



SAUROPOD PHYLOGENY AND PALAEOECOLOGY

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ABSTRACT: Phylogeny and palaeoecology are usually treated as separate research areas, although in reality they have much to offer each other. Phylogenetic information may help pinpoint functionally related character complexes, and can reveal the convergent acquisition of character states. The results of a cladistic analysis also assist in taxonomic revision, which in turn can often necessitate a re-appraisal of stratigraphic and geographic distribution. Sauropod phylogeny is currently poorly understood, although recent cladistic work is improving this situation. The results of a recent cladistic analysis, based on 174 osteological characters, are summarised. The cladogram includes several familiar aspects, such as the sister group relationship between brachiosaurids and camarasaurids, and the relatively plesiomorphic nature of *Barapasaurus* and *Vulcanodon*. Less familiar groupings include a monophyletic taxon which contains *Mamenchisaurus*, *Euhelopus* and other Chinese forms. *Opisthocoelicaudia* is removed from the Camarasauridae and placed as the sister taxon to the Titanosauridae. Morphological evolution within the Sauropoda is examined, with a particular emphasis on alterations which may have a bearing on their palaeoecology. The evolution of the dentition is traced in detail and it is suggested that the narrow peg-like teeth of diplodocids and titanosaurs were derived from the larger spatulate teeth found in other sauropods. Other observations include evidence for the convergent acquisition of particularly elongate necks and different types of tail weapon.

RESUMO: A filogenia e a paleoecologia são tratadas normalmente como áreas de pesquisa separadas apesar de terem muito a ganhar uma com a outra. A informação filogenética poderá ajudar na determinação de conjuntos de caracteres relacionados funcionalmente e podem revelar a aquisição convergente de estados de caracteres. Os resultados da análise cladística também auxiliam a revisão taxonômica que, por seu lado, pode necessitar frequentemente de uma reavaliação da distribuição estratigráfica e geográfica. A filogenia dos saurópodes é mal compreendida ainda que trabalhos recentes na área da cladística estejam a melhorar a situação. Resultados recentes obtidos a partir da análise cladística baseada em 174 caracteres osteológicos, são aqui apresentados. O cladograma inclui vários aspectos familiares, como, por exemplo, a relação de grupo irmão existente entre braquiosaurídeos e camarasaurídeos, bem como a natureza relativamente plesiomórfica de *Barapasaurus* e *Vulcanodon*. Agrupamentos menos familiares incluem o taxon monofilético que contém *Mamenchisaurus*, *Euhelopus* e outras formas chinesas. *Opisthocoelicaudia* é retirado dos Camarasaurídeos e colocado como grupo irmão dos Titanosaurídeos. É examinada a evolução morfológica dentro dos saurópodes com particular ênfase em alterações que poderão ter relevância em relação à sua paleoecologia. A evolução da dentição é descrita em detalhe e sugere-se que os dentes estreitos em forma de cravo dos diplodocídeos e titanosaurídeos, derivaram dos dentes espatulados e largos encontrados noutros saurópodes. Outras observações incluem evidências para a aquisição convergente de pescoços longos e de diferentes tipos de armas caudais.

INTRODUCTION

A paper on phylogeny might seem a little out of place in a volume concerned with sauropod palaeoecology. This is because phylogeny and palaeoecology are often investigated as if they were separate research areas. However, no overview of the Sauropoda can be truly "global" unless some account of their evolutionary history is included. There is also a pow-

erful case in support of the view that phylogeny and palaeoecology have much to offer each other.

The following discussion is divided into three main sections. Firstly, the potential value of phylogenetic information to those investigating palaeoecology is examined. Secondly, a brief account of sauropod phylogeny and classification is provided. Finally, instead of simply listing synapomorphies at a series of nodes on a cladogram, the various character state transfor-

mations are examined from the point of view of the evolution of sauropod morphology. The resulting data on "trends", correlations and convergences, could form the raw material for future palaeoecological investigations.

PHYLOGENY AND PALAEOECOLOGY

COOMBS (1990) described three major approaches to the investigation of palaeo-behaviour: functional morphology; comparison with morphologically similar extant forms; and speculation (*i.e.* "scenario building"). This list of principal methods might equally well apply to the wider field of palaeoecology (actually there are several other important approaches, including examination of ichnofossils and other kinds of organism-sediment co-occurrences - as exemplified by many of the papers in this volume). However, there is a growing realisation that a fourth approach, "phylogeny", should also be considered. HARVEY & PAGEL (1991) have discussed at length the use of cladograms in various neontological contexts. Cladograms have been less frequently used in palaeobiology, perhaps because the fragmentary nature of the fossil record has hampered phylogenetic investigations. Nevertheless, some examples do exist. For instance, WEISHAMPEL & HORNER (1994) mapped various "life history characters" (*e.g.* clutch size, hatchling size, adult size, etc.) onto a cladogram of dinosaur relationships. Phylogeny can interact usefully with palaeoecology in a number of ways, as discussed below.

CORRELATION AND CONVERGENCE

In cladistics, the anatomical structures of a taxon are treated as separate units - "characters". Although this is a necessary part of the cladistic method, we should not forget that, in the real world, an organism has to function as a well integrated whole. Alterations in one part of the body may provoke modifications elsewhere. This results in the phenomenon of correlation between characters. Correlation can cause problems in a cladistic analysis since it is intimately related to the weights given to character state transformations. Nevertheless, genuine correlations between characters may reveal much about the organisms concerned. Once a cladogram has been produced, the distribution of the character states on the "tree" may suggest correlations between two or more characters. For example, it seems likely that several derived features in the sauropod skull are related to a few basic modifications, such as changes in the size and position of the external nares. Alternatively, the cladogram might indicate that certain derived states were acquired at different nodes, making it difficult to argue that they are correlated. These considerations have an obvious value for those working on functional morphology. Indeed, the phylogenetic perspective had some influence on an investigation

of sauropod jaw musculature and feeding (BARRETT & UPCHURCH, 1994; CALVO, 1994).

Phylogeneticists often view convergent evolution as a "nuisance" - the "noise" which may obscure the true phylogenetic "signal". However, convergence has great potential value for the palaeoecologist. A well supported cladogram suggests which character states were acquired only once, and which were acquired several times independently. Convergence can strengthen arguments based on the observation of possible correlations. The more often one observes that change "A" is accompanied by change "B", the more reasonable it is to suggest a connection between these two modifications. Similarly, one might find that separate instances of a certain environmental change (*e.g.* the invasion of a new plant group) can be correlated with the convergent acquisition of certain derived states (*e.g.* changes in tooth morphology).

TAXONOMY AND DIVERSITY

One important aspect of palaeoecology is the study of fluctuations in diversity and abundance. However, confused taxonomies can render such studies difficult or even impossible. Cladistic analysis, by making synapomorphies and symplesiomorphies explicit, can help to revise taxonomies. Taxonomic revision can have a profound effect on the apparent diversity of a group. For example, UPCHURCH (1993) used the results from a cladistic analysis in his revision of the taxonomy of British sauropods. The original number of 49 species within 18 genera was reduced to 7 monospecific genera and two new unnamed forms.

A revised taxonomy may radically alter our views on the geographic and stratigraphic distribution of certain forms. For example, "*Titanosaurus*" is known from the Lower Cretaceous of Europe (HUENE, 1929a), and the Upper Cretaceous of India (HUENE & MATLEY, 1933), Argentina (HUENE, 1929b), Madagascar (DEPERET, 1896) and France (BUFFETAUT, *pers. commun.*). Given the fragmentary nature of most of this material, and the inadequate diagnosis of this genus, it seems highly likely that this wide distribution is misleading.

BIOGEOGRAPHY

As indicated above, taxonomic revision can have a profound effect on the apparent geographic range of an organism. Phylogeny and geography can interact in another way. Sauropods existed from the Jurassic-Triassic boundary to the end of the Cretaceous. During this time, Pangaea broke up into Laurasia and Gondwanaland, and then divided further into smaller units such as North and South America (SMITH, SMITH & FUNNELL, 1994). These events would have had a great effect on the distribution of large terrestrial animals like sauropods (see, for example, com-

ments on the distribution of the Diplodocidae and Dicraeosauridae, below).

From the point of view of the palaeoecologist, perhaps the most interesting aspects of sauropod biogeography are those which cannot be explained by large scale geological factors. For example, some sauropods, such as *Brachiosaurus* and *Barosaurus*, seem to have been able to reach Africa from North America (or perhaps *vice versa*) during the Upper Jurassic. However, other groups, including dicraeosaurids and titanosaurs seem to have been restricted to the Gondwanaland continents at this time. The failure of these groups to appear in North America could reflect poor preservation, but it might also have some palaeoecological significance. For example, differences in the food preferences and general habitat requirements of *Brachiosaurus/Barosaurus* and dicraeosaurids/titanosaurs, may have allowed the former to migrate or disperse, while the latter remained confined to a smaller area.

A combination of phylogeny and palaeogeography can help pinpoint biases in the fossil record. For example, the Titanosauridae appear to be very widespread, diverse and abundant in the Upper Cretaceous compared to the Middle Cretaceous. This may represent a genuine biological phenomenon, or it could simply be the result of better preservation of, or more intense collecting from, Upper Cretaceous deposits. According to SMITH, SMITH & FUNNELL, (1994), the Indian subcontinent separated from Africa during the Aptian, and remained isolated from all other land areas for the rest of the Cretaceous. At present, India is well known for its rich Upper Cretaceous titanosaurid faunas, but no sauropods are known from Middle or Lower Cretaceous deposits. Yet the isolation of India in post-Aptian times strongly suggests that sauropods were present on the subcontinent as early as the Aptian.

In short, phylogenetic information is a powerful tool for palaeoecological investigation.

A CLADISTIC ANALYSIS OF SAUROPOD RELATIONSHIPS

Our understanding of sauropod phylogeny is rather poor, especially in comparison with other dinosaur groups such as theropods and ornithischians. The unwieldy nature of much sauropod material, and the probable taphonomic bias against the preservation of complete sauropod skeletons (DODSON, 1990), may have contributed to the neglect of sauropod taxonomy and phylogeny. Cladistic analyses of sauropod relationships have been performed (YU, 1990; UPCHURCH, 1993; WILSON & SERENO, 1994), but few details have been published. The following is designed to be only a preliminary account of the cladistic analysis by UPCHURCH (1993). A much

longer formal presentation of these results will be published elsewhere (UPCHURCH, *in press*).

METHOD

The cladogram in Figure 1 is taken from UPCHURCH (1993) and was produced using PAUP 3.0n (courtesy of David Norman). The original data-matrix contained 174 osteological characters from 32 sauropodomorph taxa (including 24 sauropods). The effects of using different algorithms, alteration of character state weights, and variation in taxon number, were examined. All analyses produced small numbers of virtually identical most parsimonious trees. Further details of the results are given in the legend to Figure 1.

SAUROPOD EVOLUTION

Comprehensive reviews of the taxa included in the cladistic analysis, including details of their preservation and stratigraphic/geographic ranges, can be found in MCINTOSH (1990) and UPCHURCH (1993). HUNT *et al.* (1994) have produced a data-base covering sauropod geographic and stratigraphic distribution. Their views on sauropod classification and evolution are generally compatible with those presented below, although there are some minor differences. TABLE I outlines a tentative classification for the Sauropoda, based on the results of UPCHURCH (1993). This classification includes several new taxonomic groups, such as the "Neosauropoda" and "Nemegtosauridae". These are included purely as convenient 'labels' and will be properly diagnosed elsewhere (UPCHURCH, *in press*).

Traditionally, sauropod origins were explained in terms of a gradual evolution from prosauropod ancestors. For example, ROMER (1956) suggested that the large quadrupedal Melanorosauridae were "transitional" between the smaller bipedal prosauropods (such as *Massospondylus*) and the true sauropods. Most recent studies (SERENO, 1989; GALTON, 1990; UPCHURCH, 1993; GAUFFRE, 1994) have concluded that the Prosauropoda represent the monophyletic sister group to the sauropods. Thus, virtually nothing is known about the Upper Triassic lineage which gave rise to the first Lower Jurassic sauropods. All we can deduce from examination of other early dinosaurs, is that sauropods probably arose from rather small bipedal forms.

The best known early sauropod is *Vulcanodon*, from the Triassic-Jurassic boundary of Zimbabwe (RAATH, 1972; COOPER, 1984). Although RAATH (1972) noted several prosauropod-like features in this genus, most workers now agree that it is the most plesiomorphic of known sauropods (CRUICKSHANK, 1975; COOPER, 1984; GAUTHIER, 1986; BONAPARTE, 1986; UPCHURCH, 1993). There are several other, more fragmentary, Lower Jurassic sauropods, includ-

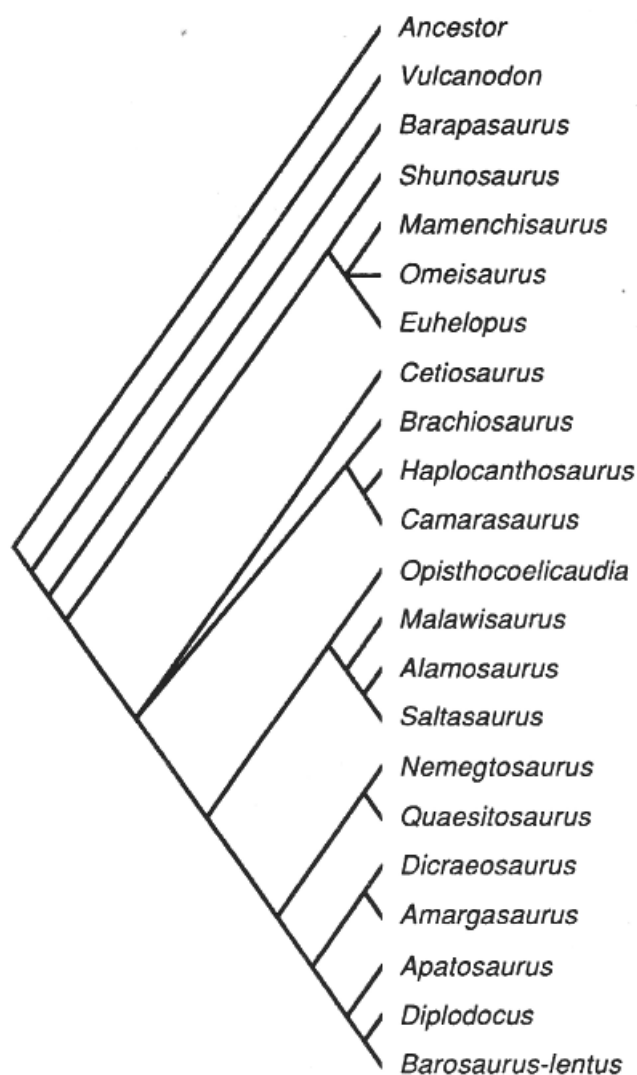


Fig. 1 - A cladogram of sauropod relationships. The original data-matrix contained 174 osteological characters for 32 sauropodomorph taxa. "Ancestor" is a hypothetical taxon which was given the plesiomorphic condition for all characters (as determined by outgroup comparison). 21 sauropod taxa were analysed using the Heuristic algorithm of PAUP 3.0n. All character state transformations were given equal weight. This analysis produced 9 most parsimonious trees which had the following tree statistics: Length = 232 steps; consistency index (excluding uninformative characters) = 0.630; retention index = 0.772; revised consistency index = 0.539. The cladogram shown here is an Adams consensus tree based on the original 9 most parsimonious trees. The topologies of these 9 trees were identical, apart from some uncertainty surrounding the interrelationships of *Mamenchisaurus*, *Omeisaurus* and *Euhelopus*, and the position of *Cetiosaurus* relative to other neosauropod groups (hence the presence of two trichotomies). Other analyses performed by UPCHURCH (1993) produced results very similar to that shown here.

ing: *Sanpasaurus*, *Zizhongosaurus* and *Kunmingosaurus* from China (DONG, ZHOU & ZHANG, 1983; DONG, 1992); *Ohmdenosaurus* from the Toarcian of Germany (WILD, 1978); and *Barapasaurus* from India (JAIN *et al.*, 1979). Characteristic sauropod footprints have also been reported from the Lower Jurassic of Morocco (JENNY & JOSSEN, 1982; ISHIGAKI, 1986). Most of these remains are too fragmentary for their relationships to other sauropods to be reconstructed. However, they do at least suggest that sauropods were geographically widespread, and perhaps taxonomically diverse, as early as the Lower Jurassic. This is consistent with the view that sauropods actually diverged from other dinosaur lineages during the Upper Triassic.

The remaining sauropods form a monophyletic group which was termed the "Eusauropoda" by UPCHURCH (1993). This is divided into two main assemblages; the Euhelopodidae and the "Neosauropoda". The Euhelopodidae are a monophyletic group containing only Chinese taxa from the Middle and Upper Jurassic, and possibly the Lower Cretaceous. Figure 1 shows that this Chinese radiation includes *Mamenchisaurus* and *Euhelopus*. These genera do not, therefore, belong in the Diplodocidae and Camarasauridae (*contra* MCINTOSH, 1990). RUSSELL & ZHENG (1993) reported skull elements, including the mandible, belonging to *Mamenchisaurus*. These strongly suggest that this genus is not a diplodocid.

The discovery of a monophyletic group entirely composed of Chinese taxa has obvious implications for our understanding of sauropod biogeography. One possibility is that a group of sauropods became geographically isolated from other forms at some point in the Lower/Middle Jurassic, and formed an endemic radiation. Geological evidence supporting the isolation of China at this time is discussed by UPCHURCH (*in press*). Several other Chinese sauropods, including *Datousaurus* (DONG & TANG, 1984), *Klamelisaurus* (ZHAO, 1993) and "*Nurosaurus*" (an undescribed form mentioned by DONG, 1992), possess features which suggest that they also belong to the Euhelopodidae. The relationships of a few Chinese genera, including the Middle Jurassic *Bellusaurus* and *Tianshanosaurus*, remain unresolved. These forms have been associated with some of the neosauropod families (MCINTOSH, 1990; JACOBS *et al.*, 1993) but there is little evidence for this (UPCHURCH, *in press*).

The "Neosauropoda" contains most of the familiar sauropod families, including the Cetiosauridae, Brachiosauridae, Camarasauridae, Titanosauridae, Diplodocidae and Dicraeosauridae. Note that "Neosauropoda" is used here in the more restricted sense of UPCHURCH (1993) rather than the more inclusive group recognised by WILSON & SERENO

TABLE I

Revised classification of the Sauropoda. Whilst the following includes several taxa not involved in the cladistic analyses, it should be noted that this classification is far from comprehensive. It is designed merely as a provisional revision, and much work on the diagnosis of some genera and species is still required. For an alternative sauropod classification, based on the review of MCINTOSH (1990), see HUNT *et al.* (1994).

Sauropodomorpha HUENE, 1932
Sauropoda MARSH, 1878**"Eusauropoda"****Vulcanodontidae COOPER, 1984***Barapasaurus* JAIN *et al.*, 1975*Vulcanodon* RAATH, 1972**Euhelopodidae ROMER, 1956***Datousaurus* DONG & TANG, 1984*Euhelopus* ROMER, 1956*Mamenchisaurus* YOUNG, 1954*Omeisaurus* YOUNG, 1939*Shunosaurus* DONG, ZHOU & ZHANG, 1983**"Neosauropoda"****Cetiosauridae LYDEKKER, 1888***Amygdalodon* CABRERA, 1947*Cetiosaurus* OWEN, 1841*Patagosaurus* BONAPARTE, 1979**Brachiosauridae***Brachiosaurus* RIGGS, 1903*Lapparentosaurus* BONAPARTE, 1986*Pleurocoelus* MARSH, 1888*Ultrasaurus* JENSEN, 1985**Camarasauridae COPE, 1877***Camarasaurus* COPE, 1877*Cathetosaurus* JENSEN, 1988*Haplocanthosaurus* HATCHER, 1903**"Titanosauroida"***Opisthocoelicaudia* BORSUK-BIALYNICKA, 1977**Titanosauridae LYDEKKER, 1885***Alamosaurus* GILMORE, 1922*Andesaurus* CALVO & BONAPARTE, 1991*Malawisaurus* JACOBS *et al.*, 1993*Saltasaurus* BONAPARTE & POWELL, 1980**"Diplodocoidea"****"Nemegtosauridae"***Nemegtosaurus* NOWINSKI, 1971*Quaesitosaurus* KURZANOV & BANNIKOV, 1983**Dicraeosauridae***Amargasaurus* SALGADO & BONAPARTE, 1991*Dicraeosaurus* JANENSCH, 1914**Diplodocidae MARSH, 1884***Apatosaurus* MARSH, 1877*Barosaurus* MARSH, 1890*Diplodocus* MARSH, 1878*Seismosaurus* GILLETTE, 1987

(1994). The Cetiosauridae are a problematic family, containing several potentially important but rather poorly known forms (*Cetiosaurus*, *Patagosaurus*, *Amygdalodon*). It is possible that this family is paraphyletic with respect to the rest of the "Neosauropoda" (UPCHURCH, *in press*).

The remaining sauropods divide into two main groups, the brachiosaurid-camarasaurid and the titanosauroid-diplodocoid clades. The Brachiosauridae were only represented by *Brachiosaurus* itself in the cladistic analysis. However, there are numerous other taxa which probably belong to this family. For example, JENSEN (1985) reported a very large form, *Ultrasaurus*, from the Morrison Formation of Colorado. *Brachiosaurus* is known from the Upper Jurassic of both North America and Tanzania, and fragmentary evidence from England also indicates the presence of brachiosaurids in Europe at this time (UPCHURCH, 1993). Members of this family are also known from the Lower/Middle Cretaceous of North America and Europe, as demonstrated by the presence of *Pleurocoelus* in Texas and Maryland (LANGSTON, 1974) and dorsal vertebrae of a brachiosaurid from the Barremian Wessex Formation of the Isle of Wight, England.

Several of the genera included within the Camarasauridae by MCINTOSH (1990) are here placed in other families. The remaining forms (TABLE I) are all Upper Jurassic genera from North America. The inclusion of *Camarasaurus* and *Cathetosaurus* is not controversial, but the referral of *Haplocanthosaurus* is somewhat unexpected. The latter genus has previously been considered to be a cetiosaurid (MCINTOSH, 1990) or a close relative of the Dicraeosauridae (BONAPARTE, 1986). Comparison of *Haplocanthosaurus* with the best preserved specimens of the English *Cetiosaurus* (at LCM¹ and OUZM²) suggest that nearly all of the similarities between these genera are, in fact, symplesiomorphies. It is also interesting to note that the only other cladistic analysis based on a large data-set has also proposed a close relationship between *Haplocanthosaurus* and *Camarasaurus* (WILSON & SERENO, 1994). It is highly likely that camarasaurids existed outside North America. Several fragmentary specimens from the Lower/Middle Cretaceous of Europe, including "*Chondrosteosaurus*" from the Isle of Wight, appear to have camarasaurid affinities.

The remaining sauropods have been grouped into two monophyletic superfamilies, the "Titanosauroidea" and the "Diplodocoidea". The latter

contains two familiar families, the Dicraeosauridae and Diplodocidae, and a new family, the "Nemegtosauridae". The earliest known diplodocoid appears to be *Cetiosauriscus stewarti* from the Callovian of Cambridgeshire, England. This form is probably more closely related to the Diplodocidae than to the Dicraeosauridae, but the possibility that it is a basal diplodocoid cannot be ruled out (UPCHURCH, *in press*).

The Diplodocidae are generally restricted to Europe and North America during the Upper Jurassic and Lower Cretaceous, although *Barosaurus* is also found in east Africa (MCINTOSH, 1990). In contrast, dicraeosaurids are only known from Africa and South America. It is tempting to regard the diplodocids and dicraeosaurids as separate (though closely related) Laurasian and Gondwanan radiations. The separation of Laurasia and Gondwanaland from the Callovian onward (SMITH *et al.*, 1994) supports this view, although it does not explain how *Barosaurus* managed to reach Africa during the Upper Jurassic.

The "Nemegtosauridae" includes two genera, *Nemegtosaurus* and *Quaesitosaurus*, from the Late Cretaceous of Mongolia (NOWINSKI, 1971; KURZANOV & BANNIKOV, 1983). Both forms are only known from isolated skulls, making it more difficult to assess their affinities. There is substantial evidence, however, that these forms are closely related to other diplodocoids. For example, both *Quaesitosaurus* and *Nemegtosaurus* possess elongate preorbital regions (BARRETT & UPCHURCH, 1994), and the latter genus has fully retracted external nares which face dorsally. Some of the cranial material assigned to "*Antarctosaurus*", a titanosaurid from South America and India, appears to belong to an unusual diplodocoid (JACOBS *et al.*, 1993; UPCHURCH, *in press*). This form cannot be placed within any of the three diplodocoid families employed here. If these interpretations are correct, it would appear that two diplodocoid lineages survived from the Upper Jurassic to Upper Cretaceous times. These lineages have apparently not yet been discovered in rocks older than the Upper Cretaceous. This illustrates just how little we still know about sauropod evolution.

The "Titanosauroidea" contains the well-known but poorly understood titanosaurs, and *Opisthocoelicaudia*. The latter has previously been interpreted as a camarasaurid (BORSUK-BIALYNICKA, 1977; MCINTOSH, 1990), but several of the synapomorphies, which support this view, are actually plesiomorphic. In addition, *Opisthocoelicaudia* and the

(1) LCM - Leicester City Museum and Art Gallery, Leicester, UK.

(2) OUZM - Oxford University Museum of Zoology, Oxford, UK.

Titanosauridae share several derived states, including extremely robust radii and ulnae.

The Titanosauridae first appear in the Upper Jurassic of Africa in the form of the fragmentary genus *Janenschia* (= "*Tornieria*", WILD, 1991). Although there are some doubts surrounding the association of the material assigned to this genus (MCINTOSH, 1990), JACOBS *et al.* (1993) and UPCHURCH (*in press*) have noted the titanosaurid nature of the caudal vertebrae and forelimb elements respectively. Lower Cretaceous titanosaurids are known from Europe (caudal vertebrae and possibly some forelimb material) and Africa (disarticulated remains belonging to *Malawisaurus*). *Malawisaurus* is particularly important since it includes some of the first cranial material that can be reliably assigned to a titanosaurid (JACOBS *et al.*, 1993). The *Malawisaurus* premaxilla has a tall ascending process, suggesting that the external nares were relatively large and placed near the rostral end of the skull. This would give the skull a somewhat brachiosaurid-camarasaurid appearance (a factor which may have contributed to WILSON & SERENO's, 1994, suggestion that brachiosaurids and titanosaurids are sister taxa. From the Aptian-Albian onwards, there are scattered reports which suggest that titanosaurids had achieved an even wider geographic range. These include *Andesaurus* from the Cenomanian of Argentina (CALVO & BONAPARTE, 1991), *Aegyptosaurus* from the Cenomanian of Egypt (STROMER, 1932), and unnamed forms from Kazakhskaya (RIABININ, 1939) and Laos (HOFFET, 1942). Titanosaurids were also probably present on the Indian subcontinent from the Aptian onwards (as explained earlier). Upper Cretaceous titanosaurid faunas are particularly well preserved and have been found in India, Madagascar and Argentina. *Alamosaurus*, from the Maastrichtian of southwestern USA, apparently represents a form most closely related to South American titanosaurids. This, combined with other evidence, has led to the suggestion that sauropods died out in the USA after the Albian, and re-invaded from South America during the Campanian-Maastrichtian via the Panamanian landbridge (BONAPARTE, 1984; LUCAS & HUNT, 1989).

In very general terms, sauropod evolutionary history can be divided into four main phases:

1 - The first phase saw the origins of the sauropods during the Upper Triassic, and the diversification and dispersal of the vulcanodontids during the Lower Jurassic.

2 - The second phase was marked by the radiation of the Euhelopodidae in China during the Lower/Middle Jurassic, and the appearance of neosauropod-like forms (cetiosaurids) elsewhere.

3 - The third phase saw the rise of familiar Upper Jurassic and Lower/Middle Cretaceous faunas. The

Euhelopodidae continued to occupy eastern Asia but elsewhere sauropod faunas were dominated by brachiosaurids and diplodocoids. The titanosaurids arose during this third phase, but appear to have formed only a relatively small component of most sauropod faunas.

4 - The fourth phase saw the disappearance of the euhelopodids, brachiosaurids, camarasaurids and most diplodocoids. From the Middle Cretaceous onwards, titanosaurids dominated most sauropod faunas. One exception to this is eastern Asia where nemegtosaurids demonstrate the continuing importance of diplodocoids. Despite the presence of these apparently "thriving" Upper Cretaceous sauropod faunas, all sauropods became extinct at the end of the Cretaceous.

SAUROPOD MORPHOLOGICAL EVOLUTION

The following discussion examines some aspects of sauropod morphological evolution. This is not intended to be a detailed list of the synapomorphies supporting the relationships in Figure 1. Rather, it is meant as a series of examples illustrating changes in sauropod morphology which may have had a bearing on their palaeobiology.

THE SKULL

Skull structure, feeding and jaw musculature: Sauropod skulls have been modified, relative to other dinosaurs, in ways which suggest alterations in the orientation and relative importance of various jaw muscles. Some of these are explored in more detail in BARRETT & UPCHURCH (1994). Examples of modifications that would have affected jaw muscle attachment and orientation include:

1 - Postorbital bar slants anteroventrally in eusauropods, rather than vertically as in other dinosaurs. The infratemporal fenestra therefore extends forwards beneath the orbit. This is seen in a mild condition in euhelopodids, and much more prominently in neosauropods.

2 - The excavated area ("fossa") around the margin of the supratemporal fenestra is reduced (euhelopodids) or absent (neosauropods). The supratemporal fenestra is reduced in diplodocoids, and faces laterally in dicraeosaurids.

3 - The ectopterygoid process of the pterygoid is shifted anteriorly in the eusauropod skull, so that it lies below or in front of the antorbital fenestra. The process remains robust in most eusauropods, but has been greatly reduced in *Diplodocus* and *Apatosaurus*.

4 - The external mandibular fenestra is greatly reduced in euhelopodids (including *Mamenchisaurus*, RUSSELL & ZHENG, 1993), and is closed in neosauropods. A similar situation is found in orni-

thopods (SERENO, 1986) and carnosaurs (GAUTHIER, 1986).

Several other alterations to the sauropod skull probably relate to changes in feeding styles. The skulls of many early dinosaurs, including basal theropods (*Herrerasaurus*, SERENO & NOVAS, 1994), basal ornithischians (*Lesothosaurus*, SERENO, 1991) and prosauropods, are triangular in dorsal view, with rather acute rostral tips. Sauropods, as in many "advanced" theropods and ornithischians, have broadly rounded snouts. Sauropods also show numerous alterations to their dentitions (see below).

Narial retraction: One of the most characteristic features of the eusauropod skull is the posterior displacement ("retraction") of the external nares. In euhielopodids, brachiosaurids, camarasaurids and titanosaurs, "partial" narial retraction has occurred: the external nares lie anterodorsal to the antorbital fenestrae, but still face laterally (Fig. 2A-B). Several other characters, including the shortening of the skull roof and the posterior shift of the contact between maxillary ascending process and the dorsal end of the lacrimal, may be correlated with narial retraction. In diplodocoids, the external nares have been displaced even further posteriorly and now lie posterior to the anterior rim of the antorbital fenestra (Fig. 2C). The external nares are smaller and the internarial bar (formed from the premaxillae and nasals) is absent, thus forming a single large opening. Unlike other sauropods, diplodocoids have external nares which face dorsally. This extreme form of narial retraction may be correlated with a profound re-arrangement of the bones of the snout. The premaxillae have become extremely elongate (anteroposteriorly), enabling them to continue to form part of the margin of the external nares. These bones have also become rather narrow transversely, and the distinction between "main body" and ascending process is much less marked than in other sauropods. At present, the functional significance of these modifications to the external nares is poorly understood.

Dentition: Sauropod dentition is often described in simple terms as either "spatulate" or "peg-like". In fact, the situation is somewhat more complex (see also CALVO, 1994). The teeth of early sauropods were probably "spatulate" and coarsely serrated. Serrations are present on the teeth of *Barapasaurus* (JAIN *et al.*, 1979), *Omeisaurus* (HE *et al.*, 1984) and *Mamenchisaurus* (RUSSELL & ZHENG, 1993). The presence or absence of serrations is variable not only at the generic level (*e.g.* they are absent in *Shunosaurus* and *Euhelopus*) but also from tooth to tooth within a single individual (RUSSELL & ZHENG, 1993).

The typical spatulate tooth has a lanceolate crown with a mesiodistally convex labial surface. This surface is normally marked by two grooves, one near each of the mesial and distal margins. These grooves

run parallel to the margins of the crown. The tooth is mesiodistally widest at a point close to its base. The mesial and distal margins are acute, and converge on a slightly recurved tip. The lingual surface is concave, both mesiodistally and dorsoventrally. This concave area is usually partly occupied by a ridge which runs along the length of the crown, curving slightly distally towards the tip. Although there are differences in proportion and absolute size, essentially spatulate teeth are known in *Barapasaurus*, euhielopodids, cetiosaurids, brachiosaurids and camarasaurids. This distribution, according to the relationships in Figure 1, would suggest that the peg-like teeth of titanosaurs and diplodocoids, were derived from the spatulate condition. There is some morphological evidence to support this view. Peg-like teeth have crowns which are longer and more slender than those of spatulate teeth. The former have also lost the concavity on the lingual surface (a reversal to the plesiomorphic state). However, in *Malawisaurus*, *Nemegtosaurus*, *Quaesitosaurus* and *Dicraeosaurus*, the peg-like teeth retain the grooves on the labial surface. Similar grooves can also be found on the lingual surface, almost as if the lingual concavity was obliterated by an increase in size of the central ridge. In *Diplodocus*, the tooth crowns show no sign of the labial or lingual grooves, and the point at which the crown starts to taper is situated very close to the crown tip.

Sauropods also show considerable variation in the positioning and arrangement of the dentition. The tooth row ends more anteriorly than in other dinosaurs (most posterior alveolus beneath or in front of the antorbital fenestra). In diplodocoids this feature is carried to extremes, with all of the teeth "crammed" into the anterior portion of the snout (Fig. 2C). This is related to the formation of the "tooth combs" (BARRETT & UPCHURCH, 1994). Sauropod teeth are also procumbent, *i.e.* the crowns "lean" forwards. Finally, the teeth in euhielopodids remain fairly constant in size along the tooth row (apart from the most posterior ones), whereas in neosauropods there is usually a marked increase in size towards the anterior end of the upper jaw.

AXIAL SKELETON

Neck lengthening: All sauropods have long necks compared to other dinosaurs, but there is also variation in relative neck length within the Sauropoda. For example, the neck in *Mamenchisaurus* forms nearly 45% of total body length, whereas that in *Dicraeosaurus* represents only about 30% (or less, depending on assumed tail length). Brachiosaurids, diplodocoids and euhielopodids (excluding *Shunosaurus*) appear to have the longest necks amongst the sauropods. The relationships in Figure 1 would suggest that these long necks were acquired convergently. This view is supported by the details of neck

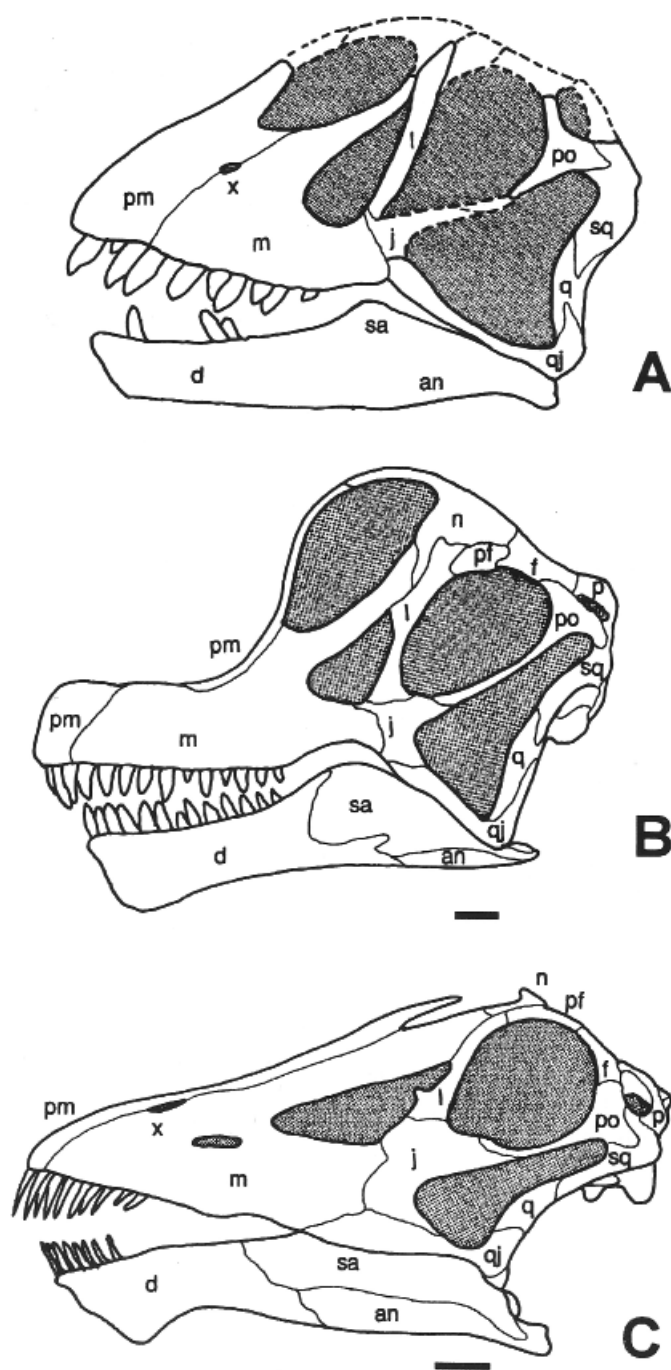


Fig. 2 - Examples of three sauropod skulls in left lateral view. **A** - *Euhelopus* (after MATEER & MCINTOSH, 1985). **B** - *Brachiosaurus* (after JANENSCH, 1935-36). **C** - *Diplodocus* (based on CM11161). Abbreviations: an - angular; d - dentary; f - frontal; j - jugal; l - lacrimal; m - maxilla; n - nasal; p - parietal; pf - prefrontal; pm - premaxilla; po - postorbital; q - quadrate; qj - quadratojugal; sa - surangular; sq - squamosal; x - premaxilla-maxilla foramen. All scale bars: 50 mm. CM - Carnegie Museum of Natural History, Pittsburgh, USA.

structure. There are at least three ways in which a neck can be lengthened: invention of new cervical vertebrae; conversion of dorsal vertebrae into cervicals; elongation of cervical vertebrae. All three sauropod groups have achieved their long necks in slightly different ways. *Brachiosaurus* has 12 (or per-

haps 13) cervicals and 12 (11?) dorsals - probably the plesiomorphic state for the "Eusauropoda". The neck has been lengthened, therefore, solely by elongation of individual cervical vertebrae. In diplodocids, there are 15 cervicals and 10 dorsals. This suggests that at least part of neck lengthening was due to the conver-

sion of dorsals into cervicals. Individual vertebrae have also been lengthened, especially in *Diplodocus* and *Barosaurus*. Finally, the euhelopodids have at least 17 cervicals, and 12-14 dorsals. Conversion of dorsals alone cannot account for the increase in cervical number, so it seems likely that the neck was lengthened by the invention of new cervicals. Individual cervicals are also extremely elongate.

Tail weapons and forked chevrons: The cladogram in Figure 1 suggests that forked or "skid-like" chevrons were acquired independently by the Euhelopodidae and the Diplodocidae/Dicraeosauridae. UPCHURCH (1993) noted some differences in the chevrons of the two groups. For example, in diplodocids and dicraeosaurids, the more anterior forked chevrons develop a slit-like opening along the ventral midline. In more posterior chevrons this slit increases in size until the left and right rami lose contact altogether. These features are absent in the chevrons of euhelopodid sauropods. BAKKER (1986) has suggested that forked chevrons allowed the tail to be rested on the ground during "tripodal" feeding (see UPCHURCH, 1994a). However, CHARIG (1980) has proposed that these elements protected subvertebral blood vessels and nerves in those forms which used their tails as weapons. Euhelopodids have rather short tails (35-40 caudals), and in *Shunosaurus* and *Omeisaurus* the tail appears to have ended in a "club" (DONG, PENG & HUANG, 1989: fig. 1-2). Diplodocids are well known for their long tails (70-80 caudals) which terminate in a distal "whiplash" (see CZERKAS, 1994, for more detail on the structure of the "whiplash"). Thus, the presence of forked chevrons might be correlated with the use of the tail as a weapon. The tail club and whiplash are clearly convergently acquired weapons, and the forked chevrons in euhelopodids and diplodocids may also have been convergently acquired. If correct, dicraeosaurids should be reconstructed with whiplash tails, whereas *Mamenchisaurus* and *Euhelopus* would have had tail clubs.

APPENDICULAR SKELETON

Relative forelimb length: The relative length of the forelimb has several palaeoecological implications. For example, the relatively long forelimbs of sauropods imply that they walked quadrupedally (as has now been confirmed by trackway evidence, e.g. BIRD, 1939; THULBORN, 1989, 1990). Particularly long forelimbs may reflect the need to raise the shoulder region, perhaps as part of a quadrupedal high browsing stance (as in *Brachiosaurus*). Shortened forelimbs would lower the shoulder region, perhaps in relation to feeding at lower levels (BARRETT & UPCHURCH, 1994). Alternatively, shorter forelimbs would shift the centre of gravity to a point near the acetabulum, making a bipedal stance more feasible (BAKKER, 1986). Unfortunately, most sauropods are

too poorly known for accurate forelimb/hindlimb ratios to be calculated. However, a brief survey of the currently available information on forelimb length is given below.

The humerus and femur of *Vulcanodon* are damaged, making it impossible to establish their lengths accurately. However, reasonable estimates of their lengths, combined with measurements from the radius, metacarpals, tibia and metatarsals, indicate a probable forelimb/hindlimb ratio of ~ 0.76 (compared to 0.6 or less in most non-sauropod dinosaurs). Euhelopodids, camarsaurids, *Opisthocoelicaudia* and titanosaurs have ratios of approximately 0.75-0.80. *Brachiosaurus* is not known from material complete enough to allow a ratio to be calculated, but the general appearance of the forelimb suggests that it would have been more than 80% of hindlimb length. Diplodocids and dicraeosaurids have forelimb/hindlimb ratios of ~ 0.66 -0.70. The position of these two families in Figure 1 indicates that their reduced forelimb length is a specialisation, and not the retention of the plesiomorphic state.

CONCLUSION

Phylogenetic data can be used in the context of a palaeoecological investigation. A cladogram may suggest correlations and convergences which are relevant to the more traditional palaeoecological approaches such as functional morphology and comparison with appropriate living analogues. Before this can occur, however, a well supported phylogeny must be established. Sauropod phylogeny has received much less attention than that of other major dinosaur groups. It is hoped that this paper, and future publications, will help to stimulate interest in this field. Sauropods have much to offer the palaeoecologist. They were a diverse, widespread and long-lived group, which attained a body form and size not seen in any extant terrestrial animals. If we are to achieve a truly "global" view of sauropod biology, we cannot escape the need to investigate their evolutionary relationships.

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