SAUROPOD FEEDING: DIFFERENTIATION AND GHOST LINEAGES

CORALIA-MARIA JIANU
Muzeul Civilizației Dacice si Romane Deva,
B-dul 1 Decembrie Nr. 39, 2700 Deva, Romania
and
DAVID B. WEISHAMPEL
Department of Cell Biology and Anatomy, The Johns Hopkins University,
School of Medicine, Baltimore, Maryland 21204,U.S.A.

REZUMAT

Unul dintre cele două mari grupe de dinozauri ierbivori – Sauropoda – este cunoscut în toată lumea începând din Jurasicul Inferior până la sfârşitul Cretacicului, având maxime în Jurasicul Superior, Cretacicul Inferior şi Cretacicul Superior.

Combinând informaţiile filogenetice cu aspectele funcţionale ale hrănirii, acest studiu lărgeşte aria estimărilor iniţiale.

Combinarea filogeniei şi cronostratigrafiei se foloseşte pentru a se detecta prezenţa aşa numitelor "ghost lineages" (strămoşi fantomă) şi distribuţia acestora în cadrul Sauropodelor. Aceştia sunt răspândiţi prin tot grupul, dar fac parte integrantă din cladele superioare.

Dacă probăm diversitatea la un interval de 2.5 milioane de ani, observăm un maxim la începutul Jurasicului, urmat de un declin în timpul Jurasicului mediu, apoi cel mai mare maxim la sfârşitul Jurasicului, în timpul căruia diversitatea temporală „a sărit" aproximativ de 7 ori (datorită cladogenezei crescute în cadrul brachiosauridelor, camarasauridelor, titanosauridelor şi diplodocoidelor). Apoi, nivelul diversităţii scade gradat pâna la sfârşitul Mesozoicului, cu un declin final abrupt începând din Campanian până în Maastrichtian.

Optimizarea grupurilor în funcţie de tipul de hrănire pe filogenie indică o radiaţie rapidă în Jurasicului Superior a sauropodelor cu dinţii în formă de con comprimat, şi de tip "peg-spoon", nivelele diversităţii acestor grupuri trofice bazate pe "ghost lineages" par să nu aibă nici o relaţie cu dinamica diversităţii printre plantele contemporane.

În cele din urmă, analizele bazate pe "ghost lineages" indică faptul că gradul nostru de cunoaştere este foarte limitat în ceea ce priveşte evoluţia modului de hrănire al sauropodelor.

INTRODUCTION Populated by drastically different creatures, the Mesozoic was almost a world of its own. Dinosaurs dominated the terrestrial realm, occupying virtually all ecosystem levels from primary consumers to top predators. Then, 65 million years ago, when an asteroid collision decimated 95% of all life on land and in the sea, all of these food-web associations completely disintegrated. Following this dramatic biotic reshuffling, many of the overarching ecosystem relationships were somehow maintained, to be rebuilt largely from a mammalian perspective.

Many attempts have been made to understand ancient trophic relationships by analogy with the modern world, especially from this mammalian point of view. In particular, investigations of herbivore-plant interactions during the Mesozoic have emphasized the ways in which synapsid and diapsid herbivores mutually related with terrestrial tracheophyte plants. By grouping faunas and floras in terms of the taxa associated with one another or the features that reflect this plant-herbivore interaction (tooth shape, foliage type, etc.), it is then possible to examine these groupings in light of their paleobiogeographic and temporal distributions. Expectations are that these groupings will provide a better understanding of possible coevolutionary patterns (e.g., Bakker 1978, Benton 1984, Tiffney 1986, Farlow 1987, Coe et al. 1987, Wing and Tiffney 1987).

In addition to its devastating climax, the Mesozoic is also particularly important in view of the profound evolutionary radiation of angiosperms beginning in the latter half of the Early Cretaceous and extending through the end of the Period (Doyle and Donoghue 1986, Crane 1989). In view of these changes in the plant realm, not only in diversity, but also in physiognomy and life histories (Crane 1987, Upchurch and Wolfe 1987), contemporary herbivores surely confronted new feeding opportunities and perhaps problems associated with the digestion of these new plants. Consequently, it is important to evaluate changes in taxonomic diversity and feeding systems among contemporary primary consumers of these angiosperms and other plants.

Two great clades of dinosaurs lived in this world of tracheophytes (e.g., angiosperms, “gymnosperms”, and “pteridophytes”). One - Ornithischia - has received the greatest interest in studies of the evolution of Mesozoic herbivory, in part because of the diversity and complexity of their chewing apparatus (Weishampel and Norman 1989, Weishampel and Jianu in press). The other great clade - Sauropodomorpha - lacks much of the masticatory sophistication of ornithischians (Dodson 1990a). However, they clearly surpassed the latter in one of the most fundamental of biological properties, that of body size (Farlow 1987). At any time during their long Mesozoic reign, sauropods were always at least an order of magnitude larger than contemporary ornithischians.

Among sauropodomorphs, we focus on sauropods in this paper (fig. 1). These long necked, long-tailed quadrupeds are, for many, the "archetypal" dinosaurs. Beyond that, sauropod diversity, biology, and phylogeny are becoming much better known than ever before in the 150 years of their study. For example, feeding differentiation, once regarded as minimal (Weishampel and Norman 1989), is now known to be fairly great based on differences in dentitions, tooth wear, jaw mechanics, neck biomechanics and browse height, gut size, and occasional presence of gastroliths (Fiorillo 1991, Barrett and Upchurch 1994, Calvo 1994a, b). In addition, phylogeny now comprises a major research effort in sauropod studies (e.g., Upchurch 1995, 1998, Wilson and Sereno 1998), with many longstanding controversies about relationships beginning to be resolved (cf. McIntosh 1990).

In our efforts to better understand sauropods (and other taxa) as dominant among Mesozoic herbivorous vertebrates, we have developed a new approach to diversity estimates. Its aim is to tease apart the relationship between taxonomic and function diversity among these herbivores on the one hand and changes among Mesozoic plants on the other (Weishampel and Jianu in press). Called "Ghost Lineage Analysis", this approach begins with traditional sources of data (e.g., a temporal census of species-level taxa; Weishampel and Norman 1989). These raw stratigraphic data are then combined with phylogenetic information to yield a stratigraphically-calibrated phylogeny. Although it does not completely correct for the inherent biases of the fossil record, ghost lineage analysis provides additional information about diversity not present in the raw fossil data. Ghost lineage analyses operate on both taxic and functional levels, the former by maintaining the continuity between sibling species and their common ancestor, while the latter by interpreting this continuity in functional (or behavioral) terms via optimization analysis. These two aspects of ghost lineage analysis are discussed following our discussion of sauropods and their groups of feeding.

SAUROPOD TAXA, DIVERSITY PATTERNS, AND FEEDING GROUPS

Sauropods have long been considered a monophyletic group, but internal relationships have been unclear until recently. Upchurch (1995, 1998) recognized euhelopodids, diplodocoids, camarasaurids, brachiosaurids, and titanosauroids as monophyletic clades, with other taxa interpolated among them (fig. 2), while Wilson and Sereno (1998), using a smaller sample of taxa, identified three of these clades (diplodocoids, brachiosaurids, titanosaurids); their study however advocated different relationships among them and between them and other taxa (fig. 3). It is not our purpose to assess the relative merits of the Upchurch and Wilson-Sereno studies in what follows. Instead, we will use Upchurch's phylogenetic analyses in our analyses, leaving the Wilson-Sereno cladogram and its diversity implications for another study.

Historically, sauropods have been best known from the Late Jurassic of North America (the famous Morrison fauna of the western United States), but most recently from the Middle and Late Jurassic of eastern Asia and the Cretaceous of South America. Taken as a whole, however, sauropods are known worldwide from the Early Jurassic through the end of the Cretaceous (McIntosh 1990, Weishampel 1990). When sampled through this interval at the species-level, sauropod diversity fluctuates dramatically on a stage-by-stage basis. There is a peak in the Late Jurassic (North American and Chinese sauropods), another less substantial peak in the mid-Cretaceous (South American sauropods), and another just prior to the end of the Cretaceous (dominated by titanosaurid sauropods from Gondwana; data from Weishampel and Norman 1989, with updates).

As the world's largest terrestrial plant-eaters, these quadrupedal herbivores ranged upwards in length to 30 m and must have been formidable plant-eaters (McIntosh 1990, Dodson 1990a). However, beyond their size, sauropods have not been regarded as having particularly complex adaptations for herbivore. Consequently, Weishampel and Norman (1989) characterized the entire clade as gut processors in large part because of their simple teeth, lack of documented tooth wear and the sporadic preservation of gastroliths in sauropods as a whole.

More recent studies have shown that this characterization is much too simple. The dentition consisted of relatively widely spaced, peg-like or spatulate teeth often restricted to the front of the mouth (Calvo 1994a, Barrett and Upchurch 1994). Calvo's (1994a) study represents the most comprehensive work on the cranial anatomy and biomechanics of feeding among sauropods to-date and we focus on his feeding groups in the following. These groups are based on details not only of the skull but also of the dentition (including wear) for all of the major taxonomic groups of sauropods.

Calvo (1994a) groups sauropods into those with peg-like teeth, spoon-like teeth, compressed cone-chisel-like teeth, and chisel-like teeth (another group - indeterminate - will not be considered here). Peg-like teeth (fig.

4), found in such diplodocids as *Diplodocus, Dicraeosaurus, Apatosaurus, Amargasaurus* are long, slender, and slightly curved lingually, restricted to rostral margin of the jaws. Tooth wear and cranial biomechanics indicate that the lower jaw was able to move propalinally (fore-and-aft) to produce modest oral processing (see also Barrett and Upchurch 1994) and that relatively soft plant material was the chief source of food. In contrast, teeth whose crown is appreciably wider than the root, that interlock with each other throughout a relatively long arcade, and that have wear are considered spoon-like (fig. 5). Found in camarasaurids and euhelopids (*sensu* Upchurch 1995, 1998; i.e., species of *Camarasaurus, Euhelopus, and Aragosaurus*), sauropods with spoon-like teeth are characterized as having a somewhat better ability to chew, both propalinally as well as transversely, than those sauropods with peg-like teeth.

Calvo's group of chisel-toothed sauropods includes species of *Titanosaurus, Antarctosaurus, Saltasaurus, Alamosaurus, Nemegtosaurus*, and *Quaesitosaurus*, taxa distributed within Titanosauroidea and Diplodocoidea by Upchurch (1998). These long, thin, and straight teeth are restricted to the rostrum (fig. 6). Ingestion (and perhaps slight oral processing) appears to be limited to orthal (up-and-down) motion of the lower jaw, as indicated by both jaw mechanics and tooth wear. Finally, those sauropods whose tooth crowns are wider than the root (but not so much as in spoon-like teeth), appear to be compressed cones in lingual view, are set in a relatively long arcade but do not interlock are considered to be compressed cone-chisel-like forms by Calvo (fig. 7). Found in species of *Brachiosaurus, Bothriospondylus*, and *Astrodon* (brachiosaurids *sensu* Upchurch 1995, 1998), both cranial biomechanics and tooth wear indicate that lower jaw movement was orthal, enabling ingestion but little oral processing of plant food.

SAUROPOD GHOST LINEAGES AND DIVERSITY PATTERNS

Before evaluating the patterns of the evolution of feeding among sauropods, it is appropriate to provide more details on ghost lineages and their affect on diversity calculations. As indicated previously, ghost lineage analysis combines phylogeny and stratigraphy in a way that identifies contiguity between ancestors and descendant sibling species and thereby better reflects diversity through time. But what are these ghost lineages? Norell and Novacek (1993) described them as the portions of the history of a taxon for which there is no direct fossil record, but which logically come from the phylogenetic continuity between ancestors and paired descendants at cladogenesis. Ghost lineages (and their durations) can be identified through the stratigraphic calibration of the phylogeny of particular groups of interest (Weishampel 1996, Weishampel and Jianu in press). For example, Figure 8a portrays the stratigraphic distribution and phylogeny of a hypothetical group of extinct organisms. When these two sources of information are combined (fig. 8b), sibling relationships often reveal the presence of missing evolutionary history that comes from the ages of any two sister-taxa. Said another way, the older of the two descendant species fixes the minimal age of the common ancestor and thereby provides evidence that some of the history leading to its younger sister species is missing from the stratigraphic record ("ancestors cannot be younger than descendants"). Thus, species occurrences in the fossil record imply, via their phylogeny, unseen aspects of diversity that are reflected in their ghost lineages. In turn, ghost lineages provide information on cladal diversity beyond that available from raw species counts and help provide a clearer picture of minimal diversity levels.

Ghost lineages are most accurately identified when the phylogeny of the group of interest is well understood and the stratigraphic occurrence of the descendant sibling species is relatively precise. At the very least, both the phylogeny and stratigraphic distribution of sauropods are presently the focus of considerable research and are becoming better understood with further discoveries and analyses. In our analyses, as previously indicated, the species-level cladogram for Sauropoda comes from work by Upchurch (1995, 1998) with interpolation of additional species from McIntosh (1990). Resolution of species on this cladogram is generally unproblematic, as most genera are monospecific. Where multispecific genera are encountered, they are positioned as unresolved sister taxa, sometimes with a starburst effect. Total number of sauropodomorph species on this cladogram is nearly 100, ranging in age from the Early Jurassic (Hettangian) through the end of the Cretaceous (late Maastrichtian; Weishampel 1990). The species-level sauropod cladogram is available from the authors.

These phylogenetic relationships are then calibrated against the earliest occurrence of each species (fig. 9). The resulting ghost lineages are not only scattered throughout the entire sauropod clade, but are also an integral part of all higher taxa.

In order to assess the relationship of ghost lineages to estimates of sauropod diversity, we conducted two sampling efforts. The first sampled the stratigraphic distribution of actual sauropod species known from the fossil record, while the second sampled their ghost lineages at 2.5 million year intervals from the end of the Cretaceous back through to the earliest occurrence of each clade of sauropods. This 2.5 million year interval was chosen in order to insure that all species as well as their ghost lineages will be sampled in view of Dodson's (1990b) calculation that dinosaur species have an approximately 5 million year duration.

Direct sampling of the fossil record of sauropods provides somewhat similar results to that identified earlier by Weishampel and Norman (1989) a peak in the Late Jurassic, several much less substantial peaks in the Early to mid-Cretaceous, and another just prior to the end of the Cretaceous (fig. 10a). In contrast, when sampling ghost lineages at 2.5 million-year intervals (fig. 10b), a vastly different pattern emerges. There is a small peak at the beginning of the Jurassic, followed by a decline through most of the Middle Jurassic, then two extremely large peaks at the end of the Jurassic, during which time diversity jumps by at least an order of magnitude (driven by increased cladogenesis in brachiosaurids, camarasaurids, titanosauroids, and diplodocoids). Thereafter, diversity levels gradually decline through the end of the Mesozoic, with a final abrupt increase and then decline from the Campanian through the Maastrichtian (driven principally by the diversification and extinction of titanosauroids).

Given these very different patterns of diversity among sauropods, as well as the increased sampling afforded by the identification of ghost lineages, it is clear that raw taxonomic counts are at best a less-than-accurate measure of diversity. At worst, however, they can be truly misleading when used to evaluate evolutionary dynamics based on patterns of diversity. By harnessing phylogenetic contiguity between ancestors and descendant sibling taxa, we have demonstrated that the use of ghost lineages can have a large impact on estimates of diversity well beyond that available directly from the fossil record.

FEEDING GROUP DIVERSITY PATTERNS AND GHOST LINEAGES

However interesting this assessment of ghosts and taxonomic data may be, it is really the diversity of feeding groups that is ultimately useful in assessing herbivore-plant interactions and/or coevolution. Consequently, we have taken Calvo's (1994a) feeding groups for particular sauropod species and deduced "ghost feeding groups" from their ghost lineages. These feeding groups, as previously described, include sauropods with peg-like teeth, spoon-like teeth, chisel-like teeth, and compressed cone-chisel-like teeth. The ghost feeding groups were then identified on the basis of optimization analysis. Optimization analysis consists of mapping of features of interest - morphological, behavioral, or ecological - down a cladogram and the optimizing them back up the tree to resolve character ambiguities at particular nodes. For example, in Figure 11, characters (a) and (b) are mapped down this cladogram by pair-wise comparisons of terminal taxa, terminal taxa and nodes, and nodes and nodes. Once the basal node is resolved - as (a) - character ambiguities are resolved (or optimized) back up the tree. In this way, it is clear that character transformation from (a) to (b) occurs prior to the most recent common ancestor of A and B.

In this study, we have used the DELTRAN optimization option of PAUP (Swofford 1985) in order to produce the minimal resolution of feeding on the sauropod tree given the available data. Because of the strictures of DELTRAN and lack of appropriate information from the fossils themselves, unresolved feeding groups are also present, located not surprisingly in many of the basal relationships among the sauropod clades.

Sampling of optimized feeding groups was again at the same 2.5 million years as the ghost lineage analyses described previously. Ghost lineage diversity of these groups is indicated in Figure 12. For the first nearly 40 million years of their evolution, the ways that sauropods fed are unknown from the perspective of the Calvo groups. These unknown feeding styles in fact are often found at relatively high levels almost to the end of the Mesozoic (see below for their % contribution to sauropod feeding diversity). Unfortunate though this situation may be, it is expected that new discoveries as well as new analyses of skull biomechanics, tooth form, and other aspects of feeding in some of the basal members of each of the sauropod clades will reduce this ubiquitous class of unknown feeding styles.

Those groups that are known, however, provide a reasonably good picture of sauropod trophic diversity when optimized as ghosts. The group with the longest duration - sauropods with compressed cone-chisel-like teeth - is also the one that dominates the Late Jurassic, the time of greatest cladal diversity. Twin peaks of diversity, each with as many as 13 species, can be identified approximately 165 to 150 million years ago. Following this acme, there is stepwise decline in diversity for approximately 45 million years, after which this feeding group disappears. Yet even during this decrease, compressed-cone-toothed sauropods are twice to five-times as diverse as are peg-toothed sauropods, their only contemporaries during the Early Cretaceous.

Sauropods with spoon-like teeth also exhibit a tight bimodal distribution, but at less than 2/3 the level seen in compressed-cone-toothed sauropods, declining between these peaks to an intermediate five species. However, these spoon-toothed sauropods have a much shorter longevity than the aforementioned compressed-cone-toothed forms - 15 million years - although their diversity increase appears to occur in concern with the latter.

Peg-toothed sauropods exhibit an abrupt increase and decrease in diversity (from 0 to 12 species and then back to a single species) over an interval of 7.5 million years. This Late Jurassic peak indicates that peg-toothed sauropods were as diverse as contemporary compressed-cone-toothed forms. Furthermore, this high level of diversity also occurs at a time of maximum sauropod diversity; that is, during the same interval as the second peak in both spoon-toothed and compressed-cone-toothed sauropods. Low-level diversity continues until approximately 135 million years ago, after which this feeding group disappears.

Sauropods with chisel-like teeth constitute the only feeding group that is present at the end of the Cretaceous, separated from all others by at least 20 million years. There is a strong increase in diversity beginning 85 million years ago and culminating in nine species some 78 million years ago. Thereafter, chisel-toothed sauropods exhibit a gradual disappearance over the next 20 or so million years.

In order to reduce the effects of different sample sizes, we have also transformed these data into percentage contributions of feeding groups (fig. 13). Most of the patterns seen in the untransformed feeding ghosts remain the same, although often to a heightened degree. For example, the percentage of unknown feeding groups dominates virtually all of the sampling intervals. Unknown feeding groups comprise a minimum of 0 to 20% during the Late Jurassic and latest Cretaceous, but maximally account for 100% of the diversity for as much as 60 million years (concentrated in the Early and Middle Jurassic and mid-Cretaceous.

From what is known about sauropod feeding, the Late Jurassic begins solely with compressed-cone-toothed forms, but sequentially and immediately thereafter includes spoon-toothed and peg-toothed sauropods through the end of the Period. The percentage of first-mentioned group fluctuates around 40-50% in the Late Jurassic, gradually declining to 0% in the Early Cretaceous, approximately 105 million years ago. In contrast, the latter two contribute from 25% to 35% over this same interval.Finally, 100% of the latest Cretaceous feeding groups are made up of chisel-toothed sauropods.

DISCUSSION

Because of the phylogenetic continuity of species within clades, it is possible to deduce minimal levels of species diversity - as well as feeding groups - beyond those species physically available to us from the fossil record. Although not fully correcting for the biases of the fossil record, ghost lineages add significant information about diversity not available from raw species. For example, raw species counts from Sauropoda under-represent minimal diversity levels by at best 75% and by as much as 100% for individual intervals of time (fig. 10). Clearly, high levels of diversity are masked by the simple-minded use of raw species data.

Even with the use of ghost-lineages, however, our analyses indicate that the major aspects of the diversification of sauropod feeding are woefully incompletely known. As indicated previously, more than 50% of all feeding groups are unknown throughout the duration of the clade. How the eventual resolution of these unknown groups turns out is also unclear, such that further discoveries could have a great impact on the patterns discussed in this paper (see also Weishampel 1996).

In the meantime, we will examine the diversity patterns at hand that come from our ghost-lineage analysis. In particular, we want to test the hypothesis changes in feeding groups among sauropods, the largest and therefore among the most trophically specialized of all terrestrial herbivores (Farlow 1987), might be expected to reflect shifts in contemporary floras, the most significant of which is the Early Cretaceous origin and radiation of angiosperms. That is, changes in the plant realm selected for or against particular aspects of feeding in sauropods, either in an adaptive or coevolutionary way.

If we regard diversity patterns as a signal for important evolutionary events linking plants and herbivores, then virtually all of the feeding diversification among sauropods took place in the Late Jurassic, well before the major radiation of angiosperms. This pattern exists in both untransformed and percentage analyses (cf. figs. 10, 11). Even the diversity decline of all but the chisel-toothed sauropods took place prior to the angiosperm radiation. The degree to which the Late Jurassic diversification of sauropod feeding was tied to the evolutionary dynamics of gymnospermous or pteridophytic plants is not known, although paleobotanical diversity studies (e.g., Niklas et al. 1980, 1985) have not identified major evolutionary changes in these plant groups at this time.

Like the case of ornithischian dinosaurs (Weishampel and Jianu in press), sauropods appear to have been little affected by changes in contemporary plants, including the initial radiation of angiosperms. However, because of the coincidence of the diversification of sauropod feeding groups in the Late Jurassic, these patterns clearly need further investigation - from the point of view of both diversity fluctuations and also the ebb and flow of features that relate to feeding on the one hand and the resistance to predation by plants on the other.

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Figure 1. A restoration of the sauropod Diplodocus, by Brian Francak

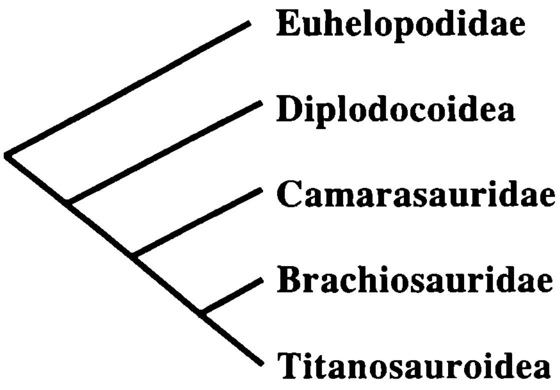

Fig. 2. – Phylogenetic relationships of the major sauropod clades identified by Upchurch (1998)

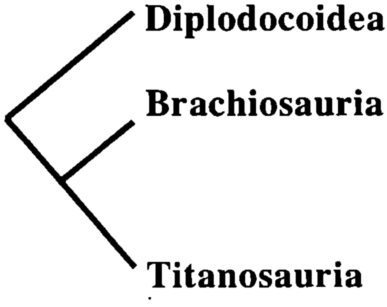

Fig. 3. Phylogenetic relationships of the major sauropod clades identified by Wilson and Sereno (1998).

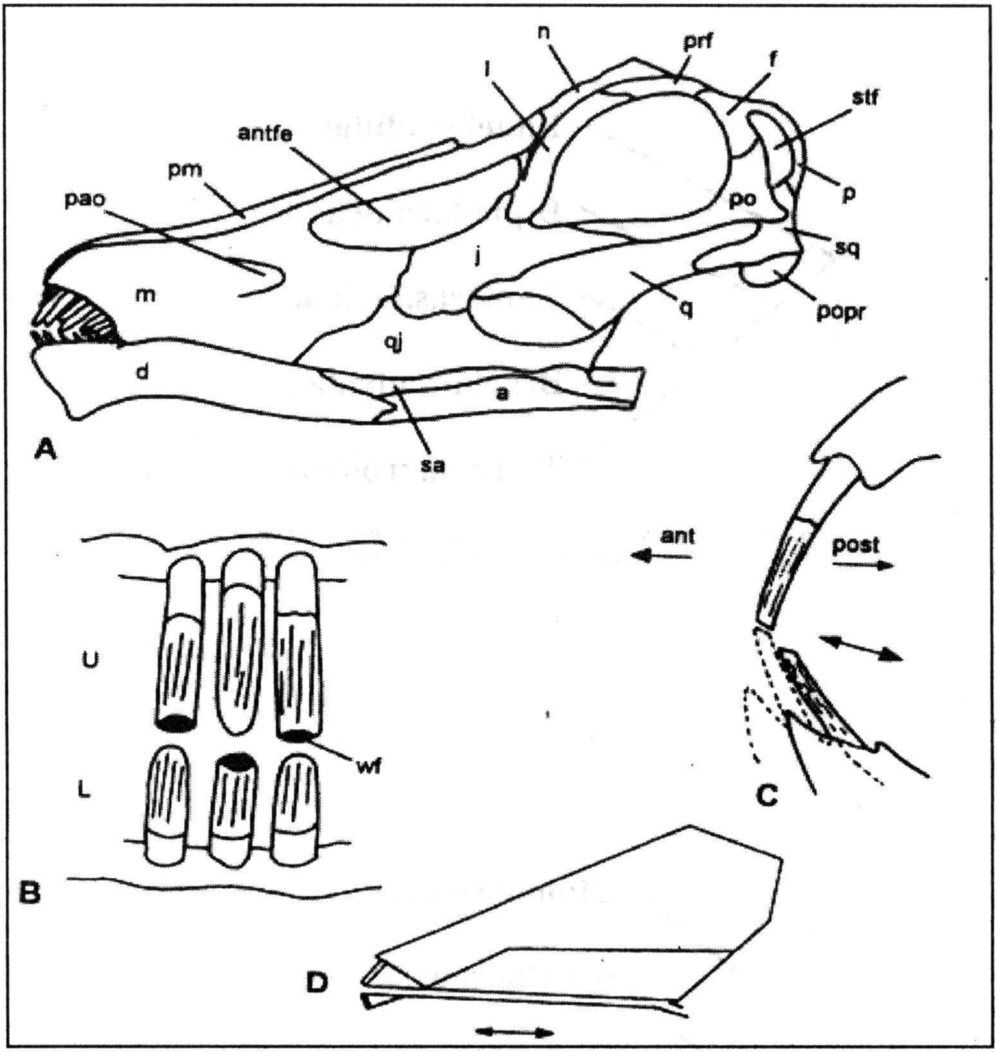

Fig. 4. – Peg-like feeding group. A. Reconstruction of the skull of Diplodocus in lateral view. B. Enlargement of premaxillary-dentary teeth in lingual view indicating wear facet position. C. Enlargement of premaxillary-dentary teeth in lateral view to show occlusion and jaw movement of the lower jaw. The double arrow shows the movement of the lower jaw. D. Kinematic abstraction of the propalinal jaw mechanism of peg-toothed sauropods. Abbreviations for Figures 4-7 – a: angular; ant: anterior; antfe: antorbital fenestra; ar: articular; bo: basioccipital; d: dentary; en: external naris; f: frontal; j: jugal; l. lacrimal; L: lower tooth; m: maxilla; n: nasal; p. parietal; pao: preantorbital opening; pm: premaxilla: po: postorbital; popr: paroccipital process; prf: prefrontal; q: quadrate; qj: quadratojugal; sa: surangular; saf: surangular foramen; scr: sclerotic ring; sf: subnarial foramen; sq. squamosal: stf: supratemporal fenestra; U: upper tooth; wf: wear facet. (from Calvo 1994a).

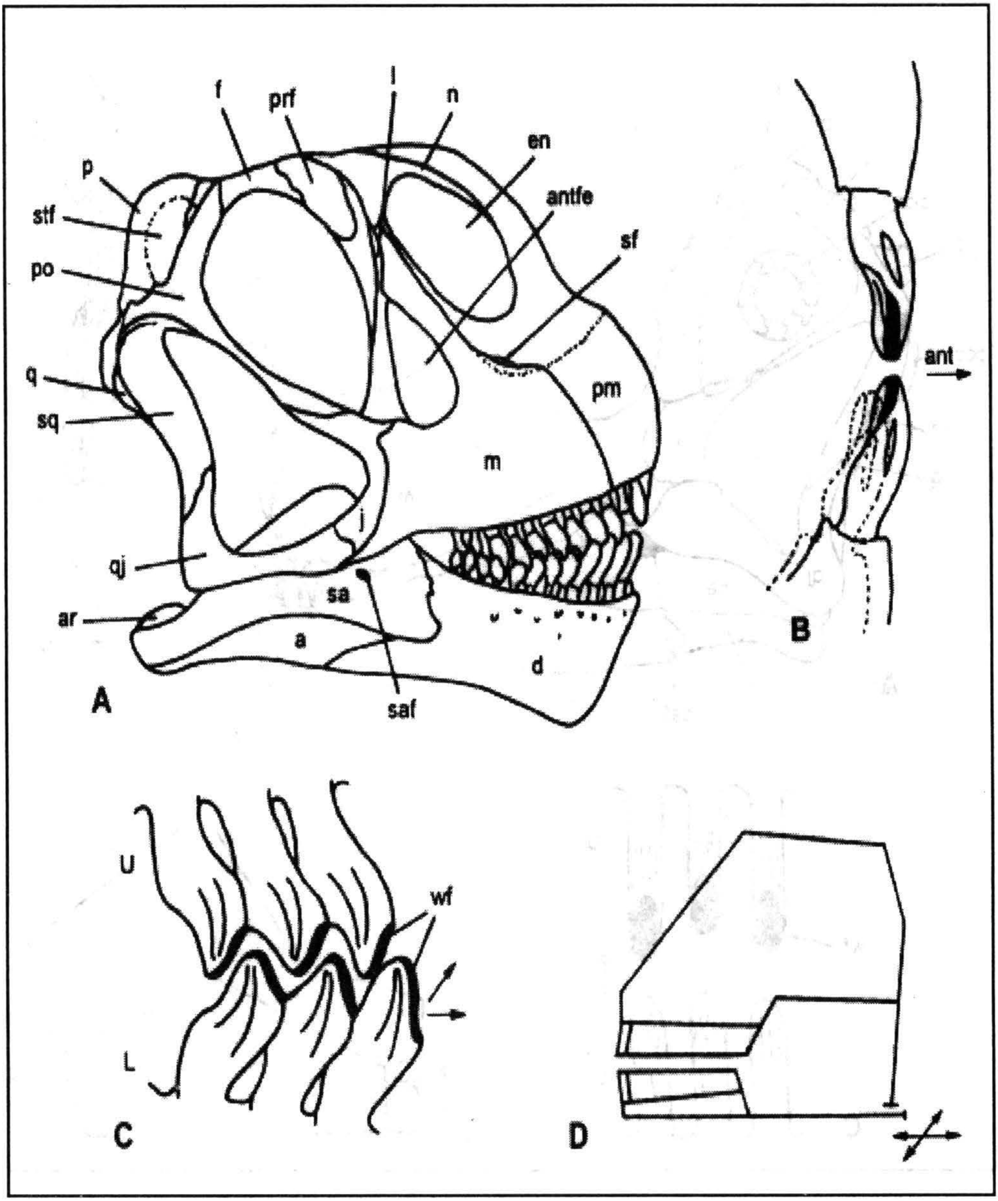

Fig. 5. – Spoon-like feeding group. A. Reconstruction of Camarasaurus skull in lateral view. B. Enlargement of premaxillary-dentary teeth in lateral view to show occlusion and jaw movement. C. Enlargement of premaxillary-dentary teeth in lingual view showing wear facet positions. Arrows indicate direction of jaw movemnt. D. Kinematic abstraction of the isognathic jaw mechanism of spoon-toothed sauropods. Abbreviations as in Figure 4. (from Calvo 1994a).

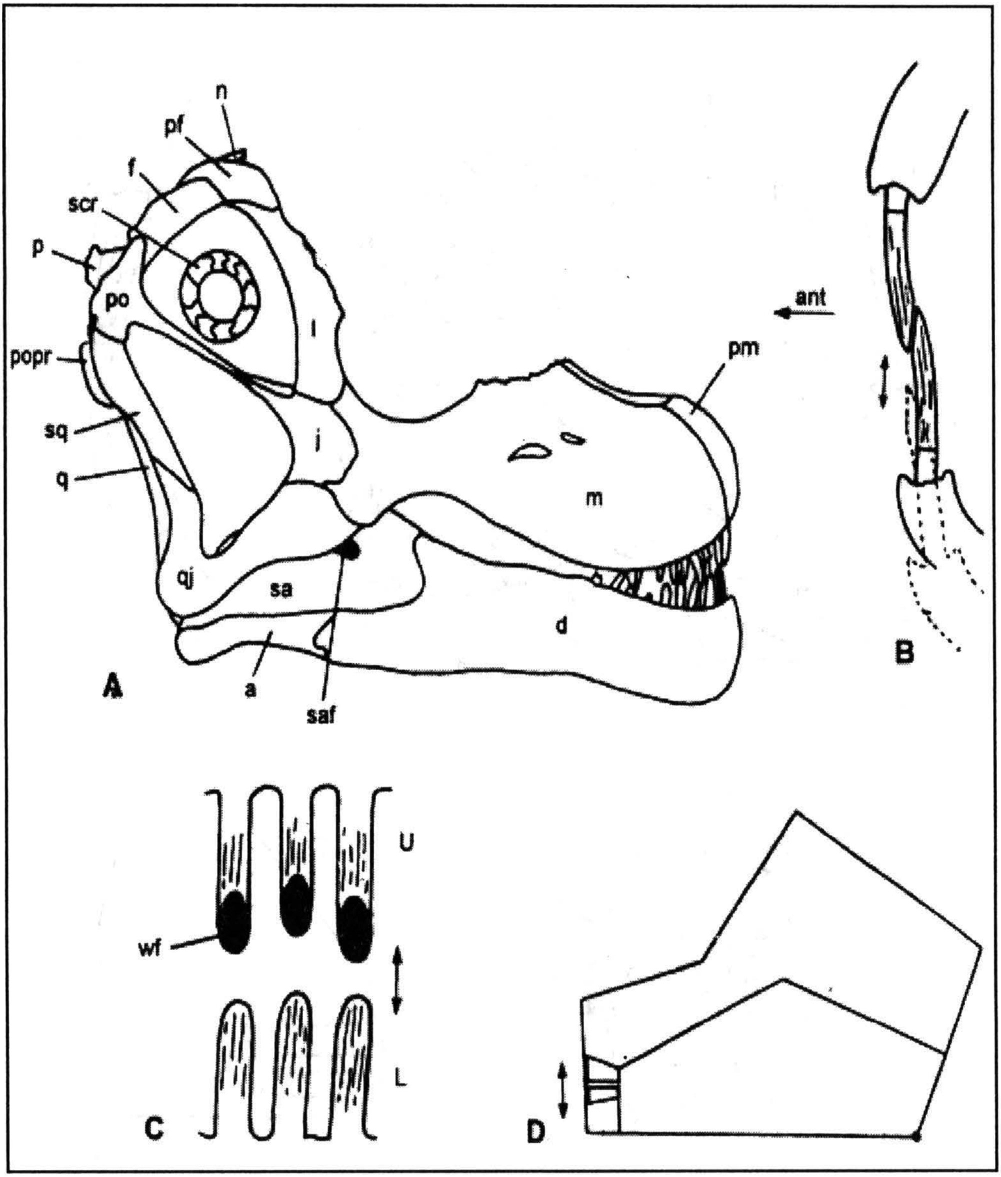

Fig. 6. – Chisel-like feeding group. A. Nemegtosaurus skull in lateral view of the skull. B Enlargement of premaxillary-dentary teeth in lateral view to show occlusion and jaw movement. C Enlargement of premaxillary-dentary teeth in lingual view showing wear facet positions. D. Kinematic abstraction of the simple hinge jaw mechanism of chisel-toothed sauropods. In (B) and (C), double arrow points out direction of movement. Abbreviations as in Figure 4. (from Calvo 1994a).

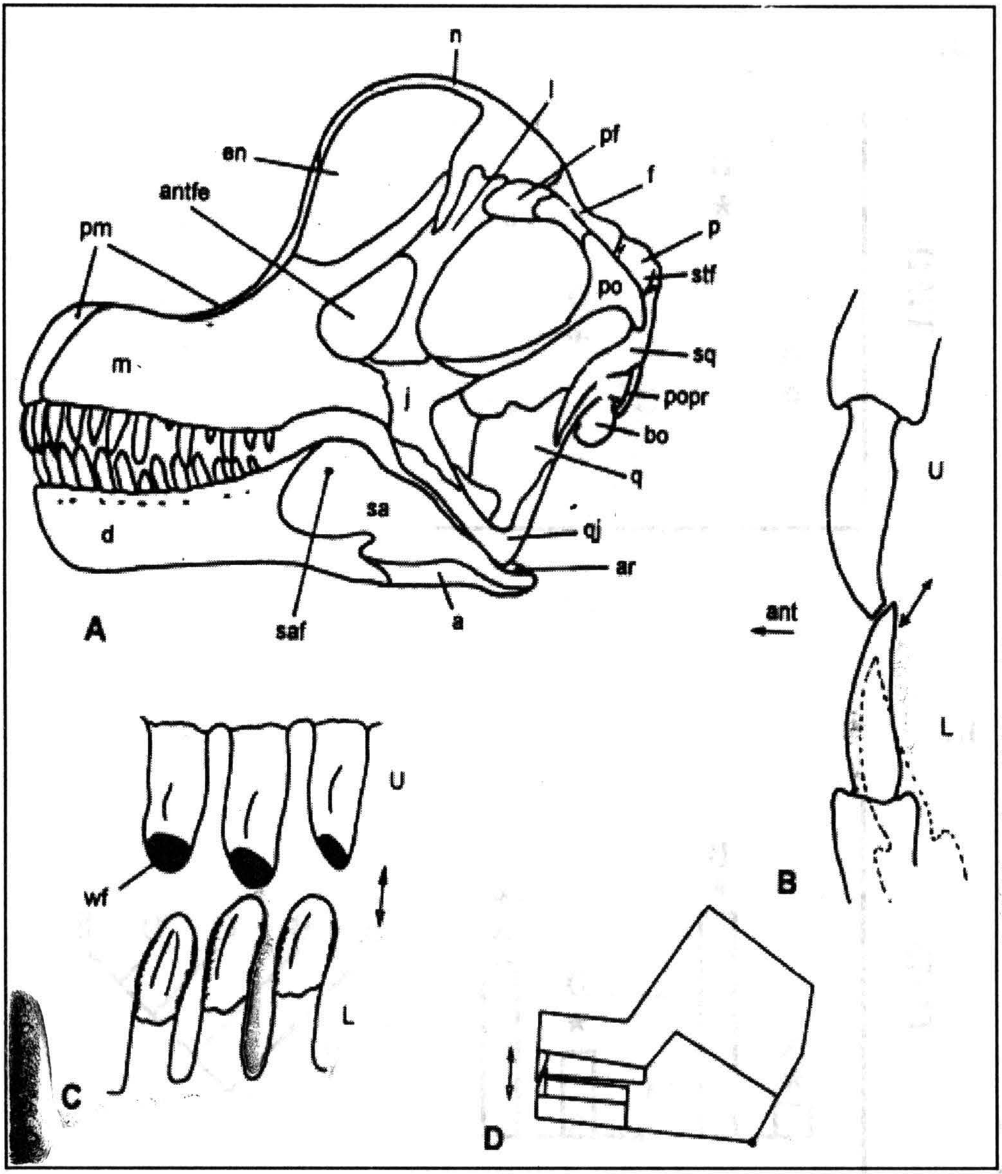

Fig. 7. – Compressed cone-chisel-like feeding group. A. Brachiosaurus skull in lateral view. B. Enlargement of premaxillary-dentary teeth in lateral view to show occlusion and jaw movement. C. Enlargement of premaxillary-dentary teeth in lingual view showing wear facet positions. D. Kinematic abstraction of the simple orthal jaw mechanism seen in compressed-cone-toothed sauropods. In (B) and (C), the double arrow indicate direction of jaw movement. Abbreviations as in Figure 4. (from Calvo 1994a.)

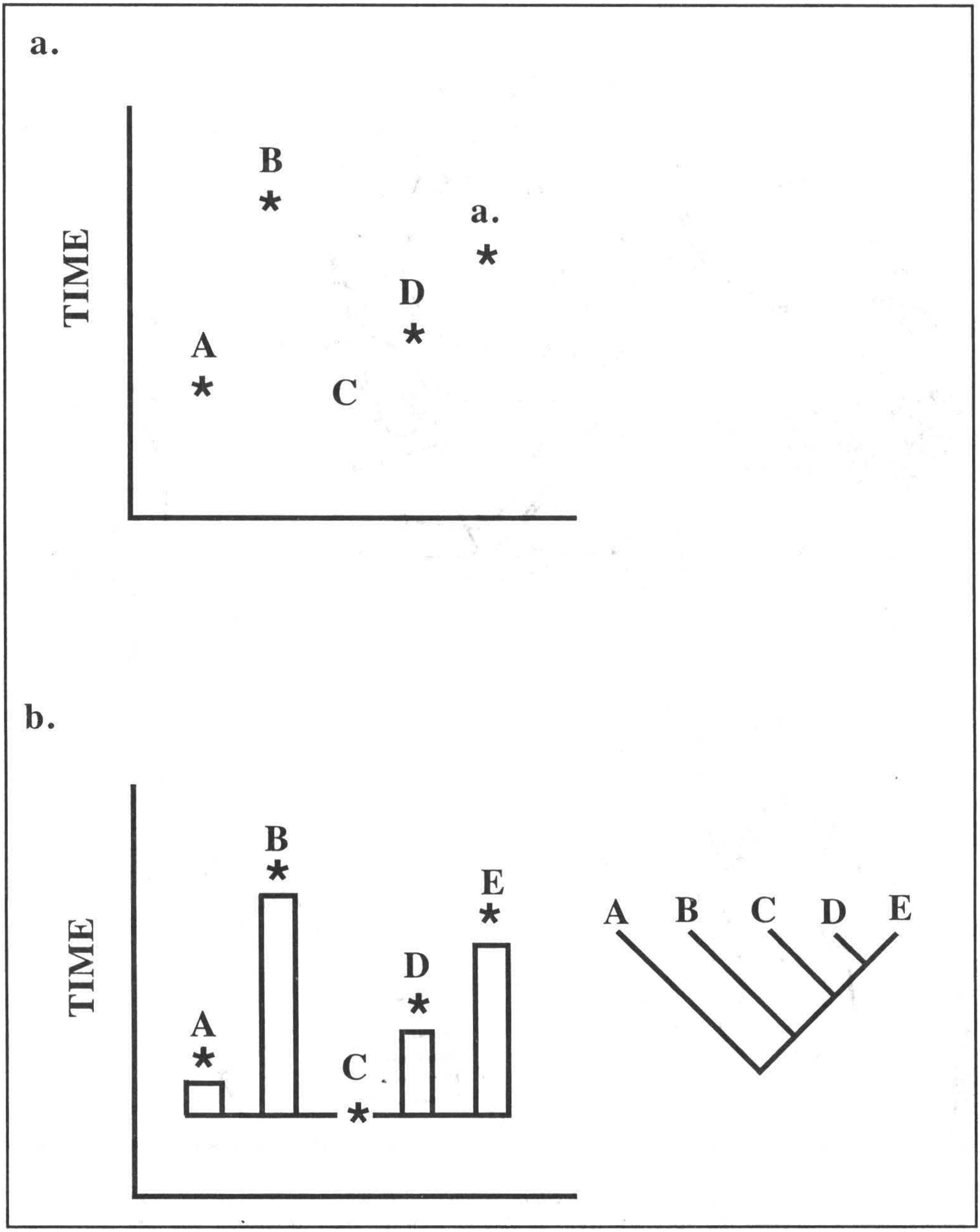

Fig. 8a. – Five hypothetical extinct species plotted against the time of their earliest stratigraphic occurrence. b. The ghost lineages (rectagular boxes) for the same five species. These ghost lineages come from the stratigraphic calibration of the cladogram indicated on the right.

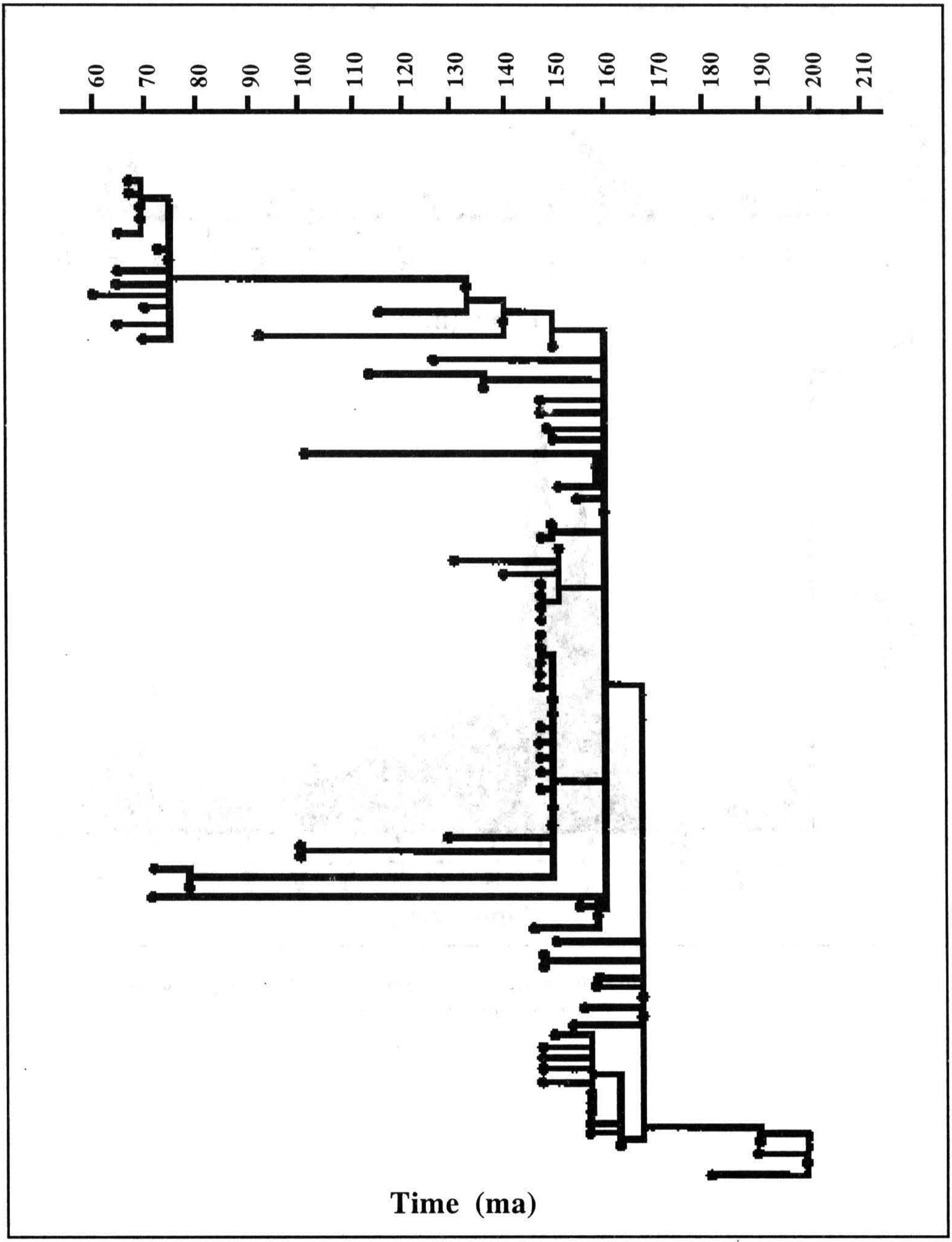

Fig. 9. – Ghost-lineage diagram of Sauropoda.

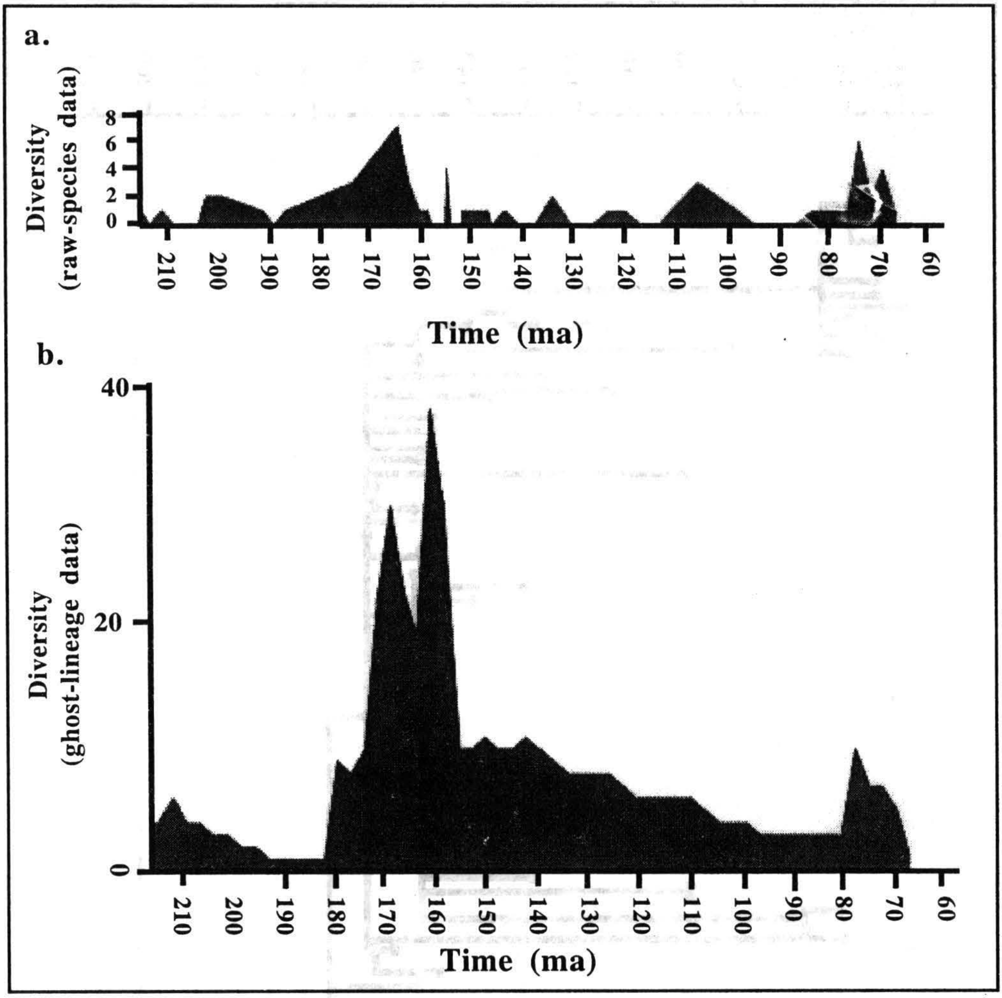

Fig. 10a. – Sauropod diversity based on raw-species data b. Sauropod diversity based on ghost-lineage data.

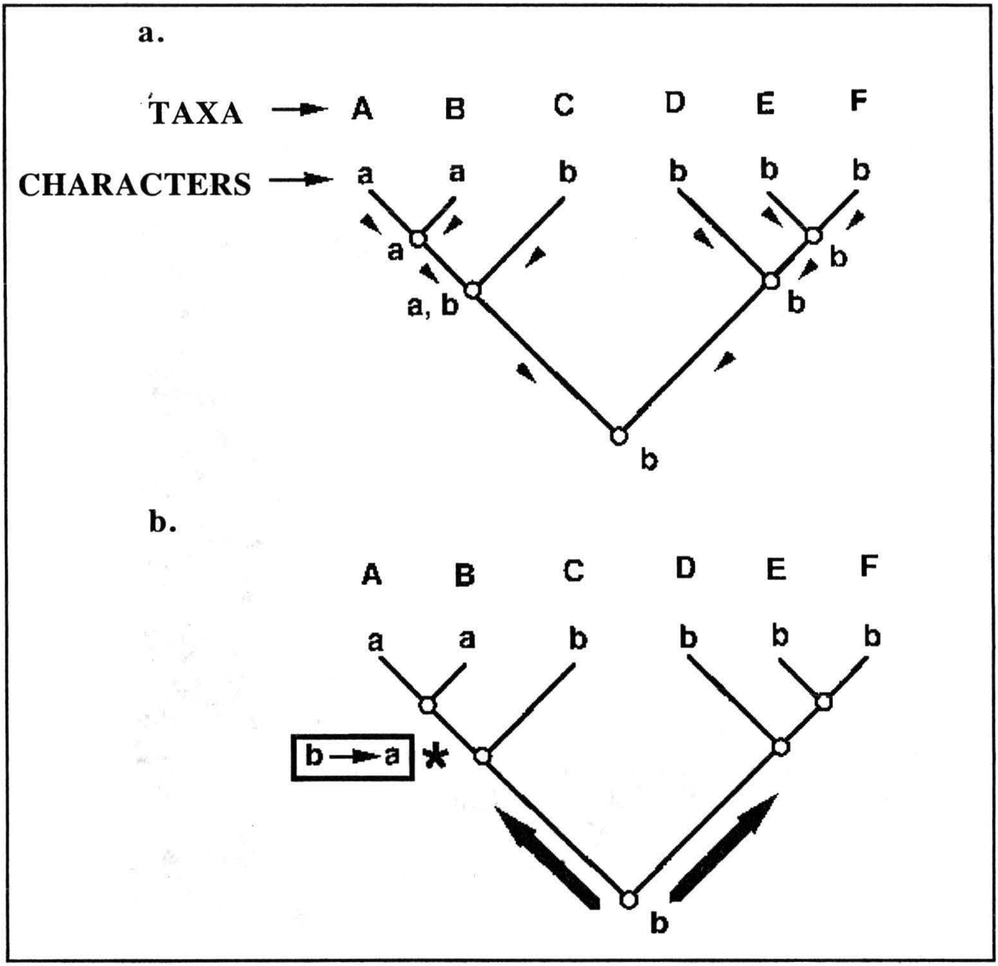

Fig. 11. Optimization analysis of two characteres (a,b) onto a cladogram of six species (A-F).

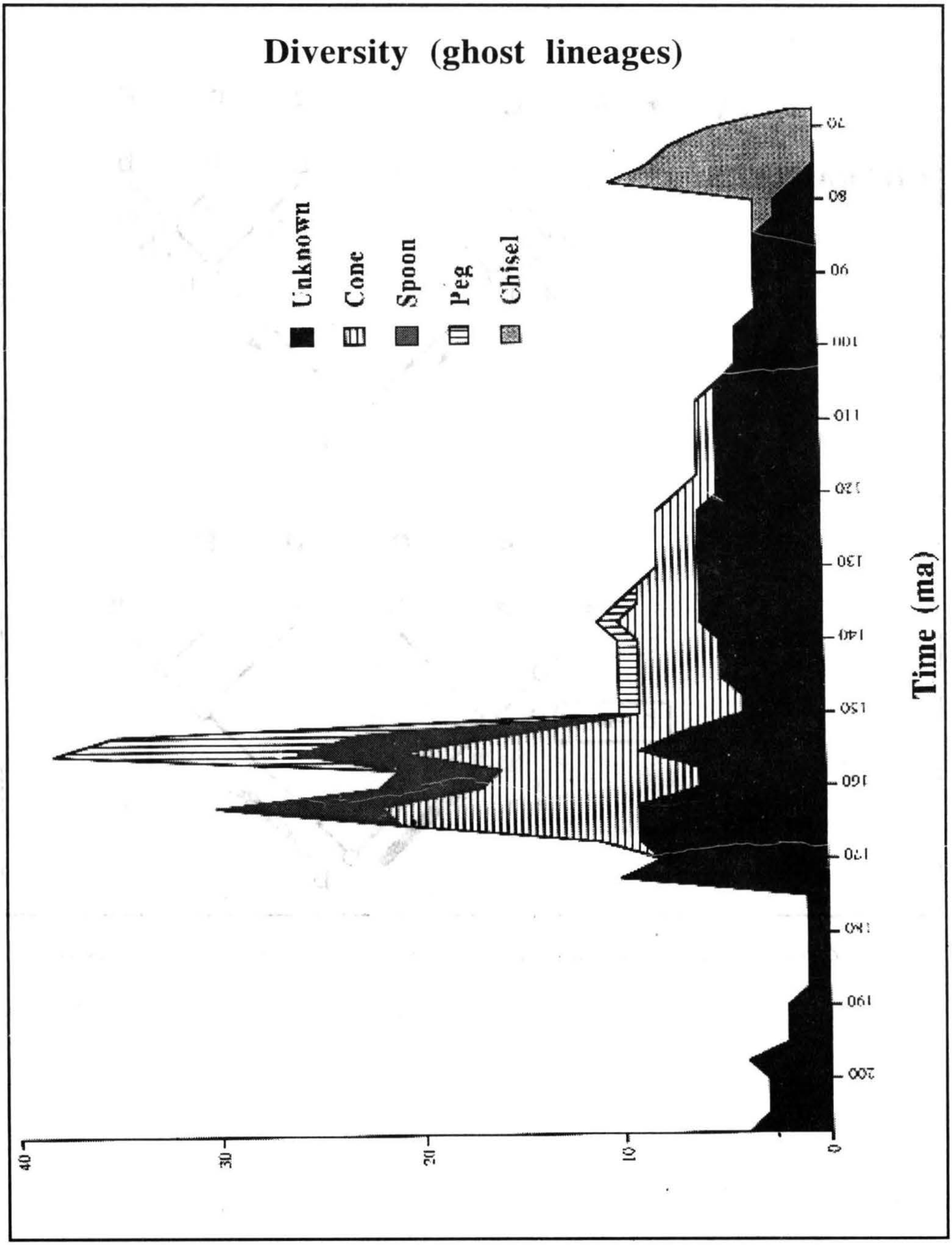

Fig. 12. – Diversity of sauropod feeding groups, based on ghost-lineage analysis.

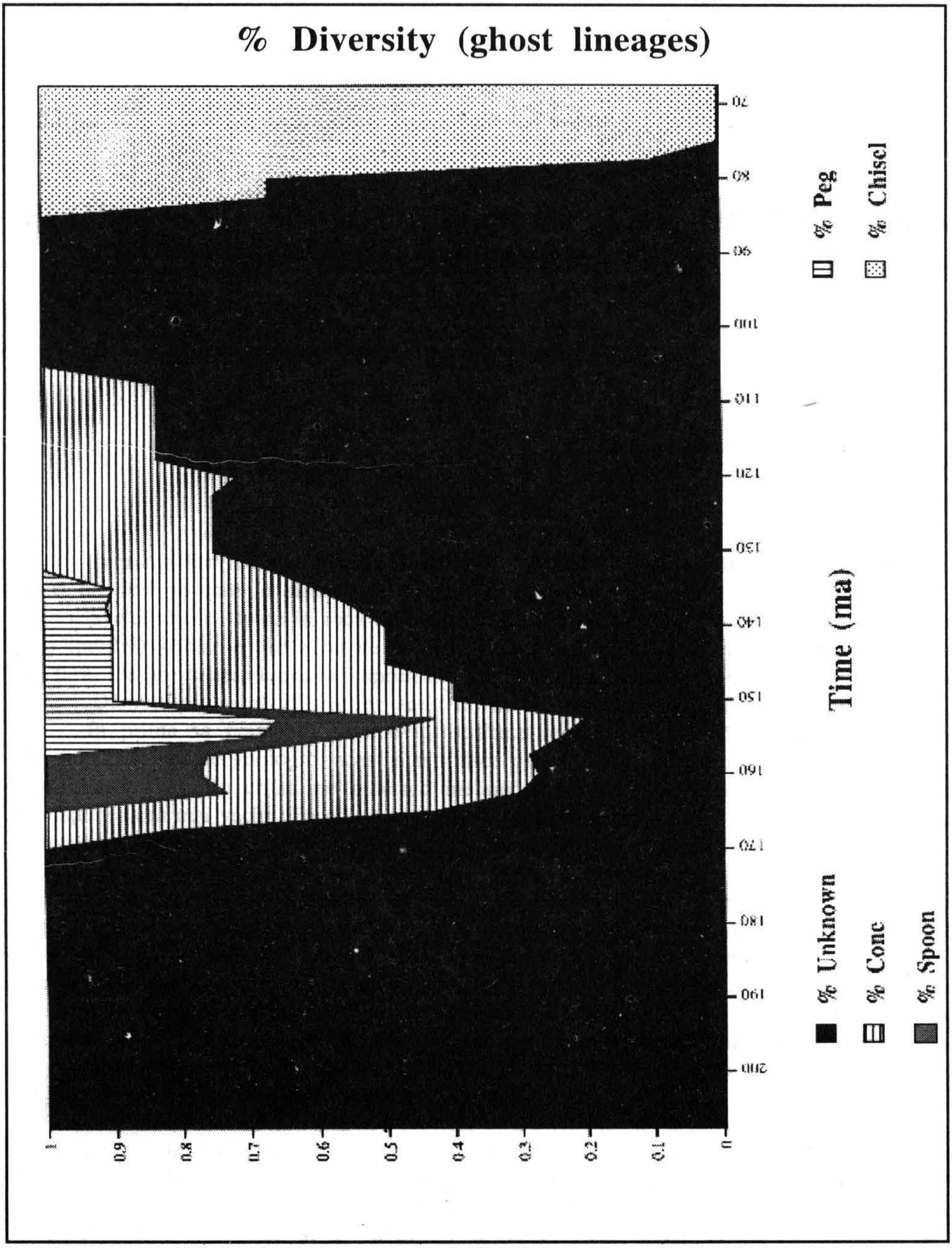

Fig. 13. – Diversity of sauropod feeding groups transformed into percentages, based on ghost-lieage analysis.