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Gondwanan dinosaur evolution and biogeographic analysis

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ABSTRACT—Gondwanan dinosaurs, though less well-known than their Laurasian counterparts, are being discovered and described at an ever accelerating pace. Dinosaurs are known from every major Gondwanan landmass, including South America, Africa, Antarctica, Australia, India, Madagascar and New Zealand. Much of the Gondwanan dinosaur literature includes speculation on vicariant and dispersal events relating to the fragmentation of Gondwana during the Jurassic and Cretaceous. These prolific biogeographic hypotheses are often inconclusive, speculative in nature, and untestable with the data at hand. To formulate well-supported biogeographic hypotheses, resolved dinosaur phylogenies and sound hypotheses of Earth history are necessary. Other factors, such as taphonomy, depositional setting, and missing taxonomic, temporal and geographic data, also contribute to understanding dinosaur faunal compositions. Additional phylogenetic information, a continuation of the current exploration and discovery, and knowledge of recent advances in tectonic plate reconstructions are paramount to developing a well-supported view of Gondwanan dinosaur biogeography. © 1999 Elsevier Science Limited. All rights reserved.

RÉSUMÉ—Bien que moins connus que leurs équivalents de Laurasie, les dinosaures du Gondwana sont découverts et décrits à un rythme de plus en plus accéléré. Ils se rencontrent dans toutes les terres émergées importantes du Gondwana, c'est-à-dire l'Amérique du Sud, l'Afrique, l'Antarctique, l'Australie, l'Inde, Madagascar et la Nouvelle Zélande. La littérature sur les dinosaures du Gondwana contient beaucoup de spéculations sur les événements de substitution et de dispersion liés à la dislocation du Gondwana lors du Jurassique et du Crétacé. Ces hypothèses biogéographiques prolifèrent, mais sont le plus souvent sans fondement, spéculatives et non vérifiables à partir des données disponibles. Pour élaborer des hypothèses biogéographiques qui se tiennent, il faut d'abord résoudre les problèmes de phylogénie des dinosaures et obtenir une histoire cohérente de la terre. D'autres facteurs, comme la taphonomie, les sites de dépôt et les données absentes de taxonomie, de datations et de géographie contribuent également à la compréhension de la composition des faunes à dinosaures. Des progrès en phylogénie, la poursuite des explorations et des découvertes actuelles et la connaissance des avancées dans la reconstruction des plaques tectoniques sont de première importance pour le développement d'une théorie cohérente de la biogéographie des dinosaures du Gondwana. © 1999 Elsevier Science Limited. All rights reserved.

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INTRODUCTION

Dinosaur remains have been collected on every major landmass that once constituted Gondwana: New Zealand, Australia, Antarctica (peninsula and mainland), Madagascar, India, South America (17 countries) and Africa (seven countries). In total, these areas have produced a diverse fauna that covers most dinosaur clades and spans the entire Age of Dinosaurs from the Late Triassic through the end of the Cretaceous Period.

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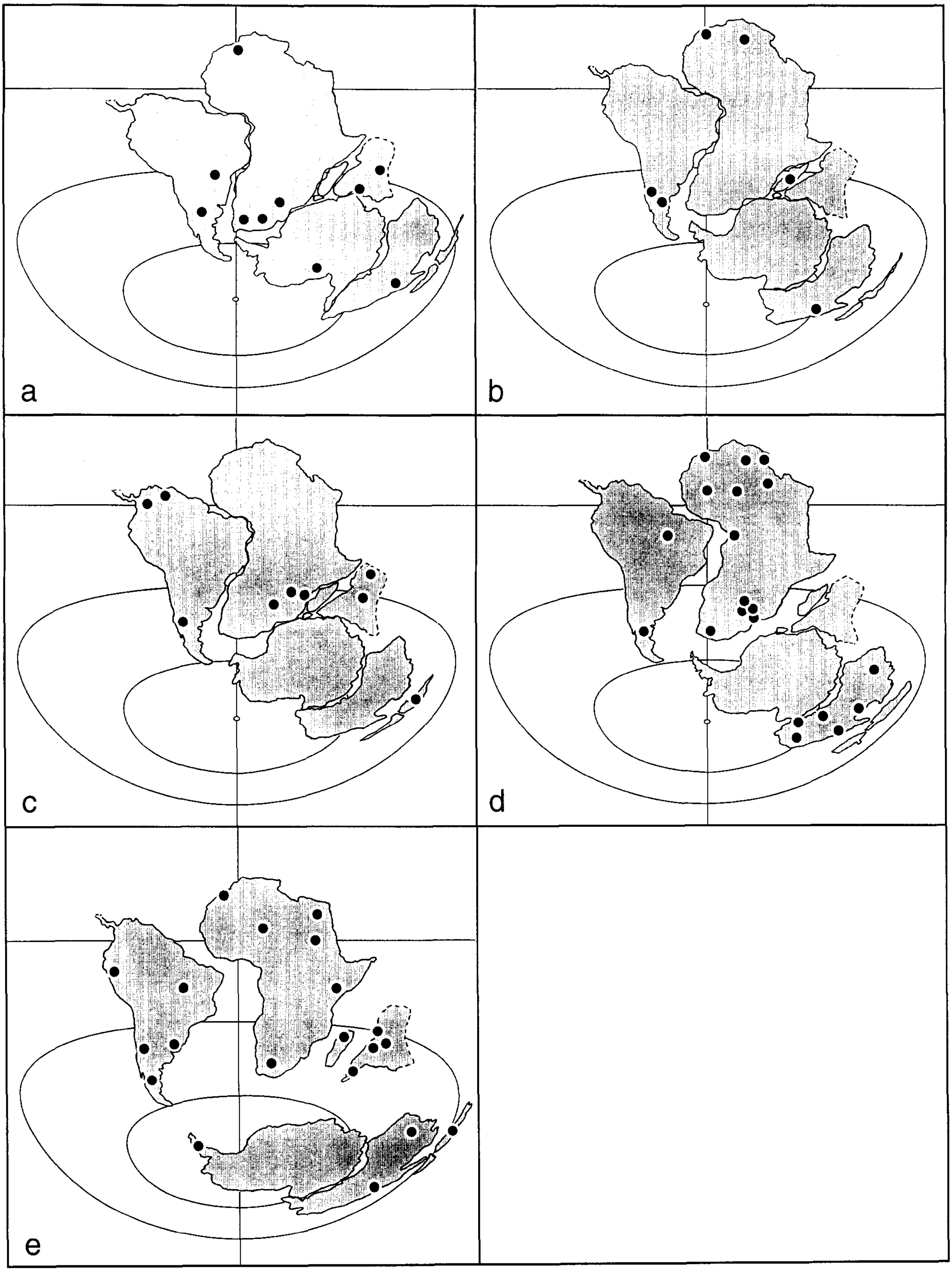

Figure 1. The distribution of Gondwanan dinosaurs through time. Latitude lines shown are the Equator, 30°S, 60°S and the South Pole; longitude is 0°. Dots represent general localities by country or state/province and are not meant to reflect each exact locality. Base maps (Lambert equal area projections) after Smith et al. *(1994). (a) Late Triassic through Early Jurassic: Argentina, Brazil, South Africa, Lesotho, Zimbabwe, Morocco, India (Madhya Pradesh, Andhra Pradesh), Australia (Queensland) and Antarctica (Transantarctic Mountains). (b) Middle Jurassic: Chile, Argentina, Morocco, Algeria, Madagascar and Australia (Queensland). (c) Late Jurassic: Colombia, Venezuela, Chile, Tanzania, Malawi, Zimbabwe, Madagascar, India (Jabulpur, Madhya Pradesh) and New Zealand. (d) Early Cretaceous: Argentina, Brazil, South Africa, Zimbabwe, Cameroon, Morocco, Algeria, Tunisia, Libya, Mali, Malawi, Mozambique, Niger, Zambia and Australia (Western Australia, South Australia, Northern Territory, Queensland, New South Wales, Victoria). (e) Late Cretaceous: Argentina, Peru, Brazil, Uruguay, Chile, Niger, Sudan, Morocco, Egypt, Kenya, South Africa, Madagascar, India (Gujarat, Madhya Pradesh, Maharashtra, Tamil Nadu), Antarctica (penninsula), Australia (Queensland, Western Australia) and New Zealand.*

Although the term 'Dinosauria' was proposed for early discoveries in Laurasia (Owen, 1842), the history of dinosaur discoveries in Gondwana reaches back nearly as far in time. In England and Europe bones and teeth, later identified as dinosaurian, began making their way into museum collections and scientific circles as early as the late 1600's. Although reports of unusual specimens later realised to be dinosaurian reach back at least to 1677, the first material originally recognised and described as a 'gigantic reptile' was a fragment of theropod dinosaur jaw (*Megalosaurus)* obtained by William Buckland in England (Sargeant, 1997). Subsequent discoveries ensued in England and elsewhere, culminating in the naming of a "distinct tribe or suborder of Saurian Reptiles...Dinosauria" in 1842 by Sir Richard Owen.

Discoveries of 'gigantic reptiles' in Gondwana quickly followed. Dinosaur remains were collected from the Lameta Beds in Jabulpur, India, as early as 1828, although they were not recognised as such until later (Sahni, 1997). In 1844, the ship *H.M.S. Fly* stopped somewhere off the northeastern coast of Queensland and collected fragments of fossil bones. These pieces were taken to England, purchased by the British Museum of Natural History in 1879, and finally studied by H. G. Seeley (1891) who named the specimen *Agrosaurus macgillivrayi* (Long, 1998). However, Long (1998) notes that "...the ship's log has no record of the locality where the fossils came from and to date there have been no other dinosaur bones collected from the north coast of Queensland, so it is difficult to be certain about *Agrosaurus* even being an Australian dinosaur."

A well-documented discovery was made in South Africa in 1845. Spurred on by the dinosaur discoveries in England, amateur naturalists Andrew Geddes Bain and William Atherstone took "a holiday excursion for the purpose of geological exploration" near their hometown of Grahamstown (Atherstone, 1857). In rocks now known as the Kirkwood Formation they discovered fragments of large bones and a partial jaw with teeth. Bain and Atherstone sent these fossils to Sir Richard Owen in England (de Klerk *et al.*, 1992), who described the jaw (maxilla) fragment 31 years later (Owen, 1876); a specimen now known as the armored stegosaur *Paranthodon africanus* (Galton and Coombs, 1981). By the early twentieth century, dinosaurs had been discovered and described in South America (e.g. Allport, 1860; Ameghino, 1904; von Huene, 1929, 1934), Madagascar (e.g. Depéret, 1896; Gautier, 1896; Thevenin, 1907), the Indian subcontinent (e.g. Lydekker, 1877; Matley, 1921, 1929), Australia (e.g. Longman, 1926) and other parts of Africa (e.g. Janensch, 1914; Stromer, 1915, 1934).

An onslaught of work throughout Gondwana in the past 30 years, including both field work and specimen analysis, has greatly increased the Gondwana dinosaur database, expanding it in number of taxa, temporal and geographic range, and systematic diversity (Fig. 1). This work covers South America (e.g. Bonaparte, 1978, 1991; Novas, 1993, 1997a; Coria and Salgado, 1996; Kellner and Campos, 1996; Kellner, 1996; Salgado *et al.*, 1997), Madagascar (e.g. Krause *et al.*, 1997; Sampson *et al.*, 1998), Australia (e.g. Molnar, 1980; Molnar and Galton, 1986; Rich and Rich, 1989; Long, 1992), Africa (e.g. Raath, 1969; Santa Luca *et al.*, 1976; Taquet, 1976; Rich *et al.*, 1983; Jacobs *et al.*, 1993; Sereno *et al.*, 1994, 1996; Rauhut, 1995), India (e.g. Jain, 1980; Chatterjee and Rudra, 1996; Loyal *et al.*, 1996) and the first discoveries of dinosaurs in Antarctica (e.g. Olivero *et al.*, 1991; Hooker *et al.*, 1991; Hammer and Hickerson, 1994) and New Zealand (e.g. Molnar, 1981; Molnar and Wiffen, 1994).

This increase in Gondwanan dinosaur research has led to some singular discoveries. For example, phylogenetic groups unique to Gondwana are now recognised, such as the theropod group Abelisauridæ (Bonaparte and Novas, 1985), to date found only with certainty in Upper Cretaceous rocks in Argentina, India and Madagascar (Sampson *et al.*, 1998). The discovery of Cretaceous dinosaur faunas in southeastern Australia, New Zealand and Antarctica, from sediments deposited at that time well within the Antarctic Circle, has led to investigations of the biological implications of dinosaur life in southern polar regions (Rich and Rich, 1989; Rich, 1996; Wiffen, 1996). For instance, the only feature thus far identified as an adaptation to low light conditions in a polar dinosaur is that of the hypsilophodontid *Leællynasaura* (a small, herbivorous, bipedal ornithischian) from the Early Cretaceous (Aptian-Albian) Otway Group, southern Victoria, Australia. This taxon shows hypertrophied optic lobes in the brain, possibly indicative of enhanced visual ability under low winter light conditions (Rich *et al.*, 1988; Rich and Rich, 1989; Rich, 1996; Vickers-Rich, 1996; Chinsamy *et al.*, 1998).

Nearly all that we know of the origin and early diversification of Dinosauria comes from two Gondwanan sequences: the 'Stormberg Group' of southern Africa, and the Agua de la Peña Group of northwestern Argentina (La Rioja and San Juan Provinces; Fig. 1a). These sedimentary sequences, spanning the Middle Triassic through Early Jurassic, contain a record of the origin and early diversification of Dinosauria (Sereno *et al.*, 1993). For example, in the Agua de la Peña Group, the dinosaur 'precursors' *Marasuchus ('Lagosuchus')* and *Lagerpeton* are found in the Chañares Formation, the early dinosaurs *Pisanosaurus, Herrerasaurus* and *Eoraptor* are from the overlying Ischigualasto Formation, and more derived prosauropod dinosaurs *Riojasaurus* and *Coloradia* and an undescribed theropod (Arcucci and Coria, 1998) from the next youngest strata, the Los Colorados Formation. The Lower Elliot Formation, Upper Elliot Formation, Clarens Formation, and Forest Sandstone of the 'Stormberg Group' (and equivalents) preserve an even more diverse fauna, including basal ornithischians (*Heterodontosaurus, Lesothosaurus ['Fabrosaurus'], Abrictosaurus, Geranosaurus, Lanasaurus, Lycorhinus*), a theropod (*Syntarsus*), and prosauropods (*Blikanosaurus, Euskelosaurus, Massospondylus, Melanorosaurus).* Both these sequences also include older strata (the Los Rastros Formation in Argentina and the Molteno Formation in South Africa) that bear small to moderate sized theropod-like tridactyl footprints that predate the earliest known dinosaur body fossils (Raath *et al.*, 1990; Forster *et al.*, 1995).

Almost every major dinosaur clade is represented in Gondwana, including representatives of sauropods, prosauropods, ceratosaurian and tetanuran theropods, basal ornithischians, ornithopods, and thyreophorans. The only clade whose presence cannot be confirmed in Gondwana are the marginocephalians (Pachycephalosauria and Ceratopsia), the dome-headed and horned dinosaurs. A pachycephalosaur *Majungatholus atopus,* previously reported from Madagascar (Sues and Taquet, 1979), has recently been demonstrated to be an abelisaurid theropod (Sampson *et al.*, 1998). Two possible occurrences of ceratopsians have been reported: *Notoceratops* in Argentina (a partial dentary, now lost; Tapia, 1918), and an unnamed specimen in Australia (an ulna; Rich and Vickers-Rich, 1994). However, due to the incompleteness of these specimens, it is currently impossible to confirm their assignment to Ceratopsia.

Despite many recent advances in Gondwanan dinosaur paleontology, we still have a fragmented picture of dinosaur diversity and distribution. Although dinosaurs are known from Upper Triassic through Early Cretaceous rocks of Gondwana, large temporal gaps occur in single geographic areas, and large spatial gaps exist for each time period. While an excellent Late Triassic dinosaur record exists in South Africa, Lesotho and Zimbabwe, little is known from these areas for the rest of the Mesozoic (an exception being the Lower Cretaceous Kirkwood Formation; de Klerk *et al.*, 1998). Conversely, while fossiliferous Upper Triassic sequences have produced a diverse dinosaur fauna in these three countries and in Argentina, Late Triassic dinosaurs are nearly unknown elsewhere in Gondwana. These temporal and geographic gaps can only be filled by additional data from future exploration and discovery.

Despite the great advances that have been made in Gondwanan dinosaur research, particularly in the past 30 years, new discoveries still lag behind those in Laurasia. For example, in a census of new dinosaur genera named from 1989 to 1995, 15 were from Gondwana while 36 were from Laurasia (Holmes and Dodson, 1997). Holmes and Dodson (1997) also tabulated that six countries account for 75% of all named dinosaur genera: only one of these, Argentina, is in Gondwana (it is ranked fifth). To date, 404 possibly valid dinosaur species have been named from Laurasia, and 100 from Gondwana; 24.8% of named dinosaur species are Gondwanan (G. Olshevsky, *pers. comm.* 1998). These numbers suggest that we have not yet attained a global understanding of dinosaur diversity and distribution.

BIOGEOGRAPHY: DINOSAURS AND GONDWANAN HISTORY

Biogeography seeks to explain the observed distribution of life on Earth by identifying the processes, or historical factors, that influenced these distributions. One historical factor of paramount importance in Gondwana was the tectonic reorganisation of the southern continents in the Jurassic and Cretaceous. How was the evolution of dinosaurs influenced by the fragmentation of the Gondwanan supercontinent? The opportunity to investigate this interplay between Earth and evolutionary history adds a unique facet to the study of Gondwanan dinosaurs.

The effects of this interplay have long been recognised by palæontologists, and biogeographic issues have formed a major focus in literature on Gondwanan dinosaurs. Hypotheses of land bridges, faunal interchange with Europe and North America, development of endemism on fragmented landmasses, dispersal pathways, and centres of origin have all been discussed. In fact, much Gondwanan dinosaur literature has either been devoted to, or discusses, these biogeographic issues (e.g. Brett-Surman, 1979; Sues and Taquet, 1979; Bonaparte, 1986, 1991, 1996; Bonaparte and Kielan-Jaworowska, 1987; Chatterjee, 1987; Buffetaut *et al.*, 1988; le Loeuff, 1991; Olivero *et al.*, 1991; Buffetaut and Rage, 1993; Casanovas-Cladellas and Santafé-Llopis, 1993; Jacobs *et al.*, 1993; Kellner, 1994; Sereno *et al.*, 1994, 1996; Krause *et al.*, 1997; Coria and Salgado, 1995; Frey and Martill, 1995; Kellner and Campos, 1996; Salgado *et al.*, 1997; Sampson *et al.*, 1998; for an early 'pre-drift' global overview see Lull, 1910).

Much of the literature on Gondwanan dinosaur biogeography has been narrative in nature (e.g. Brett-Surman, 1979; Bonaparte and Kielan-Jaworowska, 1986; Casanovas-Cladellas and Santafé-Llopis, 1993), speculating on possible distributional scenarios such as migration routes and land bridge connections. Ball (1976, p.409) points out that a narrative is "...not aimed at the discovery or confirmation of a law, it [does] not establish any new empirical fact, and it makes no positive predictions about what may be found in future investigations." In themselves, these narrative biogeographic speculations are not falsifiable, and thus do not present us with testable hypotheses. For instance, Russell (1993) discusses the origin and diversification of hadrosaurids ('duck-billed' dinosaurs) from iguanodontian dinosaurs. After observing that the oldest known skeletal remains of hadrosaurids occur in Lower Cretaceous strata in North America, Russell (1993, p.2008) states;

"...it is nevertheless tempting to speculate that the vicariance event took place on opposite shores of the Tethyan seaway. During or somewhat before Aptian-Albian time, "basal" hadrosaurs would have crossed the Tethys by means of waif dispersal from an area of origin on Neopangea—Gondwana into Europe, together with the dicræosaurian ancestors of the Mongolian *Nemegtosaurus*. From thence the animals would have dispersed into North America and (or) Central Asia."

This explanation of process, which Russell freely points out is speculative, lacks the necessary support of hypotheses of phylogenetic relationships, and invokes dispersal pathways and an area of origin that are unsupported by data. Nevertheless, speculative papers such as this have formed the necessary first step in the development of Gondwanan dinosaur biogeography by providing the initial forum for recognition and introduction of biogeographic questions, and thus the later development of testable biogeographic hypotheses.

Testability and rigour in historical biogeography has come from the advent of vicariance biogeography, which developed with the application of phylogenetic systematics (cladistics) to analyses of taxa relationships (e.g. Rosen, 1978; Nelson and Platnick, 1980). Cladistic methodology offers a testable way of reconstructing the phylogeny of groups of organisms by tracing the history of their acquisition of novel morphological characters. That is, if evolution is "descent with modification" (Darwin, 1859), then the history of descent (phylogeny) can be traced through the history of those modifications (acquisition of novel characters or synapomorphies). A resolved phylogeny ensures that the dinosaur taxa used in biogeographic analyses have evolutionary meaning. Furthermore, any taxon used in biogeographic analyses, at any taxonomic level, must be monophyletic: descended from the same common ancestor, and including all descendants of that common ancestor (i.e. it must be a complete branch of the evolutionary tree). Cladistics thus offers one of the two tools needed for biogeographic analysis: hypotheses of the branching pattern of dinosaur evolution.

The second necessary tool is a knowledge of Earth history. The timing and pattern of the movements of Gondwanan landmasses are provided by current geophysical models and tectonic plate reconstructions (e.g. Scotese, 1991; Storey, 1991; Hawkesworth *et al.*, 1992; Smith *et al.*, 1994; Hay *et al.*, *in press*; Grunow, 1999; Smith, 1999; Scotese *et al.*, 1999). While the physical separation and collision of plates obviously affect the spacial continuity of biotas, the concurrent changes these movements effect on oceanic circulation patterns and climate may induce ecological changes, further influencing biotic evolution. As with phylogenetic analyses, tectonic reconstructions are being actively researched and improved. For instance, Hay *et al.* (*in press*) suggest Indo-Madagascar and Antarctica were connected well into the Late Cretaceous across a persistent Kerguelen Plateau. The persistence, or elimination, of the Kerguelen Plateau as an island archipelago has obvious effects on the timing of the severance of spacial continuity of these landmasses and their resident biotas. The possibility exists that reciprocal illumination between phylogeny and tectonics may be able, in future, to address such issues.

The geographic distribution of constituents of a biota at any one point in time can be explained by two primary processes: dispersal and vicariance.

Dispersal requires an organism to move away from its original locality to colonise a new area (for instance, by crossing a barrier by 'jump dispersal'; Pielou, 1979). With vicariance, a taxon diverges from its sister population (by allopatric speciation) subsequent to isolation caused by the creation of a barrier. If the history of Gondwanan dinosaurs has been effected by continental fragmentation (i.e. the creation of ocean barriers), the hypotheses of vicariant evolution can be tested. This is accomplished by seeking congruence between the pattern of continental rifting and phylogenetic branching. Repeated congruence of these patterns among multiple dinosaur lineages allows a single factor to be invoked as the causal explanation—in this case the opening of ocean basins. For instance, most palæogeographic reconstructions suggest Indo-Madagascar rifted from Antarctica at about 125 Ma, and Madagascar separated from India at 85-90 Ma (e.g. Scotese, 1991; Smith *et al.*, 1994). Vicariance thus predicts that Indian and Malagasy dinosaur taxa should be more closely related to one another than either is to Antarctic taxa (e.g. Sampson *et al.*, 1998). Thus, if the sequence of rifting matched the sequence of phylogenetic branching, vicariant processes may be invoked as the causal explanation.

Vicariance and dispersal may happen in concert; they are not mutually exclusive. However, dispersal events may occur independently among multiple taxa; ten taxa may exhibit ten different dispersal patterns. Importantly, dispersal can occur independent of the pattern of continental fragmentation. Since dispersal can be invoked to explain any distributional pattern, possibilities of vicariant explanations should be exhausted before entertaining dispersalist ones (Kluge, 1988). Therefore, in seeking a biogeographic pattern among Gondwanan dinosaurs, vicariance should be tested for first.

Beard (1998, p.6), in discussing the origin of mammal groups in Asia, comments that:

"Scientific attempts to reconstruct the biogeographical history of mammals...have lagged far behind attempts to reconstruct their phylogeny. This delay is natural inasmuch as knowledge of phylogeny is a prerequisite for assessing such second-order phenomena as the historical biogeography of a clade".

The opposite situation is often true for Gondwanan dinosaurs, where biogeographic speculation often outstrips well-supported phylogenetic analyses. Cladistic analyses have resolved some relationships within Dinosauria (e.g. Gauthier, 1986; Sereno, 1986; Holtz, 1994; Forster *et al.*, 1998), but many clades still lack well-supported, low level phylogenies. Often "Existing information on dinosaur phylogenetics lacks sufficient precision to unambiguously resolve vicariant events" (Russell, 1993, p.2003).

CONTROLS IN DINOSAUR BIOGEOGRAPHIC ANALYSES

Well-supported phylogenetic hypotheses and a knowledge of tectonic plate reconstructions are the fundamental data for dinosaur biogeographic investigations. But even with this information, caution must be taken not to overinterpret results or draw unfounded conclusions from these analyses. It is as important to understand the limitations of dinosaur biogeographic analyses as it is to recognise their power.

Vicariance, dispersal and phylogeny

Many biogeographic methodologies have been developed for extant taxa, and caution must be taken when applying these techniques to fossil taxa. A fundamental part of vicariance biogeography is the identification of areas of endemism for use in constructing taxon-area cladograms, the basic methodology for combining data of Earth and evolutionary history (e.g. Kluge, 1988; see Hovenkamp, 1997 for an alternative viewpoint). An area of endemism can be defined as "...an area of non-random distributional congruence among different taxa...relatively extensive sympatry is a prerequisite" (Morrone, 1994). Since geographic ranges of a number of populations of taxa at a given point in time are needed to determine an area of endemism, it is difficult to define an equivalent unit in the fossil record. Palæontologists are limited to data from either a single point in time and space (i.e. a single horizon at a single locality), or an amalgam of limited geographic areas over a span of time (i.e. more than one horizon over a number of localities). Fossil biotas also enjoin the additional dimension of time. It is possible that no, or greatly restricted, temporal overlap occurs between dinosaur biotas. If overlap occurs, current dating methods may not allow for precise enough correlation (needed to within thousands of years at most) for confirmation. That is, an Early Cenomanian dinosaur fauna in northern Africa and an Early Cenomanian fauna in central Africa are not necessarily temporally equivalent. An area of endemism in the fossil record cannot be defined with the same precision that it can with extant taxa.

Perhaps because of this difficulty in defining geographic boundaries to areas of endemism in the fossil record, there is a tendancy to delimit them in extremely broad terms, often at the continent level (e.g. Kellner, 1994; Bonaparte, 1996; Sampson *et al.*, 1998). For example, Sereno *et al.* (1996) propose an increase in dinosaur provincialism in Africa through the Late Cretaceous, although their database consists solely of dinosaur taxa from northern Africa. If present day biotas serve as an indicator, then intracontinental variation in climate, altitude, ecological setting, and taxonomic composition of biotas were also present in the past. Thus, it is unwarranted to assume broader dinosaur provinces than are supported by the fossil record: what is true for a dinosaur fauna in one part of a continent should not be assumed *a priori* to be true elsewhere. It would be as informative to seek evidence of intracontinental differences in dinosaur faunas, as it is to pursue intercontinental variation.

Vicariant patterns can be complicated by land bridges which may allow dispersal across previously open marine barriers. Ephemeral land bridges between North America and South America (e.g. Bonaparte, 1986; Lucas and Hunt, 1989), and Europe and Africa (e.g. Rage, 1981; Dercourt *et al.*, 1985; Buffetaut *et al.*, 1988; le Loeuff, 1991; Buffetaut and Rage, 1993) have been proposed at various times during the Mesozoic. For example, Buffetaut *et al.* (1988) hypothesised that links between southern Europe and Africa, via island arcs and emerged platforms, allowed faunal interchange in the Late Cretaceous. Yet investigations such as this concerning dispersal across land bridges also first requires a well-supported phylogenetic analysis. Without phylogeny, there is no basis for linking a possible immigrant to an area of origin without first knowing its relationship to taxa on that originating landmass. Whether seeking vicariant or dispersalist processes, an understanding of phylogeny remains a necessary prerequisite.

While well-supported phylogenies are crucial to all biogeographic analyses, the level of resolution (whether one uses species, genera, families, or orders as the operative taxonomic units) may dictate what biogeographic questions can or cannot be addressed. In some biogeographic analyses, higher taxonomic level input is sufficient to suggest a pattern. For instance, le Loeuff (1991), in an effort to apply a more rigourous methodology (Parsimony Analysis of Endemicity) to a biogeographic analysis of Cretaceous dinosaurs, gained some resolution at the family level. To address other questions, the phylogenetic level employed must be at a finer resolution to reveal a biogeographic pattern. For instance, Casanovas-Cladellas and Santafé-Llopis (1993) suggest possible dispersal patterns for a family of sauropods, the Titanosauridæ, but concede their analysis is hampered by the lack of a resolved phylogenetic analysis. Without resolution at the species or genus level, the data necessary to hypothesise such dispersals does not exist.

Gaps in the records

Missing evidence, a perennial problem in palæontology, confounds numerous facets of biogeographic analysis. Incomplete skeletal material hampers phylogenetic resolution, while gaps in the geographic and temporal record restrict refinement of biogeographic areas. Only the presence of data is informative—missing data is no data at all. For instance, Sampson *et al.* (1998) discuss the known distribution of the theropod clade Abelisauridæ from Upper Cretaceous strata in Madagascar, India and Argentina. They advance the hypothesis that the close phylogenetic relationship between abelisaurids is due to retained sub-aerial connections between South America, and Indo-Madagascar, via Antarctica, long after their separation from Africa in the Early Cretaceous. However, as pointed out by the authors, there are virtually no Campanian-Maastrichtian dinosaurs known from Africa. This absence of data from Africa is uninformative, and at present limits the ability to test the hypothesis proposed by Sampson *et al.* (1998).

Lack of temporal information can similarly hinder biogeographic hypotheses. For example, Sereno *et al.* (1996) propose that coelurosaurian theropods were globally distributed by the Late Jurassic based on:

i) the occurrence of a coelurosaurian in Morocco in the Late Cretaceous; and

ii) the timing of lineage splitting that suggests coelurosaurians originated by the Late Jurassic.

Since no coelurosaurians were then known from the Late Jurassic through Late Cretaceous of Gondwana, no positive evidence existed to support their hypothesis. However, support can be lent by finding a Late Jurassic coelurosaurian in Gondwana and, in fact, an Early Cretaceous (Valanginian) coelurosaurian has recently been reported from South Africa (de Klerk *et al.*, 1998).

Interpreting the rock record

The process of fossilisation itself may constrain comparisons between dinosaur faunas. Palæoecological and taphonomic information may be necessary to ensure that direct comparisons between faunas are valid. Since animals partition themselves along ecological boundaries (e.g. Schoener, 1988), ideally one should compare fossil biotas from similar ecological spheres. Palæoecology can be addressed by understanding sedimentological and palæontological indicators of parameters such as climate and depositional setting (e.g. palynomorphs, clay composition, facies type, sedimentary and pedogenic structures, etc.). Additionally, different facies within a formation may preferentially preserve parts of the biota, parts of the individual, or preserve different taxa altogether (e.g. Smith, 1993; Rogers, 1993). If 'dinosaur fauna A' occurs in a fluvial facies with palæoenvironmental indicators suggesting a temperate, seasonal, forested environment, it may be uninformative to compare it to 'dinosaur fauna B' from an aeolian facies whose paleoenvironmental indicators suggest a semi-arid savannah environment.

A closely integrated factor is taphonomy: the study of how post-mortem processes distort the fossil record. Both geological and biological processes may bias the fossil record, including transport (resulting in autochthonous or allochthonous assemblages), time-averaging of fossil assemblages, and differential destruction and preservation of taxa (Kidwell and Behrensmeyer, 1993). Moreover, these post-mortem processes may not be uniformly applied across palæoenvironments or taxa (e.g. Smith, 1993). What is found preserved in the fossil record, and in what quantity, may not accurately reflect the original living biota. Ideally, better control of the taphonomic and palæoenvironmental setting can help assess the feasability of direct faunal comparisons.

The non-dinosaurian faunal component

Mesozoic faunas are composed of an enormous variety of taxa other than dinosaurs, including birds, crocodilians, mammals, amphibians, pterosaurs, lizards, snakes, turtles and fish. These animals, as well as a great diversity of plants and invertebrates, also have biogeographic histories. Each faunal component may have differed in its dispersal capability and reaction to ecological change. For instance, volant birds may readily disperse over long distances, even across marine barriers, but neither fresh water fish nor amphibians easily cross salt water. Dispersal capabilities likely varied between dinosaur taxa as well. Both dispersalist and vicariant processes are apt to have influenced the distributions of different components of the biota, and any single biota should exhibit a variety of biogeographic patterns. For instance, some dinosaurs and birds may not conform to vicariant patterns (indicating dispersal), but frogs, fish, and other dinosaurs may show vicariance. This type of information has potential for delineating which dinosaurs were capable of crossing marine barriers and which were not. The biogeographic histories of non-dinosaurian faunal components, while interesting in their own right, may thus help elucidate additional aspects of dinosaur evolutionary history.

CASE STUDIES OF GONDWANAN DINOSAUR BIOGEOGRAPHY

Abelisauridæ: Late Cretaceous Gondwanan theropods

Abelisauridæ is a small clade of Late Cretaceous theropods currently known with certainty from only India, Madagascar and Argentina (see Sampson *et al.*, 1998 for a discussion of the distribution of this clade; Fig. 2a). Theropods are divided into two major clades, the Ceratosauria and Tetanuræ (Gauthier, 1986). While much phylogenetic work has been done recently within Tetanuræ (e.g. Holtz, 1994; Sereno *et al.*, 1996; Novas, 1997a), and within Ceratosauria (e.g. Rowe and Gauthier, 1990), few analyses have combined genus level taxa in both major theropod clades (an exception is Holtz, 1994; Fig. 3a, b).

Ceratosaurians have generally been considered the dominant clade of theropods in Gondwana, with tetanurans predominating in Laurasia (e.g. Bonaparte, 1986; Buffetaut and Rage, 1993). This hypothesis has recently been falsified as many basal tetanurans are now known from Gondwana, such as *Cryolophosaurus, Giganotosaurus, Deltadromeus* and *Unenlagia* (e.g, Hammer and Hickerson, 1994; Coria and Salgado, 1995; Sereno *et al.*, 1996; Novas and Puerta, 1997). Regardless, current phylogenetic analyses hypothesise that abelisaurids are a unique, late surviving Gondwanan radiation of ceratosaurians (e.g. Sampson *et al.*, 1998). However, numerous authors have noted that abelisaurids share a number of synapomorphies with tetanuran theropods, notably *Carcharodontosaurus* (Holtz, 1994; Novas, 1997b; Sampson *et al.*, 1998). Often, cladistic analyses of basal tetanurans use 'Ceratosauria' as a single taxon (e.g. Coria and Salgado, 1995; Sereno *et al.*, 1996), and thus the monophyly of this clade, and where abelisaurids fall, is not tested. If abelisaurids are indeed tetanurans, then there is no Late Mesozoic Gondwanan radiation of ceratosaurians. Additionally, our understanding of tetanuran

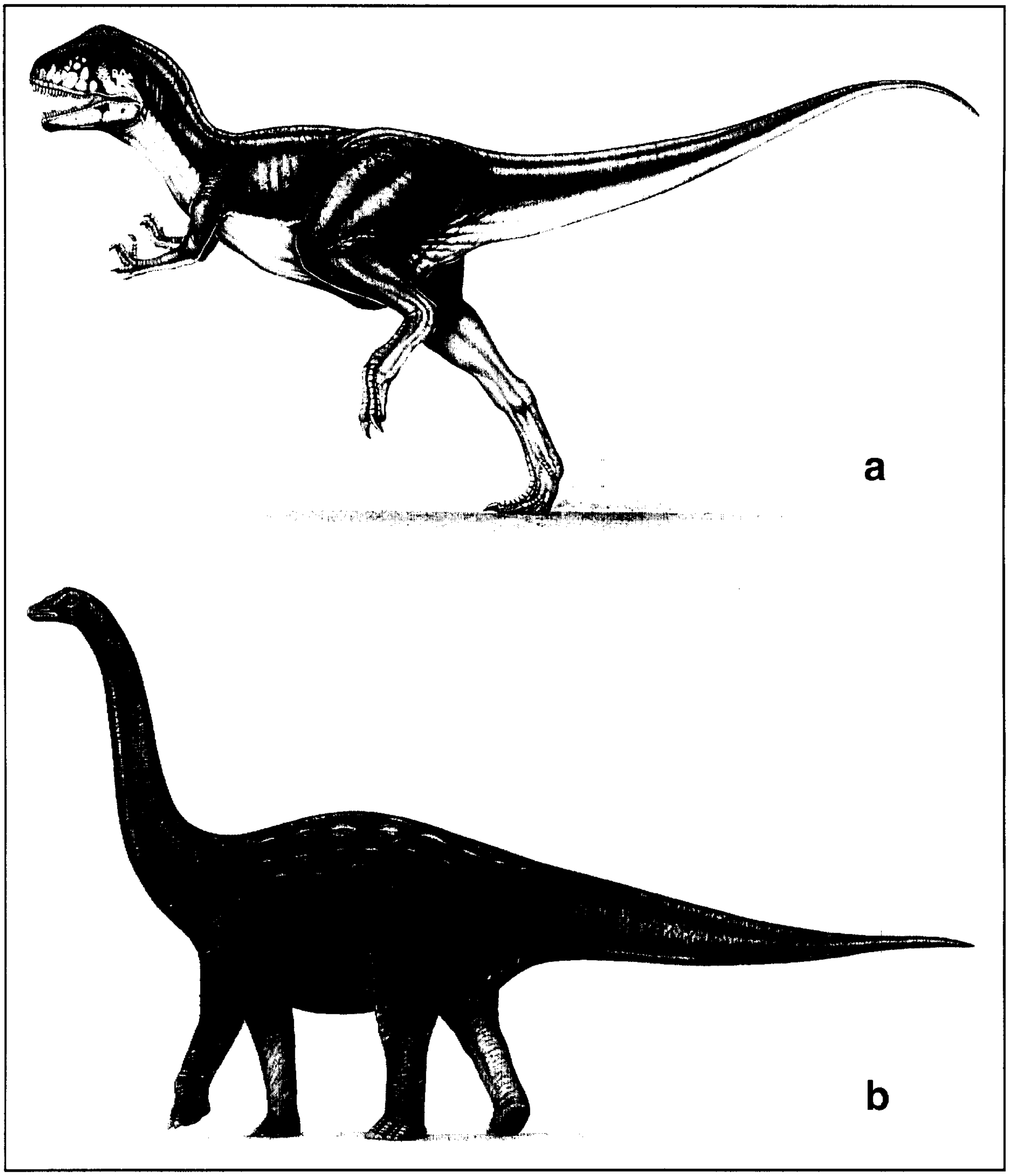

Figure 2. (a) Reconstruction of Majungatholus, *an abelisaurid theropod from Madagascar. (b) A generalised titanosaurid sauropod.*

biogeographic patterns may change with the addition of abelisaurids to this clade.

To test the placement of Abelisauridæ within Theropoda, a character matrix was constructed in part from relevant phylogenetic analyses of ceratosaurians and tetanurans (e.g. Gauthier, 1986; Rowe and Gauthier, 1990; Holtz, 1994; Sereno *et al.*, 1996). The resulting 99 character matrix was analysed using PAUP (Swofford, 1991) and McClade (Maddison and Maddison, 1992) for eleven reasonably well-known theropod genera including the abelisaurids *Majungatholus* and *Carnotaurus*, the ceratosaurians *Syntarsus, Dilophosaurus,* and *Ceratosaurus*, and the tetanurans *Carcharodontosaurus, Giganotosaurus, Tyrannosaurus, Allosaurus, Torvosaurus* and *Sinraptor* (see

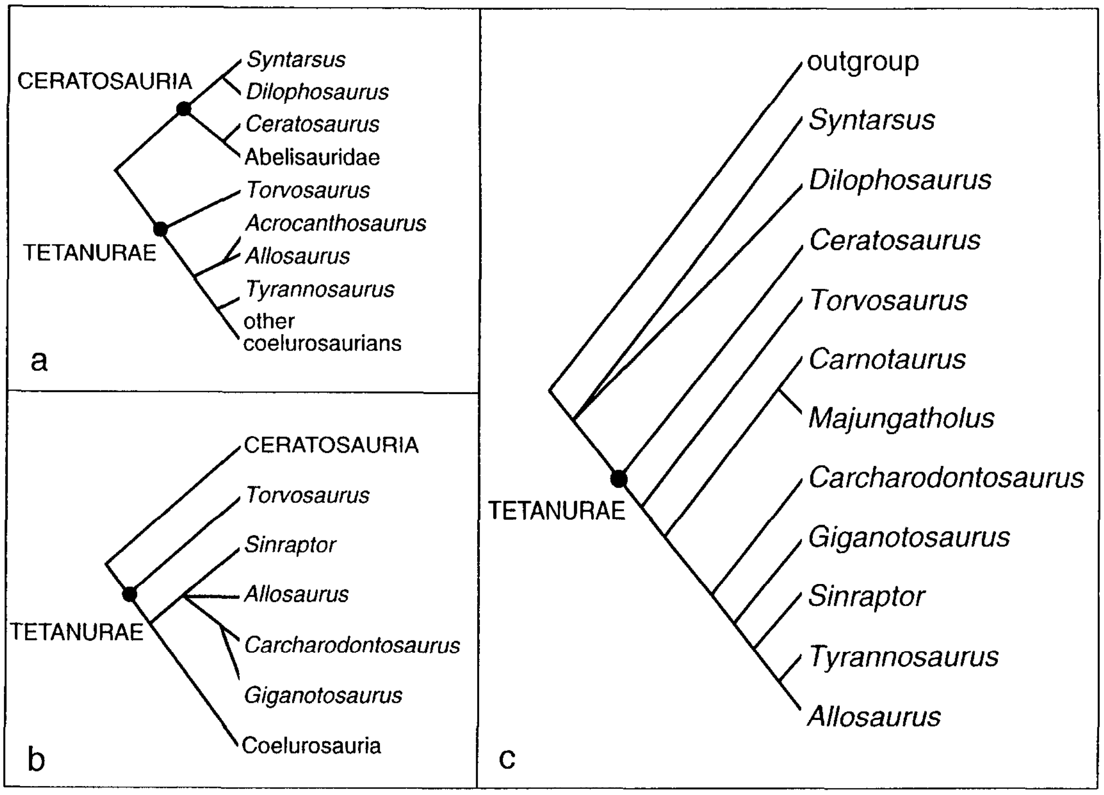

Figure 3. *Hypothesised phylogenetic relationships among theropod dinosaurs. (a) Phylogeny modified from Holtz (1994). (b) Phylogeny modified from Sereno* et al. *(1996). (c) Consensus of the two most parsimonious trees resulting from the phylogenetic analysis presented in this paper (99 characters from the cranium and postcranium; 181 steps; CI = .586; RI = .645; all characters unordered, delayed transformations).*

Fig. 3c for the consensus tree and the Appendix for the character matrix and list).

This cladistic analysis does not support Ceratosauria as a monophyletic clade, but instead pulls some 'ceratosaurian' taxa, including abelisaurids, into basal Tetanuræ. Ceratosauria is dismantled so completely that 18 additional steps are required to reunite this clade. *Carno-taurus* and *Majungatholus* are supported as sister taxa (confirming the monophyly of Abelisauridæ) within basal Tetanuræ. Regardless of their placement within either Ceratosauria or Tetanuræ, a Gondwanan radiation of a monophyletic Abelisauridæ may still be hypothesised, but genus or species level phylogenetic resolution among all basal tetanurans is necessary for further illumination.

Although admittedly preliminary, these results nevertheless suggest:

i) abelisaurids are tetanurans;

ii) there is no ceratosaurian radiation in the Late Cretaceous of Gondwana; and

iii) additional information is now available for investigating Gondwanan tetanuran biogeography due to the addition of abelisaurids.

These results demonstrate how biogeographic hypotheses can be altered by changing the hypothesis of phylogenetic relationships.

Titanosauridæ: Pan-Gondwanan sauropods

Titanosauridæ, widely distributed throughout Gondwana in the Cretaceous, is a sub-clade of the large-bodied, herbivorous Sauropoda (Fig. 2b). They are often regarded as the primary large herbivores in Gondwana during this time (e.g. Bonaparte, 1996), and were first discovered over 100 years ago in India (Lydekker, 1885). Titanosaurids are not restricted to Gondwana however, and rare remains have been reported in Laurasia, including *Alamosaurus* in North America (e.g. Gilmore, 1922; le Loeuff *et al.*, 1989). Approximately 23 titanosaurids have been named thus far (G. Olshevsky, *pers. comm.* 1998), and specimens range in completeness from whole skeletons (Holmes, 1997) to isolated vertebrae (Depéret, 1896). Unfortunately, a tendency to assign any Cretaceous age sauropod from Gondwana to Titanosauridæ has resulted in a partial 'grab-bag' taxon where "...many [taxa] are probably suspect" (McIntosh, 1990). Nevertheless, recent phylogenetic analyses support the monophyly of Titanosauridæ (Gimenez, 1992;

Upchurch, 1994; Salgado *et al.*, 1997; Wilson and Sereno, 1998), although the inclusion of much of the material assigned *a priori* to Titanosauridæ remains untested.

The lack of phylogenetic resolution within the clade has left them with little to reveal regarding biogeographic pattern. For example, titanosaurids are absent in the Late Cretaceous of North America until *Alamosaurus* appears in Maastrichtian strata, and two hypotheses have been advanced to explain this distribution. Lucas and Hunt (1989) feel that *Alamosaurus* was an immigrant from South America, dispersing across a Maastrichtian land bridge. Russell (1995), noting that Eurasian terrestrial organisms appear in India in the Maastrichtian, suggested the possibility that *Alamosaurus* was an immigrant from India after its collision with Laurasia. Tectonic models of the timing of the collision of the Indian subcontinent with Asia may provide information on the feasability of Russell's hypothesis. However, these two dispersal hypotheses can be tested through phylogenetic analyses by discovering how *Alamosaurus* is related to Indian and South American titanosaurids. If Lucas and Hunt are correct, *Alamosaurus* is predicted to be most closely related to South American taxa. If Russell's suggestion is correct, *Alamosaurus* is predicted to nest phylogeneticaly with Indian titanosaurids. As a further complication, a number of skeletons that appear to be a primitive titanosaurid were found recently in the Lower Cretaceous Cedar Mountain Formation in North America (Britt *et al.*, 1998). This new taxon suggests a third hypothesis that is also testable with phylogenetic analyses: *Alamosaurus* may belong to a separate North American lineage of titanosaurids.

There are some data pertinent to these three hypotheses. Salgado *et al.* (1997), in a cladistic analysis using postcranial characters and a limited number of titanosaurid taxa, suggest *Alamosaurus* is nested within South American taxa. However, no Indian taxa were included in their analysis, and thus the relationship of *Alamo-saurus* to these titanosaurids remains unknown. A phylogenetic analysis of all titanosaurids is required to address any of these biogeographic hypotheses.

DIRECTIONS FOR THE FUTURE

The potential for new dinosaur discoveries in Gondwana is tremendous. As this record grows, questions concerning the processes responsible for the distribution of dinosaurs across Gondwana during and subsequent to its fragmentation will continue to be addressed. Phylogenies, tectonic plate reconstructions, and an understanding of the controls needed to work with fossil biotas are necessary to formulate these biogeographic hypotheses. Often, information necessary for biogeographic analyses is incomplete and inconclusive, and many hypotheses cannot be tested by the data at hand.

There are a number of directions for Gondwanan dinosaur research to take in the future:

i) Discover more dinosaur specimens and taxa throughout Gondwana. Additional data is necessary to develop a more global view of dinosaur distributions and evolution, and to provide phylogenetic and distributional data for biogeographic analysis;

ii) Target unexplored geographic areas and temporal periods for primary field work;

iii) Increase the numbers of dinosaur palæontologists actively working in Gondwana. We must not only increase the number of palæontologists working in Gondwana, but encourage and facilitate the training of local dinosaur palæontologists within Gondwana;

vi) Construct well-supported phylogenies for dinosaur clades; and

v) Increase the dialogue between dinosaur palæontologists and those working on the timing and pattern of the break-up of Gondwana. Additionally, information from sedimentologists, stratigraphers, taphonomists, palynologists, palæobotanists, palæoclimatologists, invertebrate palæontologists and others may be crucial in developing the controls necessary for informed biogeographic analyses. Reciprocal illumination between all these fields will develop more informed, data-rich, biogeographic and palæoecological hypotheses.

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APPENDIX

Character state matrix and character list for basal theropod analysis to test abelisaurid relationships. *Herrerasaurus* and *Eoraptor* were used as successive outgroups. Characters are derived, in part, from Gauthier (1986), Rowe and Gauthier (1990), Holtz (1994) and Sereno *et al.* (1996). Tree statistics: delayed transformations, all characters unordered, two most parsimonious trees of 181 steps each, CI = .586; RI = .645.

Character state matrix

Taxa	Character states									
		10		20		30		40		50
		60		70		80		90		99
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
	00000	00000	00000	00000	00000	00000	00000	00000	00000	0000
Syntarsus	00000	00001	01000	00000	10000	00000	00010	00000	00001	00000
	12000	01010	00010	01001	01000	00110	00100	01001	10010	0100
Dilophosaurus	10000	10101	01101	??000	000??	00010	????0	00?00	00001	?0000
	120?0	0?000	00010	0?011	00000	00210	00001	00001	10000	0000
Ceratosaurus	02?10	00001	00101	10011	1002?	0002?	?1000	000??	100??	??001
	02100	1??10	001?0	???01	111?0	??0?0	00111	00?11	11010	000?
Carnotaurus	10100	00010	10111	11101	01101	0102?	?0101	10100	110??	??011
	02?01	11?1?	??100	0?001	11100	00011	00001	01?11	?????	????
Majungatholus	10100	00010	10111	11101	01101	01020	00001	10100	11001	00011
	01?01	111?0	11???	?????	?110?	?????	?????	???11	0?001	????
Tyrannosaurus	10010	11101	00201	11011	01011	1001?	01011	00001	00011	10111
	01110	10111	11110	111?2	11111	01200	11011	10101	01100	1?11
Allosaurus	11110	11101	00201	01011	1012?	00111	11000	00001	10011	11111
	01010	10111	11111	11112	11111	11211	11011	10101	01101	1111
Giganotosaurus	????1	????1	00201	??11	?1?1?	?1120	?1100	?1110	11101	1????
	?1???	1????	??001	1????	11111	11210	01010	11??1	???0?	1???
Sinraptor	10010	00011	00200	01011	01111	10021	11100	01111	10101	11?11
	01001	10011	??10?	0??11	11111	00211	11011	10101	01101	0111

Taxa	Character states									
		10		20		30		40		50
		60		70		80		90		99
Carcharodontosaurus	1?1?1	????0	10101	01011	0111?	11???	?0000	?111?	111?1	1????
	?1???	?????	?1???	?????	?????	?????	?????	?????	?????	????
Torvosaurus	121?0	????1	000??	??011	?0?11	?0?20	??0?0	?????	?????	00???
	?10?1	11???	01???	???1?	11?00	00011	?00??	??101	10101	010?

Character list

1. Maxillary toothrow extends behind anterior orbit margin (0), or restricted to in front of orbit (1).
2. Teeth in premaxilla, number: four (0); five (1); three (2).
3. Interdental plates, fusion: absent (0); present (1).
4. External mandibular fenestra: anterodorsal margin formed by dentary (0); anterodorsal margin formed entirely by surangular (1).

5. Dentary, shape of anterior end: rounded, tapers anteriorly (0); squared, slightly expanded (1).
6. Dentary-postdentary join: small, external mandibular fenestra large (0); large, external mandibular fenestra small (1).
7. Surangular-angular meet anterior to external mandibular fenenstra: absent (0); present (1).
8. Surangular, height at anterior end: low, less than 1/2 height of postentaries (0); tall, much more than 1/2 height of postdentaries (1).
9. Angular does (0), or does not (1) reach back to the level of the articular.
10. Antorbital fossa size: small rim around fenestra (0); broad, at least one-third the width of fenestra (1).
11. Nasals and maxilla, extreme pattern of rugosity on entire external surfaces: absent (0); present (1).
12. Subnarial gap: absent (0); present (1).
13. Maxillary fenestra: absent (0); small and slit-like (1); large and rounded (2).
14. Postorbital, oblique fossa across ventral side of suborbital flange: absent (0); present (1).
15. Premaxilla, subnarial process below nares: large, premaxilla contacts nasal below nares (0); reduced, maxilla reaches narial border (1).
16. Nasals: unfused (0); fused (1).
17. Nasal pneumaticity: absent (0); present, large pneumatic opening in antorbital fossa (1).
18. Snout length, pre-orbital portion of snout: longer than maximum depth of skull (0); less than or equal in length to maximum depth of skull (1).
19. Lachrimal fenestra: absent (0); present (1).
20. Prefrontal contribution to orbital margin: forms large part of orbital margin (0); greatly reduced or lost (1).
21. Jugal expressed on rim of antorbital fenestra: present (0); absent, eliminated from rim (1).
22. Postorbital processes with suborbital flange: absent (0); present, forms rear of keyhole-shaped orbit (1).
23. Nasal participation in antorbital fossa: absent (0); present (1).
24. Lacrimal crest: absent (0); present (1).
25. Prefrontal-frontal peg-and-socket articulation: absent (0); present (1).
26. Jugal pneumatic excavation: absent (0); present (1).
27. Wide contact between lacrimals and postorbitals forming a thick brow above orbits: absent (0); present (1).
28. Increased downturning of paroccipital processes: absent, paroccipital processes extend nearly laterally (0); present, paroccipital processes extend lateroventrally from occiput (1).
29. Size of lateral temporal fenestra: smaller than orbit (0); larger than orbit (1).
30. Quadrate: narrow (0), or broad (1), articular flange for quadratojugal.
31. Ectopterygoid excavation location: ventral (0); lateral (1).
32. Supraorbital notch between postorbital and prefrontal: absent (0); present (1).
33. Supratemporal fossa anteromedial corner: open dorsally (0); roofed over by shelf of frontal-parietal (1).
34. Parietal crest: flat and broad (0); sharply peaked, upper temporal fossæ nearly meet on midline (1).
35. Nuchal crest height: approximately even with (0), or rises well above (1) parietal crest.
36. Broad, arching transverse nuchal crest in posterior view: absent (0); present (1).
37. Lateral temporal fenestra, axis of orientation: vertical (0), posteroventral (1).
38. Frontal-parietal suture: present (0); obliterated (1).
39. Supraoccipital knob: narrow and small (0); well-developed, at least twice the width of the foramen magnum (1).
40. Occiput depth: deeper above foramen magnum than below (0); depth above and below foramen magnum equal (1).
41. Paroccipital processes orientation: lateral (0); posterolateral at a strong angle so that they extend far behind occiput (1).
42. Space between cultriform process and ossified sphenethmoids: widely open (0); closed or nearly closed off (1).
43. Basituberal processes position: below (0), or posterior to (1), occipital condyle.
44. Trigeminal nerve exit: one foramen (0); two foramina, separated into opthalmic and maxillo-mandibular branches (1).
45. Pneumatic basisphenoid recess: absent (0); present (1).
46. Internal carotid canal: no incision ot only slightly incised (0); deeply excavated into braincase (1).
47. Basioccipital: included (0), or excluded (1), from basal tubera.
48. Axial neural spine: unexpanded distally (0); broadened distally into a 'spine table' (1).
49. Ventral keel on axial centrum: present (0); absent (1).
50. Axial pneumatic foramina: absent (0); present (1).
51. Axial diapophysis: present, parapophyses large (0); absent, parapophyses small (1).
52. Cervical vertebrae: no (0), one (1), or two (2), pneumatic fossæ or foramina.
53. Pneumatic chambers in cervicals and anterior dorsals: single cavity (0); subdivided into sub-chambers (1).
54. Tenth presacral: a cervical (0); converted into a dorsal (1).
55. Epipophyses on cervical vetebrae: absent or very short, do not extend beyont posterior margin of zygopophyses (0); present, elongate and robust, extend well beyond posterior margin of zygopophyses (1).
56. Dorsal vertebrae, pneumatic foramina: absent (0); present (1).

57. Dorsal vertebrae, transverse processes in dorsal view: nearly uniform in width (0); triangular with broad bases that taper distally (1).
58. Sacral vertebrae, pneumatic foramina: absent (0); present (1).
59. Sacral vertebrae, number: less than five (0); five or more (1).
60. Caudal vertebrae, transition point: distal, half way back or further (0); proximal, one-third of the way back in tail or less (1).
61. Chevrons, posterior: straight (0); L-shaped, distal portions bent caudally (1).
62. Chevron bases: with posterior processes only (0); with paired anterior and posterior processes (1).
63. Scapular blade: set off slightly from acromion process and glenoid lip, moderately wide blade (0); sharply set off from acromion process and glenoid lip, narrow blade (1).
64. Scapula, distal end shape: unexpanded from blade (0); expanded from blade (1).
65. Coracoid-acromion process contact along anterior margin: continuous (0); separated by deep notch (1).
66. Coracoid posteroventral process: straight, shorter than width of glenoid (0); crescent shaped, longer than width of glenoid (1).
67. Clavicle fusion: absent (0); present, forms a furcula (1).
68. Semilunate carpal with transverse trochlea: absent (0); present (1).
69. Metacarpal III shaft diameter: more than (0), or less than (1), 50% that of metacarpal II.
70. Manus, digit number: five (0), four (1), three (2), two (3).
71. Iliac-ischiac articulation: larger (0), or smaller (1), than iliac-pubic articulation.
72. Postacetabular process: shorter than length of acetabulum (0); elongate, excedes length of acetabulum (1).
73. Ilium, preacetabular process, depth: slightly distally expanded at most, does not excede depth of ilium at acetabulum (0); dorsoventrally expanded, excedes depth at acetabulum (1).
74. Ilium, preacetabular fossa: absent (0); present (1).
75. Iliac pubic peduncle: less than twice as long anteroposteriorly as wide (0); at least twice as long anteroposteriorly as wide (1).
76. Pubic boot: symmetrical (0); longer anteriorly than posteriorly (1).
77. Pubic boot size: less than (0), or at least (1), 30% of pubic length.
78. Pubic obturator foramen: closed, single (0); double (1); open as a notch (2).
79. Ischium, distal expansion: absent (0); present (1).
80. Pubis-ischium relative lengths: pubis longer than ischium (0); pubis and ischium subequal in length (1).
81. Femur, lesser trochanter: small, distally placed (0); enlarged, proximally placed to be nearly even with the greater trochanter (1).
82. Ischium, distinct obturator process: absent (0); present (1).
83. Pelvic elements unfused (0), or fused (1), in adults.
84. Femur with anteromedially (0), or medially (1), orientated head.
85. Femur, trochanteric shelf: absent (0), or present (1), in robust individuals.
86. Femur, anterodistal intercondylar groove: absent (0); present (1).
87. Femur, entepicondylar flange: absent or small, barely distinguishable from shaft (0); present, large, well-defined and delineated from shaft (1).
88. Tibia, distal end backs calcaneum: absent (0); present (1).
89. Tibia, cnemial crest size: moderate, restricted to below proximal end, poorly set off from shaft (0); very large and well set off from shaft, rises up above level of proximal end (1).
90. Tibia, fibular crest: absent (0); present (1).
91. Tibia, sulcus along medial base of crista tibiofibularis: absent (0); present (1).
92. Fibula, proximomedial fossa: absent (0), present (1).
93. Astragalar distal condyles: distally (0), or anteroventrally (1), directed.
94. Calcaneum and astragalus, fusion to each other and to tibia in adults: absent (0); present (1).
95. Astragalus, horizontal groove across anterior condyles: absent (0); present (1).
96. Astragalus, ascending process length: short, less than 20% length of tibia (0); more than 20% length of tibia (1).
97. Metatarsal III, proximal end: rectangular (0); hourglass-shaped (1).
98. Metatarsal III shaft shape: rectangular (0); wedge-shaped, plantar surface pinched (1).
99. Pedal digit I, phalanges 1 + 2 subequal in length to III-1: absent (0); present (1).