

Paleobiogeography of trilophodont gomphotheres (Mammalia: Proboscidea). A reconstruction applying DIVA (Dispersion-Vicariance Analysis)

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ABSTRACT

*The objective of our paper was to analyze the distributional patterns of trilophodont gomphotheres, applying an event-based biogeographic method. We have attempted to interpret the biogeographical history of trilophodont gomphotheres in the context of the geological evolution of the continents they inhabited during the Cenozoic. To reconstruct this biogeographic history we used DIVA 1.1. This application resulted in an exact solution requiring three vicariant events, and 15 dispersal events, most of them (i.e., 14) occurring at terminal taxa. The single dispersal event at an internal node affected the common ancestor to *Sinomastodon* plus the clade *Cuvieronius* – *Stegomastodon*. A vicariant event took place which resulted in two isolated groups: (1) *Amebelodontinae* (Africa – Europe – Asia) and (2) *Gomphotheriinae* (North America). The *Amebelodontinae* clade was split by a second vicariant event into *Archaeobelodon* (Africa and Europe), and the ancestors of the remaining genera of the clade (Asia). In contrast, the *Gomphotheriinae* clade evolved mainly in North America. A dispersal event expanded the range of the common ancestor to *Sinomastodon* plus the clade *Cuvieronius* - *Stegomastodon* to include Asia again. A new vicariant event split North America and Asia resulting in the isolation of *Sinomastodon* in the latter, and the ancestor of the clade *Cuvieronius* - *Stegomastodon* in the former. Finally, these two genera reached South America in two independent dispersal events. This biogeographic history has been driven by sea-level changes. During the low sea-level episodes, trilophodont gomphotheres expanded its geographical distribution by means of dispersion events, and during high sea-level episodes suffered vicariant events.*

Key words: sea-level changes, dispersal, event-based biogeography method, DIVA, Cenozoic.

RESUMEN

El objetivo del trabajo fue analizar el modelo de distribución de los gonfoterios trilofodontos, aplicando un método biogeográfico basado en eventos. Se ha tratado de interpretar la historia biogeográfica de los gonfoterios trilofodontos en el contexto de la evolución biológica de los continentes que ellos habitaron durante el Cenozoico. Para reconstruir esta historia biogeográfica se ha utilizado

el programa DIVA 1.1. Sus resultados indican tres eventos vicariantes y 15 dispersivos, la mayoría de ellos (*i.e.*, 14) acontecidos en los taxones terminales. El único evento dispersivo en un nodo interno afectó al ancestro común de *Sinomastodon* más el clado *Cuvieronius* – *Stegomastodon*. Un primer evento vicariante dio lugar a dos grupos aislados: (1) *Amebelodontinae* (África – Europa – Asia) y (2) *Gomphotheriinae* (Norte América). El clado *Amebelodontinae*, por un segundo evento, se escindió en *Archaeobelodon* (África y Europa) y los ancestros de los géneros restantes del clado (Asia). En contraste, el clado *Gomphotheriinae* evolucionó principalmente en Norte América. Un evento dispersivo expandió el rango del ancestro común de *Sinomastodon* más el clado *Cuvieronius* – *Stegomastodon* para incluir Asia de nuevo. Un nuevo evento vicariante separó a Norte América y Asia, dando lugar al aislamiento de *Sinomastodon* en Asia, y al del ancestro del clado *Cuvieronius* – *Stegomastodon* en Norte América. Finalmente, estos dos géneros alcanzan América del Sur en dos eventos dispersivos independientes. Esta historia biogeográfica ha sido dirigida por los cambios en el nivel del mar. Durante los momentos donde los niveles del mar fueron más bajos los gonfoterios trilofodontos expandieron su distribución geográfica por dispersión, mientras que en los momentos en los que los niveles fueron más altos sufrieron eventos de vicariancia.

Palabras clave: cambios en el nivel del mar, dispersión, método biogeográfico basado en eventos, DIVA, Cenozoico.

INTRODUCTION

Throughout most of the Cenozoic Era, the Proboscidea were among the largest land mammals of the Earth. The earliest known record of a proboscidean, *Eritherium azouzorum*, is from the middle Paleocene land-mammal bearing sediments of northern Africa (Gheerbrant, 2009). Most Paleogene proboscideans did not look very “elephant-like”, because they were pig-sized and nearly trunk-less and tusk-less. But in the course of their evolution the proboscideans became larger, the trunk became longer, and the tusks and the cheek teeth, became larger (Göhlich, 1999). By the middle Eocene to Oligocene some proboscideans had reached the body size of a modern tapir (*e.g.*, *Moeritherium*). Others had reached even higher body masses (two tons) and show the typical columnar limbs of modern elephants (*e.g.*, *Palaeomastodon*, *Phiomia*, see Shoshani, 1998).

According to Shoshani and Tassy (1996), the Proboscidea may have undergone three major radiation events. The first occurred during the Eocene and Oligocene, and affected the earliest proboscideans (*e.g.*, anthracobunids, moeritheres, and deinotheres); the second occurred during the latest Oligocene and Miocene, and affected gomphotheres and stegodontids; finally, the third occurred from the latest Miocene to the Pleistocene, and affected the Elephantidae. All the taxa of the first radiation, except the American mastodon (*Mammot americanum*) had vertical tooth displacement, which is the usual method tooth replacement in Mammalia. *Mammot americanum* and the proboscideans depicted in the second and third radiations had a horizontal tooth displacement, a derived condition in which the size of the mandible is too short to accommodate all the enlarged premolars and molars at once. Proboscideans in the first radiation had low crowned teeth (brachyodont) with three or four plates in the upper third molar, and some taxa still had canine teeth. In the second radiation, upper third molars had up to seven plates and were brachyodont or hypsodont, and in the third radiation they had up to 30

plates and were hypsodont. Proboscideans in the first radiation were mostly browsers, whereas those in the second and third radiations were mostly grazers (Maglio, 1973).

The initial radiation of Elephantimorpha (*i.e.*, Mammutidae and Elephantidae) that replaced the archaic Elephantiformes (*i.e.*, Phiomidae, Paleomastodontidae) was centered in Africa and was primarily an event of the initial Neogene. During this period these proboscideans also expanded out of Africa, reaching all the continents except Australia and Antarctica (Göhlich, 1999; Prado and Alberdi, 2008). Their widespread distributions are probably related to their large body size: elephants require a large geographical range for resources, and they are capable of long-distance travel. In addition, some elephantimorph species (*i.e.*, mammoths and mastodons) were clearly well adapted for living in cold climates, which indicates a certain degree of environmental flexibility (Sánchez *et al.*, 2004).

The phylogenetic relationships of elephantimorphs to more archaic taxa were considered to be uncertain and were subject to considerable debate. Neogene proboscidean genera that do not fit easily into Stegodontidae, Elephantidae, or any other contemporaneous taxon, are usually placed in a group called gomphotheres. Most of these taxa were assigned to the “Bunomastodontidae” by Osborn (1936), and Simpson (1945) employed the term Gomphotheriidae to include the same group of taxa (Tobien *et al.*, 1986, 1988). The family Gomphotheriidae is considered to be a long lived ancestral stock from which a succession of other groups originated. This family was widespread throughout all continents except, again, Australia and Antarctica, but North America played a significant role in its biogeography and diversity (Lambert, 1996). From the early Miocene to the Pleistocene this continent received numerous immigrant taxa from the Old World via Beringia and *vice versa*. The diversity of gomphotheres also reached its peak during this time, with six genera known from the middle Miocene (*Gomphotherium*, *Rhynchotherium*, *Amebelodon*, *Serbelodon*, *Platybelodon*, and *Torynobelodon*), though the number of genera declined

during the late Miocene (*Gomphotherium*, *Rhynchotherium*, and *Amebelodon*) (Lambert and Shoshani, 1998). The gomphotheres were widespread throughout South America from the middle Pleistocene and became extinct at the end of the late Pleistocene (Prado *et al.*, 2005; Reguero *et al.*, 2007; Prado and Alberdi, 2008). Simpson and Paula Couto (1957) proposed that all of the gomphotheres known from South America derived from a single radiation in Central America.

Resolving the systematics of gomphotheres has long been considered to be a difficult task because of their great intraspecific variation, as well as the general diversity of the group. During the past three decades, many proboscidean genera of uncertain taxonomic position, but which show the same the pattern of dentition as gomphotheres, have been classified in the family Gomphotheriidae. Several cladistic works on proboscideans have been published since the mid-1990s (Kalb *et al.*, 1996; Shoshani, 1996; Tassy, 1990, 1994, 1996). Recently, Prado and Alberdi (2008) performed a cladistic analysis of the trilophodont Gomphotheriidae, using 12 genera as terminal taxa (Figure 1). According to these authors, these genera are members of a monophyletic group, separated from other genera of Proboscidea by one synapomorphy: trefoil shaped wear patterns on the occlusal surface of the teeth. The wear patterns vary from being a single trefoil to complex combinations of trefoils. Their cladogram rejects the hypothesis that consider *Rhynchotherium* (middle Miocene-Pliocene, North America) as a direct ancestor of South American gomphotheres, and supports that *Sinomastodon* (Late Miocene-Pleistocene, Asia) is the sister taxon of *Cuvieronius* and *Stegomastodon* (Pleistocene, North and South America) on the basis of the short mandibular symphysis and the absence of lower tusks. Additionally, Prado and Alberdi (2008) found high congruence between the stratigraphic record and the phylogenetic hypotheses.

A phylogeny and the knowledge of the geographical distributions of taxa are not, by themselves, sufficient to

resolve complex histories of speciation and chorology for any given group (e.g., Brooks and McLennan, 2002; Green *et al.*, 2002; Donoghue and Moore, 2003; Brooks *et al.*, 2004; Halas *et al.*, 2005). In the case of proboscideans, large-scale geological and/or environmental phenomena, like the changing configuration of continents and oceans, have affected their evolution and biogeography (e.g., Shoshani and Tassy, 1996, 2005; Shoshani, 1998). The Cenozoic configuration of continents and oceans has been strongly influenced by plate tectonic movements. The displacement of continents in the Southern Hemisphere during the middle Cenozoic, with the northward movement of the Indian and Australian continents, together with the counter clockwise rotation of Africa, closed down the Tethys Ocean. The history of the circum-Mediterranean area was strongly influenced by the Alpidic orogenies, which caused tectonic compression and fusion of numerous microplates between Europe and Africa. As a consequence of this compressive tectonic regime, Eurasia moved northwards and experienced considerable uplift (e.g., Tibetan Plateau, Alpine-Carpathian Chain, Anatolian Plate; see Kuhlemann, 2003). Simultaneously, the Eurasian ecosystems and landscapes were impacted by a complex pattern of changing seaways and land-bridges between the Paratethys Sea, the North Sea, and the Proto-Mediterranean Sea, as well as the western Indo-Pacific ocean (Popov *et al.*, 2004). The geodynamic changes in landscapes and environments were further amplified by drastic climate changes during the Cenozoic.

Connections among the major Laurasian geographic provinces have changed over time, for example, with the widening of the Atlantic ocean, and the intervention of intercontinental seaways. During the Tertiary, several major dispersal pathways facilitated biotic exchange between the Old World and New World, but shifting latitudes and climates rendered these paths either more, or less, accessible to organisms with different physiological tolerances and dispersal capabilities. The dispersal of land mammals depends not only on the availability of physical connections but also on the presence of habitats that can support viable populations.

In this context, the objective of our paper was to analyze the distributional patterns of trilophodont gomphotheres, applying an event-based biogeographic method on the basis of Prado and Alberdi's (2008) cladogram. Additionally, we have attempted to interpret the biogeographical history of trilophodont gomphotheres in the context of the geological evolution of the continents they inhabited during the Cenozoic.

MATERIAL AND METHODS

Biogeographical analysis. The event-based methods approach is primarily a taxon biogeography research program, since it is focused on the distributional history of a

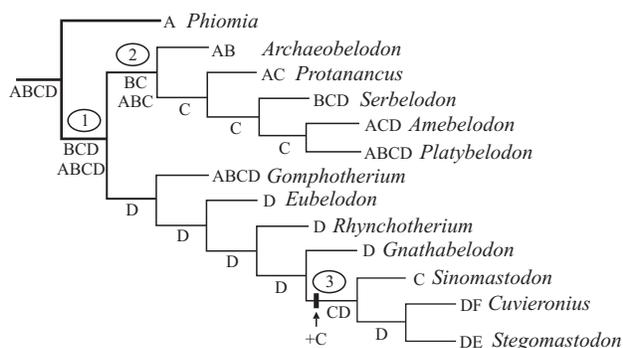


Figure 1. Prado and Alberdi's (2008) cladogram of the trilophodont gomphotheres, showing the main biogeographical events according to dispersal-vicariance analysis (DIVA). Encircled numbers indicate nodes at which vicariant events occurred; arrow indicates the unique internal dispersal event; other references as in Table 1.

particular taxon instead. As our objective was to analyze the distributional patterns of trilophodont gomphotheres, for our analysis we choose a method developed by Ronquist (1996), named dispersal-vicariance analysis (DIVA). Following Ronquist and Nylin (1990), Crisci *et al.* (2000, 2003) considered DIVA as an event-based method [but see Morrone (2005) for a different view of the use of taxonomic methods in historical biogeography].

DIVA is a biogeographic method that allows reconstruction of ancestral distributions, maximizing vicariant events and minimizing dispersal and extinction events, and allowing non-hierarchical area relationships. DIVA works by assuming that the distributions of each taxon in a phylogeny (terminals) and their ancestors (internals nodes) may be described in terms of a set of area units. If there has been a shift between the distribution of the ancestral and terminal taxa, it has occurred somewhere along the branch connecting them. To do that, DIVA uses a data matrix in which phylogenetic and distributional information of the taxon to be analyzed is included. Distributional information is encoded as the distribution of each terminal taxon of the phylogeny. Distributional areas are assigned to each internal node following two optimization rules: (a) the optimal distribution at any ancestral node cannot include any area not occupied by its descendants, and (b) the optimal set of areas for any ancestral node should include at least one area from each descendent node (Ronquist, 1997). Then, costs are assigned to changes (which represent events) between the distributional states in the descendants with respect to their immediate ancestors. Four events (or processes) are considered: vicariant speciation, dispersal, vicariance-independent speciation (*i.e.*, ‘duplication’ of a lineage within an area), and extinction. The internal nodes are then assigned the distribution state through a series of optimizations that result in the lowest cost of biogeographic events over the whole area cladogram.

To reconstruct the biogeographic history of the Gomphotheriidae we used DIVA 1.1 (Ronquist, 1996), ap-

plying an exact search according to the dispersal-vicariance optimization proposed by Ronquist (1997). This software allows inference of the ancestral distribution of a taxon and thus permits the vicariance and dispersal events that account for the geographic history of the taxon under consideration to be evaluated. To do so, the software constructs a three-dimensional cost matrix derived from a simple biogeographical model (Ronquist, 1997). The input information is the phylogenetic and distributional information encoded on the taxon-area cladogram.

The historical biogeography of trilophodont Gomphotheriidae was analyzed in terms of the phylogeny proposed by Prado and Alberdi (2008). According to the geographical distribution of the taxa (Table 1), six areas were considered as geographic units: A) Africa; B) Europe; C) Asia; D) North America; E) South American eastern area; and F) South American Andean-Patagonian area.

RESULTS AND DISCUSSION

Applying DIVA to the cladogram of Prado and Alberdi (2008), the distributional pattern of trilophodont gomphotheres has only one exact solution, requiring 15 dispersal events. All possible ancestral distributions at each node are summarized on Figure 1.

According to DIVA, there are two possible ancestral distributions for trilophodont gomphotheres at the basal node. Based on fossil record we selected the more widespread one which included: Africa – Europe – Asia – North America (Figure 1). Proboscideans are usually considered to have been endemic to Africa during the Paleogene. Shoshani and Tassy (1996: fig. 34.6) suggest that the ancestors of modern elephants “inhabited the shores of the Tethys Sea during the Eocene. From there, some [descendants] have spread to Asia, Europe, and the New World”. The recent discovery of *Erithreum melakeghebrekristosi* (a species that occupies an intermediate morphological stage between

Table 1. List of taxa considered in the analysis, with its biochron and geographic distribution. A: Africa; B: Europe; C: Asia; D: North America; E: South America eastern area; F: South American Andean-Patagonian area.

Taxon	Geological Age	Distribution
<i>Phiomia</i> Andrews and Beadnell, 1902	Late Eocene- Lower Oligocene	A
<i>Archaeobelodon</i> Tassy, 1984	Early-Middle Miocene	A and B
<i>Protanancus</i> Arambourg, 1945	Middle-Late Miocene	A and C
<i>Serbelodon</i> Frick, 1933	Middle-Late Miocene	C and D
<i>Amebelodon</i> Barbour, 1927	Middle Miocene-Pliocene	A, C and D
<i>Platybelodon</i> Borissiak, 1928	Miocene- Pliocene?	A, C, B and D
<i>Gomphotherium</i> Burmeister, 1837	Miocene- Pliocene?	A, C, B and D
<i>Rhynchotherium</i> Falconer, 1868	Middle Miocene-Pliocene	D
<i>Eubelodon</i> Babour, 1914	Middle Miocene	D
<i>Gnathabelodon</i> Barbour and Sternberg, 1935	Middle-Late Miocene	D
<i>Sinomastodon</i> Tobien, Chen and Li, 1986	Late Miocene-Pleistocene	C
<i>Cuvieronius</i> (Osborn, 1923)	Late Miocene-Pleistocene	D and F
<i>Stegomastodon</i> (Pohlig, 1912)	Late Pliocene?-Pleistocene	D and E

Phiomia and *Palaeomastodon*, meaning that all three are gomphotheres) in late Oligocene deposits of eastern Africa (Shoshani *et al.*, 2006), helps us to better understand the biogeographical implications of the early proboscidean radiation between Africa and Arabia, as well as improve the analysis of the relationships among elephantimorphs, phiomiids and palaeomastodonts (Sanders *et al.*, 2004; Prado and Alberdi, 2008). Nevertheless, the phylogenetic position of this species was uncertain and Shoshani *et al.* (2006) tentatively included it as family *incertae sedis*; for this reason Prado and Alberdi (2008) do not include this form in the cladogram.

The earliest known African gomphotheres (*Gomphotherium* sp.) occur in East Africa at Mfwangano and Mwit (east Turkana, Kenya), both early Miocene localities (20–17 Ma). Primitive elephantoids, represented by genus *Eozygodon*, reached the Indo-Pakistani subcontinent during the earliest Miocene about 22–21 Ma (Tassy, 1989; Kalb *et al.*, 1996; Lukas and Bendukidze, 1997), or perhaps earlier, as recently scanty evidence for the presence of elephantoids (referred as *Elephantoidea* indet.) was also found from the late Oligocene of Pakistan (Antoine *et al.*, 2003). This implies that the first, short-lasting dispersal corridors had evolved already during the Aquitanian Age (around 25–23.8 Ma). The time of this proposed dispersal corresponds to a phase of lower temperatures (as a consequence of the preceding Mi-1 Glaciation of Antarctica), lower sea-levels, an acceleration of the Tibetan Plateau uplift, and the rifting of the Red Sea (Haq *et al.*, 1987; Zachos *et al.*, 2001).

According to DIVA, a vicariant event (node 1, Figure 1) took place resulting in two isolated groups: Amebelodontinae (Africa – Europe – Asia) and Gomphotheriinae (North America). This distribution could have been achieved during the earliest Miocene, during the previously mentioned environmental conditions (Haq *et al.*, 1987; Zachos *et al.*, 2001). Additionally, DIVA shows that *Gomphotherium* emigrated from North America to the Old World (Figure 1). The first gomphotheres in North America came from several widespread localities from the Great Plains during the early to middle Barstovian “Land-mammal Age” (16–14.5 Ma; Middle Miocene). Lambert and Shoshani (1998) suggest a rapid spread of gomphotheres during the early Barstovian, or perhaps that the arrival of gomphotheres in North America from the Old World took place earlier than currently thought (as is possible deduce from the fossil distribution in Figure 2). DIVA does not support a dispersal event. Consequently, this result implies that gomphotheres must have been present in North America before the early Barstovian.

Gomphotherium is recorded for the first time in Europe at the end of the Mammal Neogene Zone MN3 (20–17 Ma), at the same time that other immigrant proboscideans (*i.e.*, the deinother *Prodeinotherium* Ehik, 1930, and the mammutid *Zygodolophodon* Vacek, 1877) first appear in the European record (Mein, 1975, 1999; Tassy, 1989; Koufos *et al.*, 2003). According to Steininger (1999), this wave of proboscidean immigration is dated at 19–18.5 Ma. The

northern expansion of early elephantid immigration into Western Europe, where they dispersed rapidly, started during the middle late Burdigalian Age (Early Miocene), an event previously referred to as the “Proboscidean Datum Event” by Madden and Van Couvering (1976; see also Tassy, 1989; Rögl, 1999). This is a time interval corresponding to the increased temperatures, and elevated sea-levels, of the “Mid-Miocene Climatic Optimum” (Haq *et al.*, 1987; Zachos *et al.*, 2001). Additionally, during the Early Miocene time (Burdigalian Age) the strong movements of the Savić tectonic phase changed the paleogeographic patterns in the circum-Mediterranean area. The rotation of Africa finally closed the gap between it and Eurasia, and the Arabian Peninsula collided with the Anatolian Plate. The so called “Gomphotheres land bridge” was established, and continental faunal exchange in both directions started around 19 Ma (Fortelius *et al.*, 1996; Bernor *et al.*, 1996). Subsequently, this event was recognized as being composed of multiple immigration events (Tassy, 1989, 1996; Koufos *et al.*, 2003). In Asia, the earliest gomphotheres (*Gomphotherium*) come from the Bugti Hills (Pakistan) dated around 18.3 Ma (Jacobs *et al.*, 1989).

According to DIVA, the Amebelodontinae clade was split by a second vicariant event (node 2, Figure 1): *Archaeobelodon* Tassy, 1984 was confined to Africa and Europe (in Africa around 19–16 Ma, and in Europe around 15.5–13 Ma following Pickford, 2003), and the ancestors of the remaining genera of the clade were confined to Asia. This vicariant event probably took place around the Early to Middle Miocene boundary (Burdigalian–Langhian). For a short time, the Mediterranean–Indo-Pacific seaway reopened. During this phase of open seaways, the Eurasian and African mammal dispersions were interrupted, and these seaways could explain the vicariant event that split Amebelodontinae.

Archaeobelodon is recorded for the first time in Europe during the Mammal Neogene Zone MN4. According to Steininger (1999), *Archaeobelodon* is part of a second wave of proboscidean immigration that took place between 18 and 17.5 Ma, a hypothesis not supported by DIVA. All other Amebelodontinae genera (*i.e.*, *Protanancus*, *Serbelodon*, *Amebelodon*, and *Platybelodon*) had widespread distributions which are implied from a minimum of two areas for *Protanancus* (Africa and Asia) to a maximum of four areas for *Platybelodon* (Africa, Asia, Europe, and North America). All of these widespread distributions resulted from independent dispersal events for each genus, since all of their ancestral distributions are restricted to Asia. These dispersal events (eight of the 15 postulated according to DIVA results, Figure 1) occurred after the final closure of the circum-equatorial oceanic current system that caused worldwide cooling and an increased accumulation of the East Antarctic ice sheet during the Langhian (early Middle Miocene), around 15 Ma (Kennett, 1995). Later, a new marine regression (Serravallian, late Middle Miocene) reestablished the “Gomphotheres land bridge” (Eastern

Mediterranean area: Balkan Peninsula, Aegean Sea, Asia Minor and Middle East, Koufos *et al.*, 2005). In addition, during the early Late Miocene (Tortonian) the sea-level fell drastically (see Haq *et al.*, 1987), and it was probably during this time that *Serbelodon*, *Amebelodon* and *Platybelodon* reached North America via Beringia, where to be in contact with Gomphotheriinae (Figure 2).

The Late Cenozoic opening of the Bering Strait ended the separation of the Arctic and North Pacific oceans that had persisted for about 100 million years, since the Albian period of the middle Cretaceous (Marincovich *et al.*, 1990). Since Hopkins (1967) published "The Bering Land Bridge", many geological and paleontological works concerning the Bering Strait and its adjacent areas have accumulated. The earliest known opening of Bering Strait is signaled by the presence in southern Alaskan Neogene strata of the marine bivalve mollusk *Astarte*, which had dwelled throughout the Cenozoic in the Arctic and North Atlantic oceans (Marincovich and Gladenkov, 2001). The periods of a land connection of the continents during the Pliocene are thought to have been at 4.8, 3.7, 2.5 and 2 Ma based on mammalian fossils, while marine connections between the Arctic and Pacific are suggested at around 4.2-3.0, 2.5 and

2.2 Ma, mainly based on transgressive facies of the land sections and shallow marine benthic fossils (Gladenkov *et al.*, 1991).

According to DIVA (Figure 1), the other major group (Gomphotheriinae) had evolved in isolation in North America since the Middle Miocene. At this time, the ancestor of this group, which had reached North America via Beringia during the earliest Miocene, became isolated due to higher sea-levels that occurred during Middle Miocene (see Haq *et al.*, 1987). Most ancestral distributions of the Gomphotheriinae clade were restricted to North America. *Gomphotherium* achieved a widespread distribution, colonizing Asia, Europe and Africa. This event probably took place during the aforementioned Tortonian sea-level fall. Thus, *Gomphotherium* crossed to Asia via Beringia by a migratory route that was the converse of that followed by *Serbelodon*, *Amebelodon* and *Platybelodon*. This dispersal of *Gomphotherium* from North America to Asia, Europe, and Africa, contradicts the "classical" hypothesis that proposes a dispersal in the opposite direction (*e.g.*, Shoshani and Tassy, 1996).

A major biogeographic event of the Gomphotheriinae clade is represented by the dispersal of the ancestor of



Figure 2. Map showing the distribution of gomphotheres. Symbols: □: *Phiomia*, North Africa; ○: *Protanancus*, North Africa and Asia (China, Mongolia, Turkey and Pakistan); △: *Archaeobelodon*, North Africa and Europe (France and Spain); ●: *Serbelodon*, China and North America (California and Nebraska); ∇: *Amebelodon*, North Africa, China, and North America; ◀: *Platybelodon*, East Africa, South Asia, China, Mongolia, Europe, and North America; >: *Gomphotherium*, North and East Africa, South Asia, China, Europe, and North America; ■: *Rhyncotherium*, North America; ◊: *Eubelodon*, North America (Nebraska); *: *Gnathabelodon*, North America (Kansas); ◆: *Sinomastodon*, East Asia, China, and Mongolia; ☼: *Cuvieronius*, North and South America; X: *Stegomastodon*, North and South America.

Sinomastodon plus *Cuvieronius-Stegomastodon*. This unique dispersal event occurred at an internal node. The ancestor of these three genera expanded its range from North America to North America plus Asia. This event took place via Beringia, most probably during the sea-level fall of the Messinian-Zanclean (latest Miocene-early Pliocene; see Haq *et al.*, 1987).

At the end of the Zanclean the sea-level increased again, resulting in a new vicariant event (node 3, Figure 1) which affected this clade by splitting North America and Asia. Thus *Sinomastodon* evolved in isolation in Asia, being recorded in Early Pliocene sediments of China (Tobien *et al.*, 1986; Tassy, 1996). In contrast, *Sinomastodon*'s sister group (*Cuvieronius-Stegomastodon*) evolved in North America; this clade subsequently dispersed to South America during the Great American Biotic Interchange (GABI).

The GABI was a major event in late Cenozoic biogeography as taxa from North and South America moved across the land bridge that formed with the emergence of the Isthmus of Panama (Simpson, 1950, 1980; Patterson and Pascual, 1972; Webb, 1976, 1985, 1991; Morgan, 2002, 2005). Recent studies indicate that this event was complex and started during the Miocene (Cione and Tonni, 1995; Ortiz-Jaureguizar, 1997, 2001; Scillato-Yané *et al.*, 2005; Woodburne *et al.*, 2006; Reguero *et al.*, 2007; Carlini *et al.*, 2008a, 2008b), but the main phase of the GABI occurred from about 2.7-1.8 Ma (Gelasian, early Pleistocene), with laggards lasting until about 1.0 Ma (Calabrian, late Pleistocene). A later phase occurred from about 0.8 Ma to virtually modern times and resulted in mainly southern enrichment (Woodburne *et al.*, 2006).

The new land bridge functioned as an ecologically selective dispersal corridor (Webb, 1978; Simpson, 1980). Biogeographic data indicate three major types of Plio-Pleistocene habitat corridors existed on the Panamanian land bridge: mesic tropical forest, mesic savanna, and xeric scrub savanna (Webb, 1978). During the humid interglacial phase, rain forests dominated the tropics, and the principal biotic movement was from Amazonia to Central America (south to north). During the more arid glacial phase, when savanna habitats predominated and extended well into tropical latitudes, the directional pattern reversed, and biotic forms moved from north to south (Webb, 1991).

Before the interchange, *Cuvieronius* (Gomphotheriidae), *Mammuthus* (Elephantidae), and *Mammut* (Mammutidae) were recorded in Florida and Honduras. There appears to be no obvious biological explanation why *Mammuthus* and *Mammut*, which might have been expected to cross the Panamanian land bridge, did not reach South America. The reason may be found in the diet and habitat preferences of these genera. *Mammut* have relatively low-crowned molars with zygodont crests. This dental morphology led to the recognition of mastodons as browsers (Webb *et al.*, 1992). Mammoths (*Mammuthus*) have high-crowned molars with closely spaced enamel lophs coated with cement, which identifies them as grazers (Davis *et al.*, 1985). Isotopic

analyses confirm this hypothesis (MacFadden and Cerling, 1996). The gomphotheres from West Palm Beach, Florida, and from the middle Pleistocene of South America have $\delta^{13}\text{C}$ values that are intermediate between the isotopic values for browsers and grazers (Koch *et al.*, 1998; Connin *et al.*, 1998). Mammoth and mastodon species were more specialized feeders than *Cuvieronius*, which was a mixed-feeder. Sánchez *et al.* (2004) propose that the different feeding preferences among mastodons, mammoths, and gomphotheres could explain why only the bunodont forms reached South America.

The some members of Gomphotheriinae crossed into South America during the GABI event; it apparently did so during the more arid glacial phase, when savanna habitats extended broadly through tropical latitudes (Prado *et al.*, 2005). *Cuvieronius* and *Stegomastodon* reached South America in two independent dispersal events. *Stegomastodon* ranges from early Blancan to early Irvingtonian. Although the genus was considered as the more specialized grazer within the American gomphotheres, it has been redefined as a mixed feeder with tendencies toward both browsing and grazing (Prado *et al.*, 2005). This feeding habit indicates that the genus may have been adapted to warm to temperate open grasslands.

According to Prado *et al.* (2005), *Cuvieronius* dispersed across the Andean corridor, whereas *Stegomastodon* dispersed along the eastern and Atlantic coastal areas of the continent. *Cuvieronius hyodon* is geographically restricted to the Andean Region in Ecuador, Peru, Bolivia, and Chile. It inhabited an arid landscape. This species seems to have been adapted to a temperate-cold climate, since in the inter-tropical zones it has been only found at the highest altitudes, while in Chile it expanded to the littoral zone. The latter surely offered similar living conditions, in terms of temperature, as the Andes corridor. *Stegomastodon* seems to have predominated in lower latitudes, where it occupied savannahs or xerophytic pasture areas, and consequently it would have been better adapted to warm or temperate climatic conditions. *Stegomastodon waringi* was recorded in the Santa Elena peninsula in Ecuador, and in Brazil and Uruguay (Alberdi *et al.*, 2002, 2007; Gutiérrez *et al.*, 2005). *Stegomastodon platensis* was recorded in the Middle to latest Pleistocene of Argentina, especially the Pampean Region, and also during the Late Pleistocene in Uruguay, Paraguay and Chile. All of these species became extinct at the end of the Pleistocene. The only exceptions in the Proboscidea were the African and Indian elephants. Owen-Smith (1987, 1999) has argued that the extinction of mega-mammals (more than 1000 kg) transformed a minor extinction pulse, that was affected by climate change, into a major extinction cascade because mega-mammals (such as proboscideans) were "keystone herbivore species" that had greatly raised diversity at the patch level. With the mega-mammals gone, natural processes such as woody regeneration and shrub invasions of grassy glades progressed unimpeded, thus reducing carrying capacity for non-migratory grazers.

CONCLUSIONS

The application of DIVA resulted in an exact solution requiring three vicariant events, and 15 dispersal events, most of them (*i.e.*, 14) occurring at terminal branches. The single dispersal event at an internal node affected the common ancestor to *Sinomastodon* plus the clade *Cuvieronius* – *Stegomastodon*.

The ancestral distribution for trilophodont gomphotheres included Africa – Europe – Asia – North America (Figure 1). This distribution could have been achieved during the earliest Miocene, a time of low sea-levels and low temperatures. A vicariant event took place which resulted in two isolated groups: (1) Amebelodontinae (Africa – Europe – Asia); and (2) Gomphotheriinae (North America). The Amebelodontinae clade was split by a second vicariant event: *Archaeobelodon* (Africa and Europe), and the ancestors of the remaining genera of the clade (Asia). In contrast, the Gomphotheriinae clade evolved mainly in North America. A dispersal event expanded the range of the common ancestor to *Sinomastodon* plus the clade *Cuvieronius* - *Stegomastodon* to include Asia again. A new vicariant event split North America and Asia resulting in the isolation of *Sinomastodon* in the latter, and the ancestor of the clade *Cuvieronius* - *Stegomastodon* in the former. Finally, these two genera reached South America in two independent dispersal events.

The biogeographic history of trilophodont gomphotheres has been driven by sea-level changes. During low sea-level episodes, trilophodont gomphotheres expanded their distribution by means of intercontinental dispersion events, and during high sea-level episodes they underwent vicariant events.

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