111 01100 01101 01001 10000 01000 00111 11000 10010 00000 01100 00000 00001 00000 01000 00000 10110 01000 01000 12001 21011 00000 1

Spinostropheus   ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?12?? ??100 10000 10111 102?? 111?? ?000? ???01 ????? ????? ???1? ????0 ????? 1???? ????? ????? ?

Elaphrosaurus   ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?1(12)?? ??100 1000? 11111 00210 11?00 ?1?00 11101 11100 11110 10110 ?0100 ?10?0 121?1 101?? 011?? ?

Deltadromeus   ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ???0? ????? 10101 1?0?? ????? ????? ??1?0 ?1100 121?1 11?11 0110? ?

Ceratosaurus   00001 21000 00010 00000 01000 00000 00000 00000 ?11?1 10000 11101 11001 11100 11000 11211 112?0 10012 00011 01210 ?1?00 01000 00101 1111? 111?0 10?11 11110 1(01)111 11101 11110 0010? ?

Ekrixinatosaurus   1??1? 0??00 1???? ?100? 1?11? ???1? ????? ?1??? ?1??? ????? ????? ????? ????1 ??0?0 ?1??? ??21? 0011? 01??? ?1(12)?? ?0?0? 10??? ????? ????? 1??11 1111? ????0 ?11?1 1???1 ??1?0 0???? ?

Rugops   11111 01001 11110 10001 110?? ????1 11111 ????? ????? ????? ????? ????? ????? ?1010 1???? ????? ????? ????? ????? ?0??? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?

Ilokelesia ?1??? ????? ????? ????? ??11 1101? ?????
????? ???1 ????? ????? ????? ????? ????? ?1??? ??210
10112 010?1 11??? ????? 1011? ????? ????? ????? ?????
????? ????? ????? ????? ??11 ?

Aucasaurus 11?11 21?01 1??1? ?1?2? ???0? ????1 10?1?
????? ????? ????? ????? ????? ????? ??0?? ????? ???1? ?????
?1??? ??(12)?? ???11 1??0 10111 11111 ?1111 ?111? ??1?0
?1?11 1?1?1 111?? 00111 1

Carnotaurus 11111 21?01 10110 11121 11111 11111
10111 11110 111?? ?1001 11?11 1?111 11111 11010 11211
11210 11112 01011 11211 11111 10110 10111 11111 11111
1111? 11110 ?111? ?11?? ??1?? ?0??? ?

Abelisaurus 11111 21?01 ?1011 11021 11110 1011? 111?1
1?111 ?10?? ?1001 1??1? ??1?? 1???? ???10 1???? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ?

Rajasaurus 11??? ????? ????1 ?1111 111?? ????? ???1?
????? ?1111 ??01? ????? ?211? ???10 11010 112?? ??21?
1???? 0?011 11210 ?11?? ?0??? ????? ????? 0?0?? 1??1
??11 ?1111 111?1 ????? 00??? ?

Indosaurus ????? ????? ????1 11111 111?? ????? ?????
????? ?11?? ???1? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ?

Majungatholus 11111 21001 11011 11111 11111 10011
11011 11111 11111 11011 11111 12111 11111 11010 11211
11210 10112 01011 11(12)11 11111 00110 10111 111?1
?1111 111?1 1??11 ?1??1 11111 11111 00111 ?

Genusaurus ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ?0(12)?? ????? ????? ????? ????? 1?1?1 1?1?? ????0
?12?1 ?11?? ????? ????? ?

Laevisuchus ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ?1??? ???11 ?001?
010?? ?0??? ????? ?0??? ????? ????? ????? ????? ????? ?????
????? ????? ????? ?

Masiakasaurus 01?1? 01110 ????0 00000 ???00 1000?
001?? ????? ??11 ?1001 ????? ??11? 11100 11101 11211
11211 10011 010?? ?0(12)01 11101 001?0 1?11? 1?1?0
111?? ??11 11?10 11211 11111 11111 11111 ?

Noasaurus 0??1? 01110 ????? ????? ????? ????? ?????
????? 1???? ????? ????? ????? ????? ??101 11(12)?? ???11
?1011 0?0?? ????? ????? ?010? ????? ????? ????? ?????
????0 ????? ????? ????? 1???? ?

Velocisaurus ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????0 ?????
1??1 1111? 111?? ?

Appendix 3. Theropod specimens examined

Comparative theropod materials used in this study are presented below in a phylogenetic hierarchy. All specimens were examined firsthand or as casts, except those indicated by an asterisk (of which only published materials and photographs were studied). Taxa in bold were included in the phylogenetic analyses.

Institutional abbreviations

Additional institutional abbreviations are listed in the text under 'Operational Taxonomic Units'.

THEROPODA

Herrerasaurus ischigualastensis (MCZ 7063, 7064; PVSJ 53, 373, 407)

NEOTHEROPODA

COELOPHYSOIDEA

Dilophosaurus wetherilli (UCMP 37302–03, 77270)

COELOPHYSIDAE

Coelophysis bauri (AMNH 2701–8, 2715–53, 7243, 7246; MCZ 4326, 4331–32; UCMP 129618)

Syntarsus kayentakatae (MNA V.2623*)

Syntarsus rhodesiensis (QG 1, 203, 208, 302, 691)

CERATOSAURIA + TETANURAE

Porcieux maxilla (Méchin collection)

CERATOSAURIA

Betasuchus bredai (BMNH 32997)

Ceratosaurus nasicornis (MWC 1.1; UMNH VP 5728; USNM 4735; BYU-VP 4838, 4853, 4908, 4951–2, 5008, 5010, 5092, 8937–8, 8974, 8907, 8982, 9099, 9108, 9141–4, 9152, 9161–3, 9165)

Ceratosaurus? roechlingi (HMN MB.R.1926, 1934, 1935, 1938, 2160, 2166, 37, 68, 69)

Deltadromeus agilis (SGM Din-2; BSP 1912 VIII*)

Elaphrosaurus bambergi (HMN MB.R.38–44, 1755, 1756, 1762)

Genyodectes serus (MLP 26–39*)

ABELISAUROIDEA

Compsosuchus solus (GSI K27/578*)

Jubbulpuria tenuis (GSI K20/612*, K27/614*)

Ligabueino andesi (MACN-N 42)

Ornithomimoides? barasimlensis (GSI K27/531*, 541*, 604*, 682*)

Spinostropheus gautieri (MNHN 1961–28; MNN TIG6)

Tarascosaurus salluvicus (FSL 330201–3)

Noasauridae

Noasauridae indet. (GSI K20/337A-C*, 626B*, K27/524*, 532*, 534*, 552*, 556*, 559*, 561*, 571*, 574*, 587*, 589*, 592*,

599*, 605–616*, 625*, 629–631*, 637–645*, 647–650*, 655*, 657*, 662*, 665–667*, 669, 670*, 681*, 694*, 697*, 712*)
Genusaurus sisteronis (MNHN Bev-1)
Laevisuchus indicus (GSI K20/613*, 614*, K27/588, 696)
Masiakasaurus knopfleri (FMNH PR 2108–2182; UA 8680–8696)
Noasaurus leali (PVL 4061)
Velocisaurus unicus (MUCPv-41)
Abelisauridae
Abelisauridae indet. (AMNH 1955, 1960, 1753; GSI K19/581*, K20/336A-B*, 619, K27/362*, 396*, 399*, 497, 524, 526, 527, 529*, 530*, 532, 533*, 535, 536*, 538, 539, 540*, 543–546*, 548, 550, 551*, 554*, 558*, 560*, 563, 564*, 566–568*, 569, 570*, 572, 573*, 575, 577, 579*, 580, 588, 590, 591*, 593–596*, 598*, 603*, 612*, 617, 618*, 619, 620*, 621, 627*, 628, 632, 633*, 636, 646, 648, 651, 652*, 654, 656*, 658, 659–661*, 663*, 664*, 667, 668*, 671–676*, 677, 678–680*, 683*, 684, 686*, 687, 688, 689*, 690–91, 692*, 693, 698*, 699*, 705, 707*, 708–710, 711*; ISI R163; MPM-99*; UNPSJB-PV 247*)
Abelisaurus comahuensis (MPCA 11908)
Aucasaurus garridoi (MCF-PVPH 236)
Carnotaurus sastrei (MACN-CH 894)
Coeluroides largus (GSI K27/562, 574*, 587*, 595*, 695*)

Dryptosauroides grandis (GSI K20/334*, 609*, 615*, 623–5*, K27/547*, 549*, 555*, 601*, 602*, 626*)
Ekrixinatosaurus novasi (MUCPv-294*)
Ilokelesia aguadagrandensis (MCF-PVPH 35)
Indosaurus matleyi (GSI K27/565, 548*)
Indosuchus raptorius (GSI K20/350*, K27/685*)
Lametasaurus indicus (GSI [lost]*)
Majungasaurus crenatissimus (MNHN MAJ-1, MAJ-4; FMNH PR 2008, 2100; UA 8678; FSL 92.289, 92.290, 92.306, 92.343)
Ornithomimoides mobilis (GSI K20/610*, 614B, K27/586*, 597*, 599*, 600*)
Pycnonemosaurus nevesi (DGM 859-R*)
Quilmesaurus curriei (MPCA PV-100)
Rajasaurus narmadensis (GSI 21141/1-33)
Rugops primus (MNN IGU1)
Xenotarsosaurus bonapartei (UNPSJB-PV 184/PVL 612*)
TETANURAE
ALLOSAUROIDEA
Allosaurus fragilis (CM 11844; MCZ 3897; MOR 693; USNM 4734; UMNH VP 6000)

Supplementary Data

Note added in proof

Recently Allain *et al.* (2007) reported on a new ceratosaur from the Early Jurassic (Pliensbachian–Toarcian) Toundoute beds of Morocco, *Berberosaurus liassicus*. Although incomplete, a number of features clearly identify this important new form as the earliest known ceratosaur. The authors presented a phylogenetic analysis that supported *Berberosaurus* as a primitive abelisauroid and noted that it shortened the missing stratigraphic interval between Ceratosauroidea and Coelophysoidea.

It is beyond the scope of this note to evaluate the analysis of Allain *et al.* (2007) in detail. However, *Berberosaurus* exhibits several character states found only among basal ceratosaurs, e.g. *Ceratosaurus*-like dimorphism in the morphology of the proximal femoral trochanters, lack of a prezygapophyseal–epipophyseal cervical lamina, an accessory fossa on the dorsal surface of the cervical transverse process and the mediolateral proportions of the distal tibia. Inclusion of *Berberosaurus* in our character–taxon matrix places it outside both Abelisauroidea and *Ceratosaurus* and we tentatively consider it to be a basal ceratosaur.

Such a position is more stratigraphically congruent. If *Berberosaurus* were an abelisauroid it would actually lengthen the overall stratigraphic debt by forcing back the origins of every more primitive ceratosaur taxon. In addition, although *Berberosaurus* does shorten the gap between the origins of Ceratosauria and Coelophysoidea, it effectively eliminates the gap between Ceratosauria and Tetanurae, which is also known from the Early Jurassic but not prior. *Berberosaurus* is therefore an important extension of the ceratosaur lineage into the Early Jurassic.

Reference

Allain, R., Tykoski, R., Aquesbi, N., Jalil, N.-E., Monbaron, M., Russell, D. & Taquet, P. 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurus. *Journal of Vertebrate Paleontology* **27**: 610–624.