EAST OF EDEN: ASIA AS AN IMPORTANT CENTER OF TAXONOMIC ORIGINATION IN MAMMALIAN EVOLUTION

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ABSTRACT

The continuity of phylogenetic descent requires that sister taxa originate at the same time and in the same place. Phylogenetic constraints on biostratigraphy and paleobiogeography are imposed by this simple rule, but these relationships have frequently been overlooked or underappreciated. Highly corroborated paleobiogeographic hypotheses are supported by both phylogenetic and biostratigraphic datasets. Based on this approach to paleobiogeographic reconstruction, Asia is identified as the most likely ancestral area for a large number of placental mammal clades, including Perissodactyla, Artiodactyla, Cetacea, Dinocerata, Tillodontia, Arctostylopidae, Pantodonta, Coryphodontidae, Rodentia, Alagomyidae, Lagomorpha, Primates, and Hyaenodontidae.

Contrary to many traditional notions regarding North American mammalian evolution, few higher-level mammal taxa seem to have originated in North America. Rather, North America has functioned primarily as a biogeographical cul-de-sac of Asia since at least late Cretaceous time. Iterative dispersal of higher-level mammal clades into North America from Asia has been the dominant mode of modernization of the North American mammalian biota throughout the Cenozoic Era. This "East of Eden" model agrees with paleogeographic reconstructions, which severely constrain potential source areas for mammalian immigrants to North America subsequent to early Eocene rifting in the North Atlantic. As in the case of the Grand Coupure and the Great American Interchange, East of Eden dispersal is characterized by immigrant taxa hailing from the larger landmass (in this case, Asia) being far more likely to colonize the smaller landmass (in this case, North America) than vice versa.

Three closely staggered East of Eden dispersal events during the interval spanning late Tiffanian (Ti5) through basal Wasatchian (Wa0) are interpreted as the result of a single sustained climatic warming trend. Progressive reduction of latitudinal temperature gradients over the course of this late Paleocene–early Eocene interval allowed three consecutive waves of Asian endemic mammals to disperse across Beringia and successfully colonize North America: Dinocerata and Arctostylopidae (Ti5); Rodentia, Tillodontia, and Coryphodontidae (Clarkforkian; Cf1); and Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae (Wa0).

In light of the East of Eden paleobiogeographic model, previous attempts to correlate early Paleogene Asian Land Mammal Ages (ALMAs) have probably underestimated their antiquity. The Gashatan ALMA probably correlates with the latter half of the Tiffanian and possibly the earliest part of the Clarkforkian. The Bumbanian ALMA may correlate with the remainder of the Clarkforkian and the early part of the Wasatchian.

INTRODUCTION

The phylogeny and adaptive radiation of late Cretaceous and early Cenozoic mammals took place on a dynamic geographical backdrop that was unlike that familiar to us today, but one that also differed from the monotonous conditions afforded by the supercontinent of Pangaea (and subsequently, Laurasia and Gondwanaland) earlier in the Mesozoic. This constantly changing geographical setting undoubtedly influenced the course of mammal phylogeny, perhaps in ways more numerous than one can easily imagine (cf. McKenna, 1983a). Indeed, the breakup of large Mesozoic landmasses into smaller continental plates has itself been cited as a factor underlying the radiation of early mammals and birds (Hedges et al., 1996). Regardless of whether or not the model of Hedges et al. (1996) proves to be accurate, it is clear that geographic segregation of certain landmasses resulted in marked endemism in their native mammal faunas. A prime example is the celebrated "splendid isolation" of South America, which supported an adaptive radiation of mammals remarkable both for its endemism and its evolution of basic bauplans strikingly convergent on those found elsewhere in Mammalia (e.g., Simpson, 1980; Cifelli, 1993).

However, even in the case of island continents like South America, new paleontological discoveries are demonstrating that faunal and geographic links to other continents were at times both striking and pronounced (de Muizon and Marshall, 1991, 1992; Pascual et al., 1992; Woodburne and Case, 1996).

Scientific attempts to reconstruct the biogeographical history of mammals, particularly over the critical late Cretaceous–early Cenozoic interval during which much of mammalian higher-level taxonomic diversity was generated, 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. Yet I will argue below that the reciprocal illumination between phylogeny and biogeography has been significantly underexploited by paleomammalogists in recent years. My goal here is to explore some of the logical interrelationships among phylogeny, biogeography, and biostratigraphy as they relate to the early evolution of mammals in Asia.

PHYLOGENY AND PALEOBIOGEOGRAPHY

Biogeographic hypotheses are implicit within all phylogenetic hypotheses. That is, by positing that two clades are sister taxa, one also postulates that these clades originated in the same geographic region. Furthermore, because speciation is a local (rather than global) phenomenon, it is theoretically possible to reconstruct the region of origin of any particular clade at some level of geographic precision below that of the Earth as a whole. The level of geographic precision that may be desired in reconstructing the region of origin of a given clade varies from taxon to taxon. For example, reconstructing the continent on which the living marsupial genus *Macropus* originated is biogeographically uninteresting because it and its immediate relatives are, and apparently always have been, confined to Australia and nearby islands. On the contrary, identification of the continental landmass that originally spawned all Metatheria is hotly debated, and resolution of this issue would represent a real advance in our knowledge of mammalian historical biogeography (cf. Szalay and Trofimov, 1996). As in the latter case, it is currently unrealistic to attempt to specify the region of origin of such higher-level taxa as living and extinct orders of placental mammals at geographic scales below that of the continent.

Operationally, paleobiogeographic hypotheses regarding the region of origin of a clade are contingent on phylogenetic reconstructions of that clade and closely related outgroups. In terms of parsimony alone, it is possible to treat the known geographic ranges of living and fossil taxa as "characters" to be optimized at interior nodes on a cladogram (Fig. 1). Use of such biogeographic "characters" in phylogeny reconstruction is emphatically not advocated here, if for no other reason than to maintain the independence of phylogenetic and biogeographic datasets. Rather, a posteriori optimizations of these biogeographic "characters" at interior nodes on a cladogram can serve as working hypotheses regarding the area of origin of a clade. Such phylogenetically derived hypotheses regarding the region of origin of a clade are then available for further evaluation in the light of other relevant datasets. Examples of datasets that are useful for comparison with these phylogenetically derived biogeographic reconstructions include the fossil record of the clade and geophysical data pertaining to the likelihood of the clade's dispersal and/or vicariance. Ronquist (1997) has recently outlined a parsimony-based method for reconstructing geographic distributions at interior nodes of a cladogram that is similar in many ways to that employed here.

Highly corroborated hypotheses regarding the region of origin of a clade are those in which phylogenetically derived biogeographic reconstructions are unambiguous and are congruent with other datasets, particularly a dense fossil record for the clade. In cases in which there is strong congruence between phylogenetically derived biogeographic reconstructions and the fossil record, consensus regarding the region of origin of a clade can actually be far stronger than that regarding the phylogeny of a clade. For example, it is virtually universally accepted that the human clade (that is, living humans + all fossil species that are more closely related to humans than to our nearest living outgroups, *Pan* and *Gorilla*) originated in Africa (e.g., Wood, 1992; Strait et al., 1997). This consensus is based on 1) unambiguous optimizations that reconstruct Africa as the ancestral geographic range at the interior node defining the human clade (i.e., all basal species within the human clade, as well as successive outgroups, are restricted to Africa); and 2) congruence between this phylogenetically derived biogeograph-
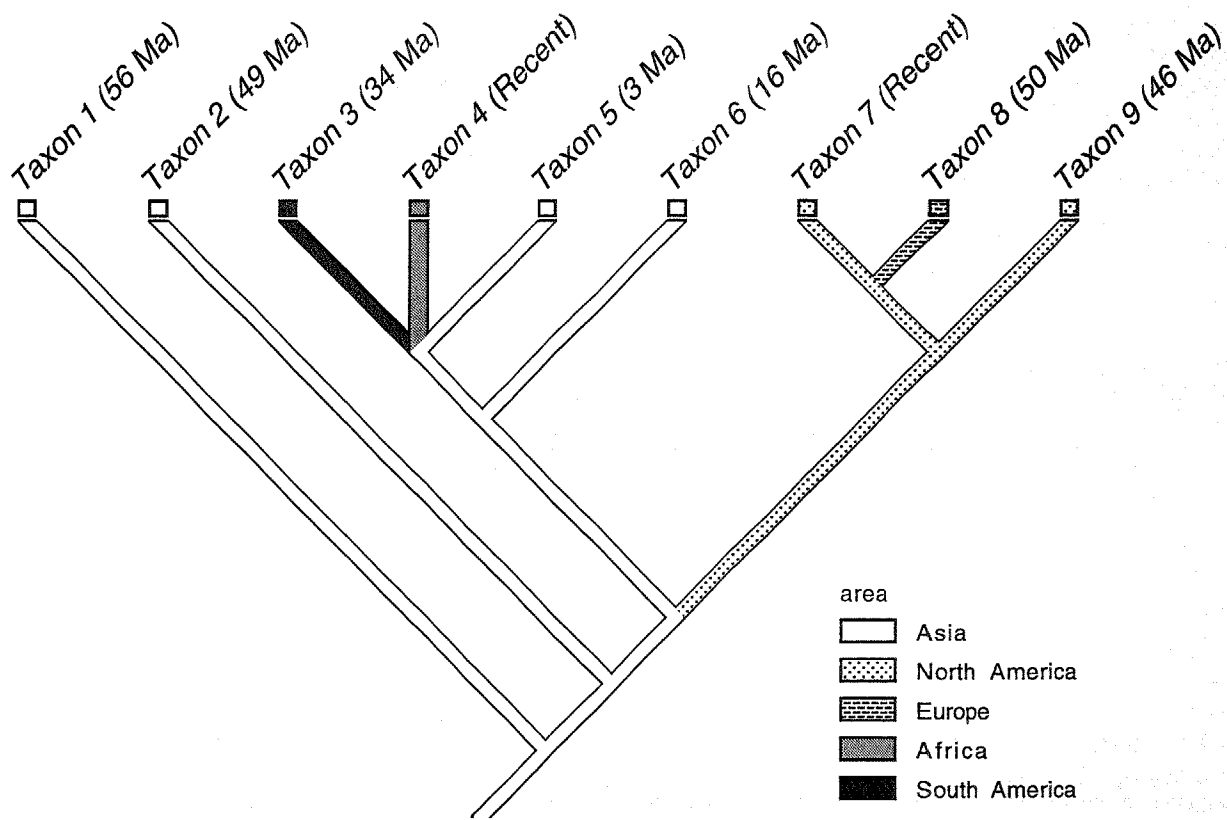
Fig. 1.—A phylogenetically derived biogeographic reconstruction for a hypothetical clade consisting of nine living and fossil taxa. Age of terminal taxa is shown in parentheses. Each terminal taxon is restricted to one of the five geographic areas (continents) shown at the lower right, as follows: taxa 1, 2, 5, and 6 are endemic to Asia; taxon 3 occurs in South America; taxon 4 occurs in Africa; taxa 7 and 9 are endemic to North America; taxon 8 occurs in Europe. A posteriori optimization of the geographic distributions of terminal taxa on this tree topology unambiguously reconstructs Asia as the continent on which the entire clade originated, with subsequent dispersal to South America (taxon 3), Africa (taxon 4), North America (ancestor of taxa 7, 8, and 9), and Europe (taxon 8). In this example, the phylogenetically derived biogeographic reconstruction is congruent with the fossil record because taxon 1 is both the oldest and most basal member of the clade.

ic reconstruction and the fossil record of the human clade, which is far older in Africa than elsewhere (cf. White et al., 1994). Importantly, the broad consensus regarding an African origin for the human clade is likely to withstand ongoing debate over details of this clade's phylogeny.

Although biogeographic reconstructions of the area of origin of a clade are operationally contingent on phylogenetic reconstructions of that clade, the possibility of reciprocal illumination between paleobiogeography and phylogeny remains. That is, biogeographic evidence that two clades that are thought to be sister taxa actually did originate in the same region can be viewed as corroborating the original phylogenetic hypothesis. For example, several anatomical lines of evidence support the monophyly of the supraordinal taxon Glires, which encompasses the orders Rodentia and Lagomorpha (e.g., No-

vacek et al., 1988; Novacek, 1990). Felicitously, the fossil record suggests that both Rodentia and Lagomorpha originated in Asia (e.g., Li and Ting, 1993; Meng et al., 1994). In this case paleobiogeographical data that are independent of the anatomical data on which Glires rests are consistent with a major prediction of Glires monophyly—that rodents and lagomorphs shared a common area of origin.

Alternatively, in cases in which taxa believed to be sister groups show discordant biogeographical patterns, the disjunct areas of origin inferred for the sister taxa require explanation. Frequently, apparent conflicts such as these can be attributed to the incompleteness of the fossil record (i.e., the sister taxa actually did share a common region of origin, but this is obscured by the vagaries of fossil preservation). This interplay between phylogeny and bio-

geography is analogous to that between phylogeny and the stratigraphic ranges of sister taxa (the "ghost lineage" concept of Norell [1992, 1993]; also see Weishampel [1996]). Less frequently among mammals, disjunct distributions may have resulted from large-scale geophysical processes causing vicariance. Of course, when evidence for the disjunct origination of taxa reputed to be sister groups is strong and seemingly inexplicable by the preceding criteria, it is always prudent to reassess the level of support for the phylogenetic reconstruction underlying the conflict.

WHY FOCUS ON ASIA?

Several paleogeographic and paleobiogeographic factors peculiar to Asia conspire to make it an ideal candidate to have served as an important theater of mammalian diversification during the late Cretaceous and early Cenozoic. These include the large area of contiguous terrestrial habitats subsumed within the Asian continent, the precocious development of varied environmental conditions there, and the central position occupied by Asia with respect to other continental landmasses during this interval of time.

GEOGRAPHIC AREA AND TAXONOMIC DIVERSITY

As recently reviewed by Rosenzweig (1995), larger areas support greater biotic diversity than do smaller areas. This ubiquitous ecological pattern holds over geographic scales ranging from islands within an archipelago to continents. Today, the vast Eurasian continent is the world's largest continuous region of dry land. Despite the ebb and flow of epicontinental seas, Asia probably maintained this status throughout much, if not all, of the Cenozoic (e.g., Smith et al., 1994). Hence, one can reasonably infer that the diversity of mammals inhabiting Asia during the late Cretaceous and early Cenozoic exceeded that on other continents at this time. Indeed, considerations of area alone may underestimate mammalian diversity on Asia because of the precocious development of faunal provincialism there.

As will become evident below, the vast area encompassed by the Asian landmass and the high taxonomic diversity of Cenozoic mammals inferred to have lived there resulted in numerous instances in which Asian endemic mammal taxa successfully colonized other landmasses. In agreement with MacArthur and Wilson's (1967) equilibrium theory, only rarely did exotic mammals from other landmasses successfully invade Asia.

PALEOENVIRONMENTAL HETEROGENEITY AND FAUNAL PROVINCIALISM

Evidence for faunal provincialism within Asia during the late Cretaceous and early Cenozoic is abundant, almost certainly reflecting the formation of highly divergent habitats there at this time. In particular, the semiarid to arid conditions that so typify central Asia today can be traced back to the Campanian, when extensive eolian dune fields developed in the Gobi Basin along the Chinese–Mongolian frontier (Eberth, 1993; Jerzykiewicz et al., 1993). This precocious development of relatively arid conditions in central Asia may have been tied to rejuvenation of the Tian Shan range, uplift of which began to cast a rain shadow over the Tarim and Turpan basins in Xinjiang as early as the early Cretaceous (Hendrix et al., 1992). In contrast to the persistently more xeric conditions in central Asia, more mesic habitats undoubtedly prevailed in lower-latitude parts of Asia and in areas nearer to the ancient coastlines of Tethys and the Pacific Ocean during much of the late Cretaceous and early Cenozoic (e.g., Tong, 1994).

Unsurprisingly, fossil mammal faunas from these latter areas can differ markedly from those derived from the more "classic" localities known from Mongolia and northern China. Examples of this phenomenon include: 1) the diversity of late Cretaceous "zhelestid" ungulatomorphs now known from coastal plain depositional settings in Uzbekistan, but which remain unknown from drier habitats in central Asia (Archibald, 1996; Nessov et al., 1998); 2) the apparent absence of multituberculates in numerous Paleocene basins of central and southern China, which contrasts with their relative abundance and diversity in Gashatan faunas of northern China and Mongolia (Sloan, 1987; Meng et al., 1998; Wang et al., 1998); 3) the presence of numerous taxa showing North American affinities (including Epoicotheriidae, Carpolestidae, Paromomyidae, Paramyidae, and others) in the Bumbanian Wutu fauna of Shandong Province, China (Tong and Wang, 1998), none of which are recorded in the similar-aged mammal fauna known from the Bumban Member of the Naran Bulak Formation in southern Mongolia; and 4) the presence of such unusual and distinctive taxa as the primates *Tarsius*

eocaenus, Macrotarsius, and *Adapoides,* didelphid marsupials, and palaeotheriid perissodactyls in the middle Eocene Shanghuang fissure fillings of southern Jiangsu Province (Beard et al., 1994; Qi et al., 1996), which contrasts with their absence or extreme rarity in similar-aged faunas from the interior of the Asian continent.

Despite comparatively good geographic representation of early Cenozoic mammal-bearing sites within China, a potentially critical part of the early Cenozoic record of Asian mammal evolution continues to elude us. That is, aside from the late Eocene Pondaung fauna of Burma (e.g., Colbert, 1938; Holroyd and Ciochon, 1995) and the roughly coeval Krabi fauna of southern Thailand (e.g., Ducrocq et al., 1995, 1996; Chaimanee et al., 1997), we have no knowledge of the late Cretaceous and early Cenozoic mammals of southeastern Asia. Judging from its Recent biota, this area holds great promise as an important theater of mammalian phylogeny and diversification. At the very least, southeastern Asia has served as a Neogene refugium for such ancient mammalian clades as Tupaiidae, Galeopithecidae, and Tarsiidae (Ducrocq et al., 1992; Beard, 1998). Should significantly earlier mammalian faunas be recovered from this region, they too can be expected to differ from those known from more interior regions of Asia.

PALEOGEOGRAPHIC LINKS WITH OTHER CONTINENTS AND LANDMASSES

Among the three Laurasian continents of Europe, Asia, and North America, it is fair to characterize Asia as playing a central role in terms of paleogeography and paleobiogeography (Smith et al., 1994). That is, following the early Eocene rifting in the North Atlantic that ultimately separated northwestern Europe from Greenland (Ritchie and Hitchen, 1996), overland dispersal among Laurasian continents was (at least intermittently) possible between Asia and Europe and between Asia and North America, but not directly between North America and Europe. Cenozoic dispersal between Asia and the other two Laurasian continents must have been controlled largely by eustatic sea level and climate, as opposed to large-scale tectonics. The Obik Seaway east of the Ural Mountains formed a marine barrier between Asia and Europe during much of the early Paleogene (McKenna, 1983a; Smith et al., 1994), while the high northern latitude position of the Beringian region acted as a strong filter between Asia and North America that was especially dependent on climatic conditions (see below).

In contrast to the climatically and eustatically mediated relationships between Asia and other Laurasian landmasses, paleogeographic links between Asia and remnants of Gondwanaland were mainly dependent on large-scale tectonics. The most obvious of these resulted from the collision between the Indian subcontinent and the southern margin of Asia, which occurred during the early Paleogene (Beck et al., 1995). Krause and Maas (1990) view this collision as having highly significant biogeographic ramifications for the mammalian biota of Asia and other Laurasian landmasses, an opinion that is not endorsed here (see below).

Faunal data show unambiguously that paleobiogeographic links existed between Asia and the Afro–Arabian landmass during the Paleogene, but such critical factors as the mode of dispersal (at best via a strong filter, more likely via sweepstakes dispersal across the eastern Tethys), the timing of interchange, and the pathways by which dispersal occurred remain unknown (cf. Holroyd and Maas, 1994). Nevertheless, the distributions of certain mammal clades imply that these taxa were able to disperse between Asia and Afro–Arabia. In at least some cases dispersal between these landmasses may also have involved Europe as an intermediary. Taxa that are critical for demonstrating Paleogene dispersal between Asia and Africa include Primates (documented in Africa as early as late Paleocene; see Sigé et al., 1990), Proboscidea (documented in Africa as early as late Paleocene; see Gheerbrant et al., 1996), Rodentia (documented in Africa as early as middle Eocene; see Vianey-Liaud et al., 1994), Anthropoidea (documented in Africa as early as middle Eocene; see Godinot, 1994), Embrithopoda (documented in Africa as early as late Eocene; see Gagnon, 1997), and Anthracotheriidae (documented in Africa as early as late Eocene; see Ducrocq, 1995). Many, but not all, of these taxa are inferred to have originated in Asia (see next section). For early Asian records of Anthropoidea and Embrithopoda, see Beard et al. (1994, 1996) and Maas et al. (1998), respectively.

PHYLOGENETIC AND PALEONTOLOGICAL EVIDENCE FOR THE ORIGINATION OF MULTIPLE HIGHER-LEVEL MAMMAL CLADES IN ASIA

In light of the phylogenetic and paleontological criteria established earlier, hypotheses on the paleobiogeographic origins of selected higher-level clades of placental mammals are briefly evaluated here. Taxa that achieved widespread distributions and/or taxa that have proven to be biostratigraphically significant are emphasized, but this treatment is not meant to be exhaustive. Phylogenetically derived biogeographic reconstructions are obviously driven by the phylogenetic reconstructions upon which they are based. Because phylogenetic reconstructions for many of the taxa discussed below remain contentious, there are significant possibilities for refinement of these paleobiogeographic reconstructions in the future.

PROBOSCIDEA

Undoubted proboscideans are prominent members of early Tertiary mammal faunas in Africa (Mahboubi et al., 1984; Gheerbrant et al., 1996), and it seems highly probable that a major part of proboscidean evolution took place on that continent. However, anthracobunids, which are widely considered to be either basal proboscideans or proboscidean sister taxa, are restricted in their known distribution to the early Tertiary of Asia (Wells and Gingerich, 1983). Embrithopods, which are also frequently mentioned as basal members or sister taxa of Proboscidea (Court, 1992), are known from the early Tertiary of northern Africa and southwestern Asia (Maas et al., 1998). Because of these Asian records of basal proboscidean relatives, Fischer and Tassy (1993:232) concluded that, "The more evidence we gather, the less likely becomes the long-held assumption of an African endemic origin of hyracoids and proboscideans. Recent collections of stem tethytherians and stem proboscideans from Asia and China . . . now suggest an origin outside Africa and perhaps in Asia."

The phylogenetic reconstruction of Proboscidea and their fossil relatives published by Fischer and Tassy (1993), with emended relationships among advanced proboscideans as suggested by Court (1995) and Gheerbrant et al. (1996), implies unambiguously that the stem lineage for Proboscidea originated in Asia (Fig. 2). If so, early dispersal from Asia to Africa of the clade comprising advanced proboscideans is indicated by the late Paleocene age of *Phosphatherium escuilliei* (Gheerbrant et al., 1996). The fossil record of early pro-

boscideans and their putative sister taxa does not contradict this phylogenetically derived biogeographic reconstruction, because such basal Asian taxa as the Nongshanian genus *Minchenella* are likely to be as old, if not older, than the earliest African proboscidean, *Phosphatherium*.

PERISSODACTYLA

Perissodactyls (excluding hyracoids, which are sometimes included in this order; cf. Prothero and Schoch, 1989) are common elements of most early Tertiary Holarctic faunas of basal Eocene or younger age. In contrast, FADs ("First Appearance Datums"; see Woodburne, 1996) for this order are much later in former Gondwanan landmasses. The FAD for perissodactyls in Africa is early Miocene, at which time both rhinocerotids and chalicotheriids are recorded (e.g., Coombs, 1989; Prothero et al., 1989). In South America the FAD for perissodactyls (in the form of Tapiridae and Equidae) is even younger, corresponding to the "Great American Biotic Interchange" about 2.5 million years ago (Webb, 1985).

Despite this evidence that perissodactyls inhabited the northern continents well before their first appearances in Gondwanan terrains, several workers have posited an origin for Perissodactyla in lower-latitude remnants of Gondwanaland. For example, Gingerich (1989:90) pointed to Africa as the likely ancestral homeland for Perissodactyla and other higher-level mammal taxa (including Artiodactyla, Primates, and Hyaenodontidae), citing resemblances between perissodactyls and African Eocene hyraxes as evidence in favor of this viewpoint. Biogeographically more complicated is the hypothesis advocated by Krause and Maas (1990:95–96), who suggested that perissodactyls and other higher-level mammal taxa (see above) may have originated on the Indian subcontinent prior to its collision with Asia. Under this hypothesis the Indian subcontinent functioned as a "Noah's Ark" (cf. McKenna, 1973, 1983a) during the late Cretaceous and Paleocene until it docked onto the southern margin of Asia sometime near the Paleocene–Eocene boundary. More traditional hypotheses regarding the landmass on which perissodactyls originated have cited all three Holarctic continents as prime suspects. However, earlier suggestions that perissodactyls may have originated in Central America or the southern part of North America (Morris, 1966; Sloan, 1969;
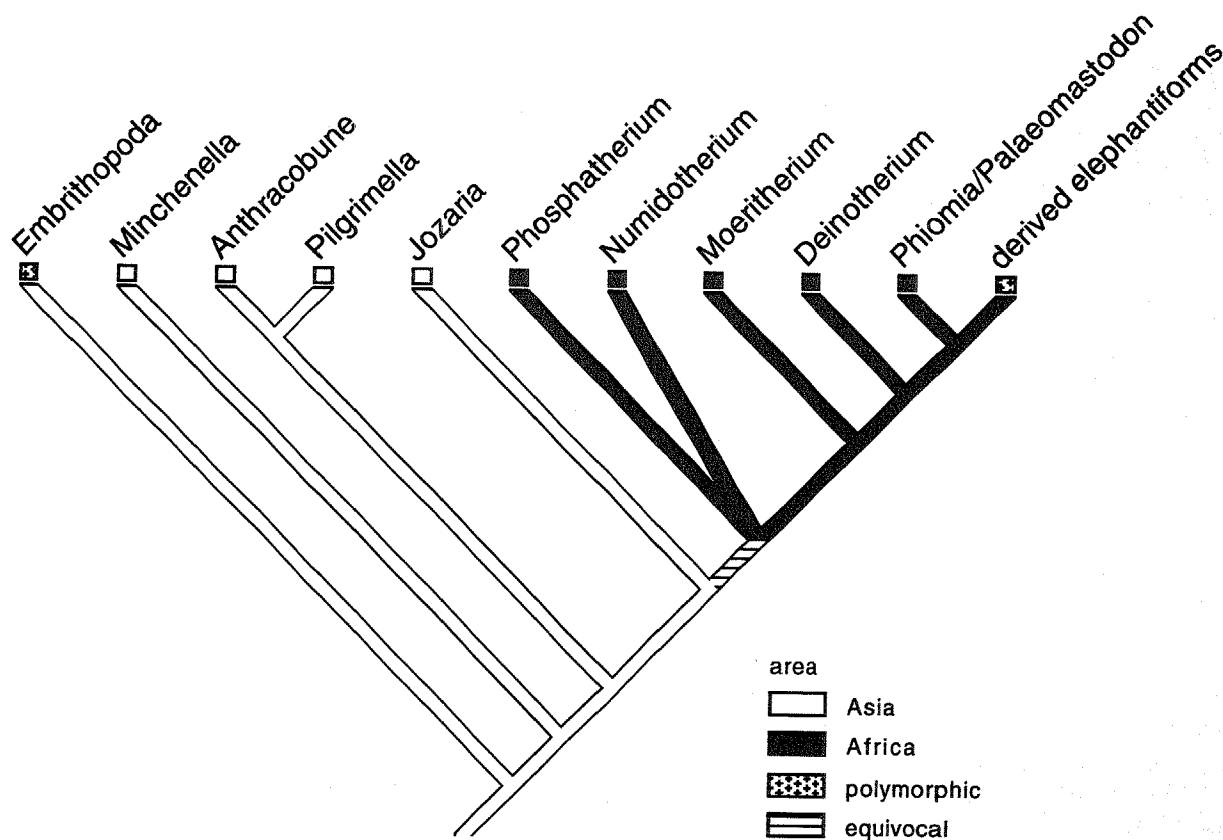
Fig. 2.—A phylogenetically derived biogeographic reconstruction for Proboscidea (sensu lato). The tree topology depicted here is based on Fischer and Tassy (1993), with emended relationships among advanced proboscideans as suggested by Court (1995) and Gheerbrant et al. (1996). Note that the stem lineage for Proboscidea is unambiguously reconstructed as endemic to Asia, followed by early dispersal of advanced proboscideans to Africa. In this and subsequent figures, terminal taxa occurring in more than one geographic region were coded as "polymorphic" for purposes of a posteriori optimization based on parsimony.

Gingerich, 1976; Schiebout, 1979) have now been largely abandoned (Gingerich, 1989; Krause and Maas, 1990). Similarly, although it has been suggested that the earliest North American perissodactyls dispersed to that continent from Europe (Hooker, 1980; Godinot, 1981, 1982), no recent worker has argued for a European origin for Perissodactyla (Krause and Maas, 1990). In contrast, the discovery of the Nongshanian perissodactyl-like mammal *Radinskya yupingae* in the Nanxiong Basin, Guangdong Province, China (McKenna et al., 1989), gives the hypothesis that perissodactyls originated in Asia renewed viability.

The past decade has witnessed a great resurgence in interest in reconstructing perissodactyl phylogeny, but no single phylogenetic reconstruction has achieved consensus. Furthermore, the possible sister-group relationship between Perissodactyla and Hyracoidea among living mammals continues to be debated (Fischer, 1989; de Jong et al., 1993; Fischer

and Tassy, 1993; Shoshani, 1993; Springer et al., 1997). Here, the Paleocene mammal *Radinskya yupingae* is accepted as the closest known sister group of Perissodactyla. Otherwise, the phylogeny for Perissodactyla published by Prothero and Schoch (1989:fig. 28.2), with emendations regarding equoid relationships as suggested by Hooker (1994), forms the basis for the phylogenetically derived biogeographic reconstruction undertaken here. Although frequent dispersal has greatly complicated the reconstruction of perissodactyl paleobiogeography, current knowledge of perissodactyl phylogeny indicates that Asia served as a persistent center of taxonomic origination throughout this clade's history (Fig. 3). In particular, the hypothesis that perissodactyls originated in Asia is unambiguously supported by the phylogenetic relationships depicted in Figure 3.

Three lines of evidence indicate that this phylogenetically derived biogeographic reconstruction is
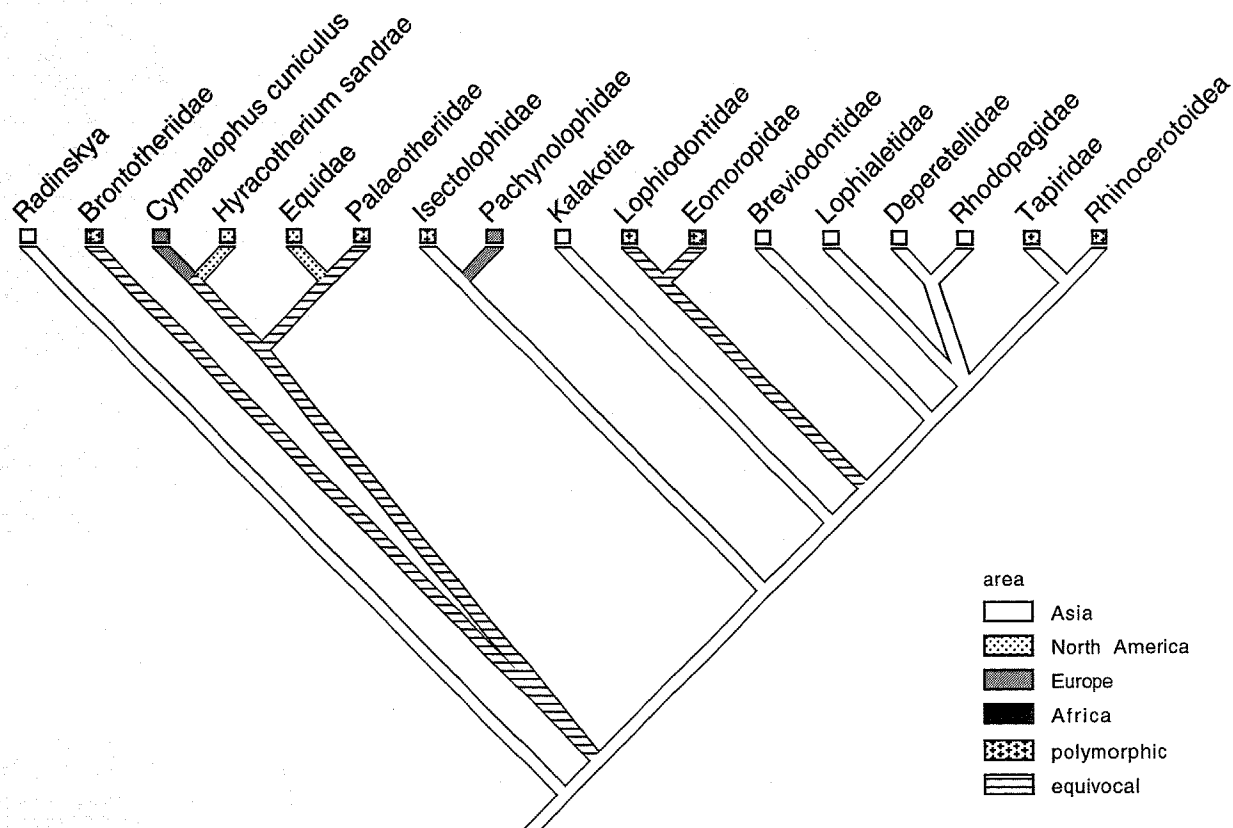
Fig. 3.—A phylogenetically derived biogeographic reconstruction for Perissodactyla. The tree topology depicted here is based on Prothero and Schoch (1989:fig. 28.2), with emendations regarding equoid relationships as suggested by Hooker (1994) and with *Radinskya yupingae* as the closest known sister group of Perissodactyla. Note that an Asian origin for Perissodactyla is unambiguously supported, and that Asia appears to function as a persistent center of origin for various perissodactyl clades throughout the history of the order.

concordant with the fossil record of perissodactyls. First, the Asian Nongshanian genus *Radinskya*, accepted here as the nearest sister group of perissodactyls, is undoubtedly older than perissodactyls from other continents (McKenna et al., 1989). Second, an indeterminate genus and species of perissodactyl showing morphological similarities to *Lambdotherium* occurs in the Bayan Ulan fauna, of Gashatan age, in Nei Mongol Autonomous Region, China (Meng et al., 1998). As is the case for *Radinskya*, the *Lambdotherium*-like perissodactyl from the Bayan Ulan fauna is clearly older than the earliest perissodactyls known from North America and Europe, which occur in basal Wasatchian and basal Sparnacian faunas, respectively (Meng et al., 1998; Wang et al., 1998; also see below). Finally, a growing diversity of Bumbanian perissodactyls in Asia (Chow and Li, 1965; Ting, 1993; Wang and Tong, 1996) may also be at least as old as the earliest perissodactyls known from North America and Europe (see below). Congruence between the phylo-

genetically derived biogeographic reconstruction depicted in Figure 3 and the fossil record of early perissodactyls underscores the strong support for the hypothesis that perissodactyls originated in Asia.

ARTIODACTYLA

As is the case for perissodactyls, artiodactyls are common elements of Holarctic mammalian faunas as early as the basal Eocene. The FAD for Artiodactyla in Africa is much later, consisting of anthracotheres from Nementcha, Algeria, and locality L-41, Fayum Depression, Egypt, that are thought to be late Eocene in age (Rasmussen et al., 1992; Ducrocq, 1995). The earliest South American artiodactyls date to roughly 2.5 million years ago (the "Great American Biotic Interchange"), when Camelidae, Cervidae, and Tayassuidae dispersed into South America from North America (Webb, 1985).

Previous hypotheses regarding the continent on which artiodactyls originated have varied largely

along the same lines as those regarding perissodactyl origins (see above). In particular, early suggestions (Sloan, 1969; Gingerich, 1976; Schiebout, 1979) that artiodactyls may have originated in either the southern part of North America or in Central America are no longer supported (Gingerich, 1989; Krause and Maas, 1990). Morphologically primitive European species of the early artiodactyl *Diacodexis* are known (Godinot, 1978, 1981; Estravis and Russell, 1989; Smith et al., 1996), suggesting to some authors that the earliest North American artiodactyls dispersed to that continent from Europe (Godinot, 1981, 1982; Estravis and Russell, 1989; Smith et al., 1996). However, because of the abrupt (and possibly synchronous) appearance of artiodactyls near the beginning of the Eocene in Europe and North America, most recent workers favor an origin for Artiodactyla outside both of these continents. As a result, an African origin for artiodactyls was proposed by Estravis and Russell (1989) and Gingerich (1989), despite the very late FAD for artiodactyls on that continent. Alternatively, Krause and Maas (1990) favored an artiodactyl birthplace on the late Cretaceous–early Tertiary Noah's Ark formed by the Indian subcontinent. Finally, study of the basal artiodactyl species *Diacodexis pakistanensis* led Thewissen et al. (1983) to propose an Asian origin for the order.

Assessing the early historical biogeography of artiodactyls on the basis of phylogenetic data is severely constrained by the absence of recognizable sister taxa for the order. Early suggestions that artiodactyls evolved from arctocyonid condylarths (Sloan, 1969; Van Valen, 1971) are now largely discounted (Rose, 1987). More recent studies cite Cetacea (+ Mesonychidae) as a potential sister group to Artiodactyla, or even as a nested clade within the suiform radiation (Irwin and Árnason, 1994; Philippe and Douzery, 1994; Randi et al., 1996). Until sister taxa of artiodactyls are more firmly established, phylogenetically derived biogeographic reconstructions for the order are best restricted to the analysis of ingroup relationships alone. Phylogenetic relationships among the diversity of living and fossil taxa of artiodactyls continue to be debated, but recent overviews agree that the fundamental dichotomy among Artiodactyla is that between Recent pigs, peccaries, hippopotamuses, and their fossil allies on the one hand, and all other artiodactyls on the other (Gentry and Hooker, 1988; Miyamoto et al., 1993). Allocation of the fossil taxa traditionally included in the basal, paraphyletic family Dichobunidae to the Selenodontia or Neoselenodontia has

been advocated by Gentry and Hooker (1988). This phylogenetic reconstruction is followed here, primarily because it is consistent with the advanced, neoselenodont-like postcranial anatomy known for *Diacodexis* (Rose, 1982, 1985). In order to simplify the analysis, only basal dichobunids are included to represent the diverse Neoselenodontia here.

Based on the phylogenetic reconstruction of basal neoselenodontians by Smith et al. (1996:fig. 1) and that for suiforms published by Gentry and Hooker (1988:fig. 9.8), biogeographic reconstruction of the continent on which artiodactyls originated is equivocal (Fig. 4A). Europe and Asia emerge as equally parsimonious optimizations for the basalmost node on the artiodactyl cladogram, as they do for the nodes at the base of the suiform and neoselenodontian radiations, respectively. Comparing the result from this phylogenetically derived biogeographic reconstruction with the fossil record of artiodactyls provides modest support for the view that Asia, rather than Europe, was the continent on which artiodactyls originated. Foremost among the fossil evidence supporting an Asian origin for artiodactyls is the unnamed taxon of basal suiform known from the Bumbanian Wutu fauna of Shandong Province, China (Tong and Wang, 1998). This critical taxon was not included in the phylogenetically derived biogeographic reconstruction undertaken here, because its phylogenetic position with respect to other suiforms has not yet been evaluated in detail. However, its great age and primitive anatomy open the possibility that the Wutu suiform comprises the sister group of all other suiforms. If so, addition of this taxon to the phylogenetically derived biogeographic analysis undertaken here would throw the weight of parsimony to the side of Asia as the unequivocal site of origin for both Suiformes and Artiodactyla (Fig. 4B). Indeed, an Asian origin for Suiformes is virtually inescapable in any case. Not only is the Bumbanian record from Wutu far older than any suiform known from other continents, but most family-level taxa of suiforms are widely acknowledged to have arisen in Asia. These include Anthracotheriidae (e.g., Suteethorn et al., 1988; Ducrocq, 1994a, 1995; Holroyd and Maas, 1994), Entelodontidae (e.g., Lucas and Emry, 1996), and Tayassuidae (e.g., Ducrocq, 1994b). Although supporting evidence remains weak, an Asian origin for Artiodactyla is the most likely hypothesis given current knowledge.

Cetacea

Following their acquisition of fully marine habits, cetaceans rapidly dispersed to achieve their current
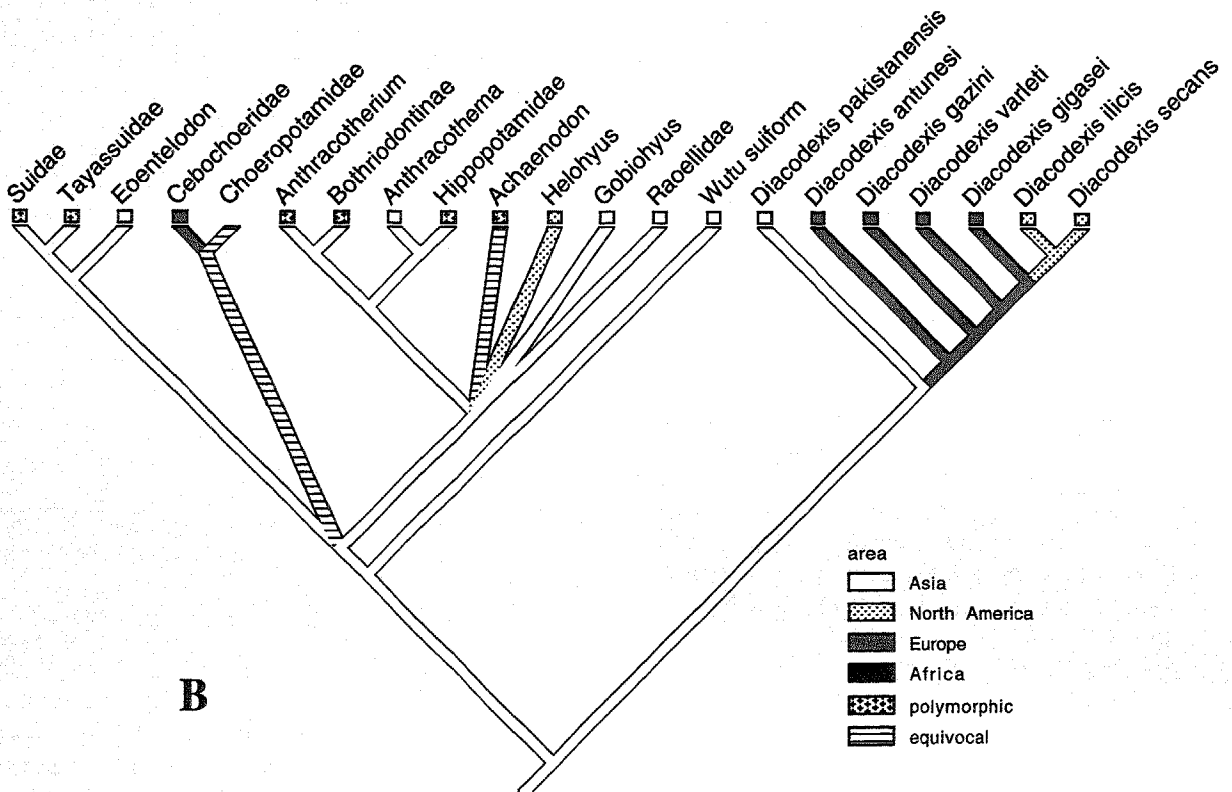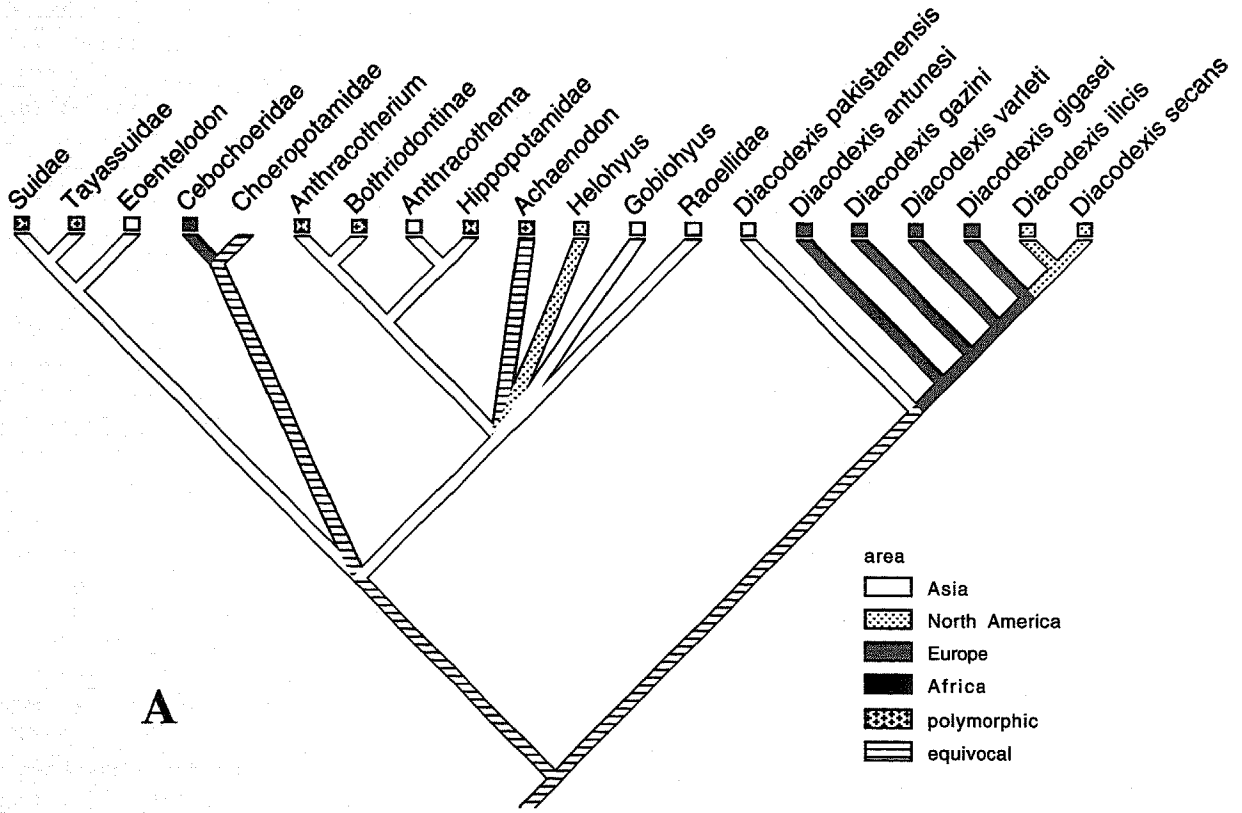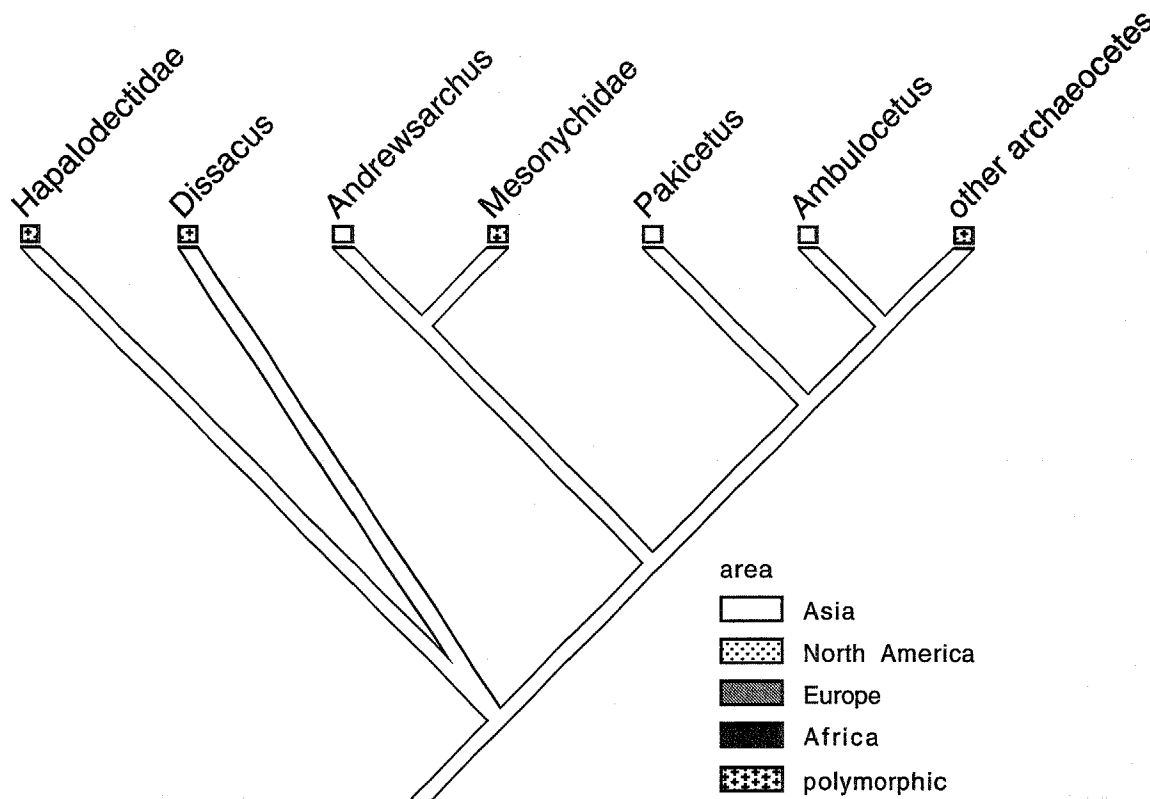
Fig. 5.—A phylogenetically derived biogeographic reconstruction for Cetacea. The tree topology depicted here is based on Thewissen (1994:fig. 4). Note that an Asian origin for Cetacea is unambiguously supported.

worldwide range. However, basal cetaceans show a much more restricted geographic distribution, currently limited to Pakistan and India (Gingerich et al., 1983; Thewissen, 1994; Thewissen et al., 1994, 1996). Accordingly, most modern workers have advocated a geographic origin for Cetacea on the eastern margin of the Tethys Sea, probably near the Indian subcontinent (e.g., Thewissen et al., 1994). Cetacean sister taxa are widely believed to lie within the fossil assemblage often referred to as "mesonychians" (Van Valen, 1966; Gingerich et al., 1983, 1994; Thewissen, 1994), which are well known from all three Holarctic continents.

Thewissen's (1994:fig. 4) phylogenetic reconstruction of basal cetaceans and their relatives provides unambiguous support for the conventional

view that cetaceans originated in Asia (Fig. 5). Because such phylogenetically basal taxa as *Pakicetus* and *Ambulocetus* are also the oldest cetaceans currently recognized in the fossil record, this phylogenetically derived biogeographic reconstruction of cetacean origins is consistent with their fossil record. As such, the hypothesis that cetaceans originated near the margin of Tethys in southern Asia can be considered quite robust.

PANTODONTA

Pantodonts are known primarily from Asia and North America, where they are represented in faunas as old as Shanghuan and late Torrejonian, respectively. A single species, *Alcidedorbignya inopinata*, is known from the early Paleocene of Bo-

←

Fig. 4.—Phylogenetically derived biogeographic reconstructions for Artiodactyla. A. Tree topology based on Smith et al. (1996:fig. 1) for basal neoselenodontians and Gentry and Hooker (1988:fig. 9.8) for suiforms. B. Same topology as A, but with unnamed suiform from Wutu Basin, Shandong Province, China (see Tong and Wang, 1998), inserted as the sister taxon of all other suiforms. Note that with the Wutu suiform excluded from the analysis (A), optimization of the center of origin for the order is ambiguous, with both Europe and Asia being equally parsimonious solutions. If the topology is altered by addition of the Wutu taxon as the most basal member of Suiformes (B), an Asian origin for Artiodactyla is unambiguously supported.
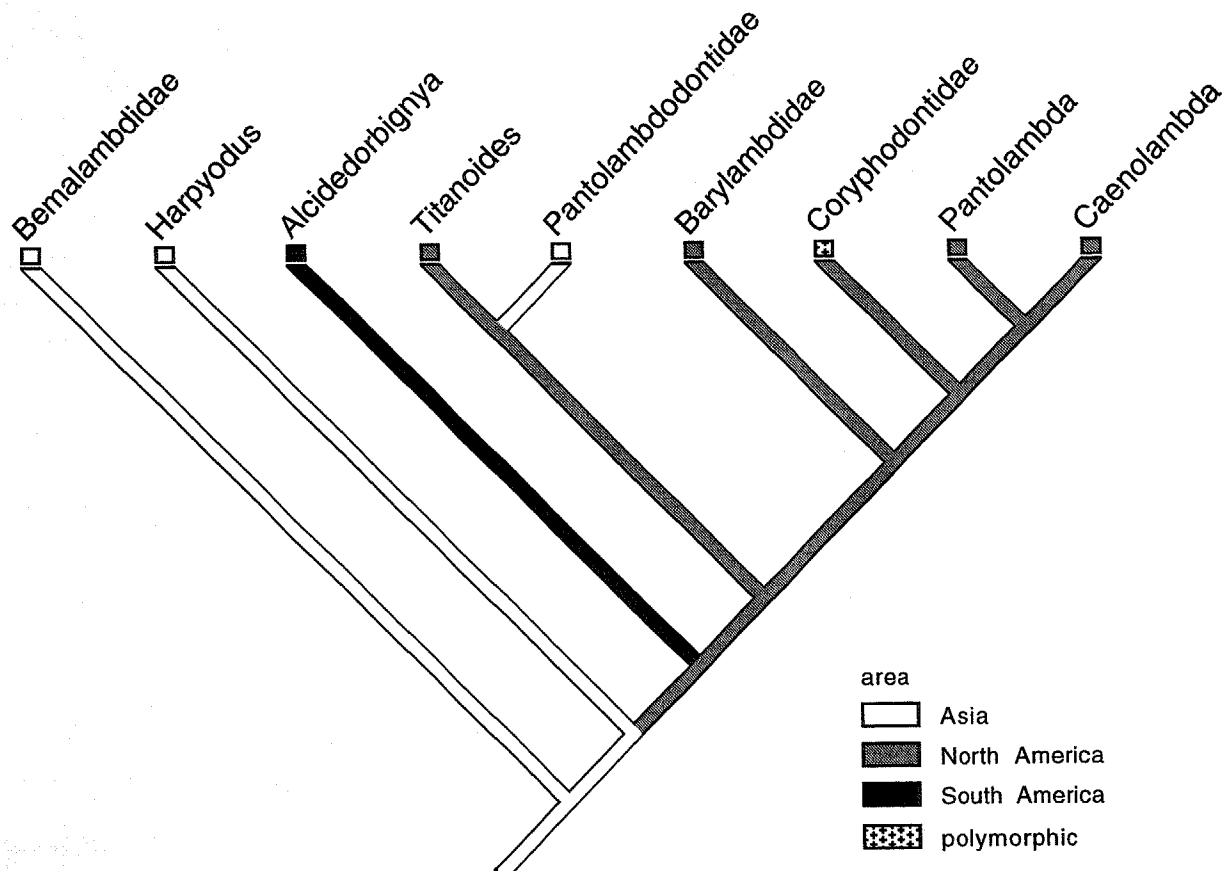
Fig. 6.—A phylogenetically derived biogeographic reconstruction for Pantodonta. Tree topology is based on de Muizon and Marshall (1992) and Lucas (1993). Note that an Asian origin for pantodonts is unambiguously supported. In this case, geographic character states were treated as "ordered," on the assumption that dispersal between Asia and South America must have involved North America as an intermediary.

livia (de Muizon and Marshall, 1992), and several species of *Coryphodon* are recorded from the Sparnacian of western Europe (e.g., Lucas, 1982, 1989). An Asian origin for pantodonts has been supported by several workers (e.g., Chow and Wang, 1979; Krause and Maas, 1990). Alternatively, de Muizon and Marshall (1987) noted that pantodonts may have originated in South America, based on the early record of *Alcidedorbignya* there. Indeed, the early dispersal history of pantodonts is difficult to explain because *Pantolambda*, the earliest pantodont currently recorded in North America (from zone To3), is significantly younger than either the Asian or South American FADs for the order. Presumably, part of the early history of North American pantodonts is yet to be documented in the fossil record, because North America must have served as a corridor for dispersal of early pantodonts between Asia and South America, regardless of where the order originated.

Phylogenetic reconstructions for pantodonts advocated by de Muizon and Marshall (1992) and Lucas (1993) suggest unequivocally that Asia was the continent on which pantodonts originated, because the two basalmost pantodont clades known to date, Bemalambdidae and *Harpyodus*, are restricted to that continent (Fig. 6). The fossil record does not contradict this phylogenetically derived biogeographic reconstruction because the early Shanghuan pantodont records known from the Nanxiong Basin in Guangdong Province, China, are probably roughly coeval with *Alcidedorbignya* in Bolivia (cf. Lucas and Williamson, 1995; Wang et al., 1998).

CORYPHODONTIDAE

The distinctive pantodont family Coryphodontidae is known from many Holarctic faunas (e.g., Lucas, 1984, 1989; Lucas and Tong, 1987; Uhen and Gingerich, 1995), but there is no consensus regarding the continent on which Coryphodontidae origi-
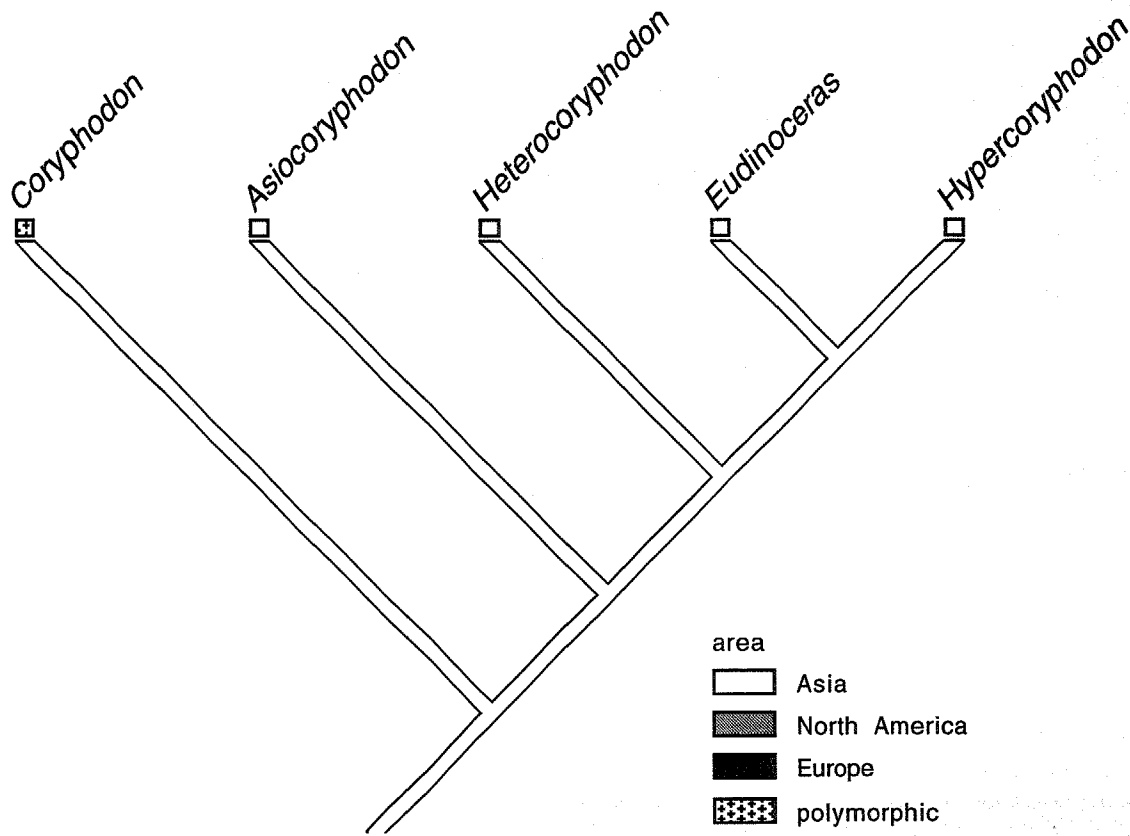
Fig. 7.—A phylogenetically derived biogeographic reconstruction for Coryphodontidae. Tree topology is based on Lucas and Tong (1987:fig. 7). Based on analysis of ingroup relationships among coryphodontids, an Asian origin for the family is unambiguously supported. However, this result conflicts with that shown in Figure 6. See text for further discussion.

nated. Such primitive North American Paleocene pantodonts as *Pantolambda* and *Caenolambda* have been cited as the closest known sister taxa to Coryphodontidae (e.g., Lucas, 1982, 1993), a finding which, if demonstrated to be true, would imply a North American origin for the family (cf. Fig. 6). However, as Krause and Maas (1990:88) recognized, ". . . *Pantolambda* is so primitive relative to *Coryphodon* that the two forms can be allied only indirectly . . . a strictly ancestor–descendant relationship between *Pantolambda* (or *Caenolambda*) and *Coryphodon* is not defensible on present evidence, and no structural intermediates from the fairly well-sampled late Tiffanian of the Western Interior have turned up. . . ." Uhen and Gingerich (1995:284) concurred, noting that "The appearance of *Coryphodon* in the Clarkforkian of North America with no identifiable North American ancestry, suggests that *Coryphodon* may have immigrated from some other continent at this time."

A phylogenetically derived biogeographic reconstruction based on ingroup relationships within Cor-

yphodontidae (Lucas and Tong, 1987:fig. 7) unambiguously points to Asia as the continent of origin for the family (Fig. 7). However, this result conflicts with that shown in Figure 6, in which a North American origin for coryphodontids is favored because of the nested phylogenetic position of coryphodontids as a whole among more primitive North American pantodonts. Because the phylogenetic position of coryphodontids with respect to other pantodonts continues to be debated, an Asian origin for the family (based on Fig. 7) is preferred here. Assessing whether the fossil record of coryphodontids supports or conflicts with an Asian origin for the family is problematic, because of difficulties in establishing intercontinental correlations that are independent of mammalian biostratigraphy during this interval (see below).

TILLODONTIA

Tillodonts are known from all three Holarctic continents. In North America and Europe, tillodonts first appear relatively late (early Clarkforkian and
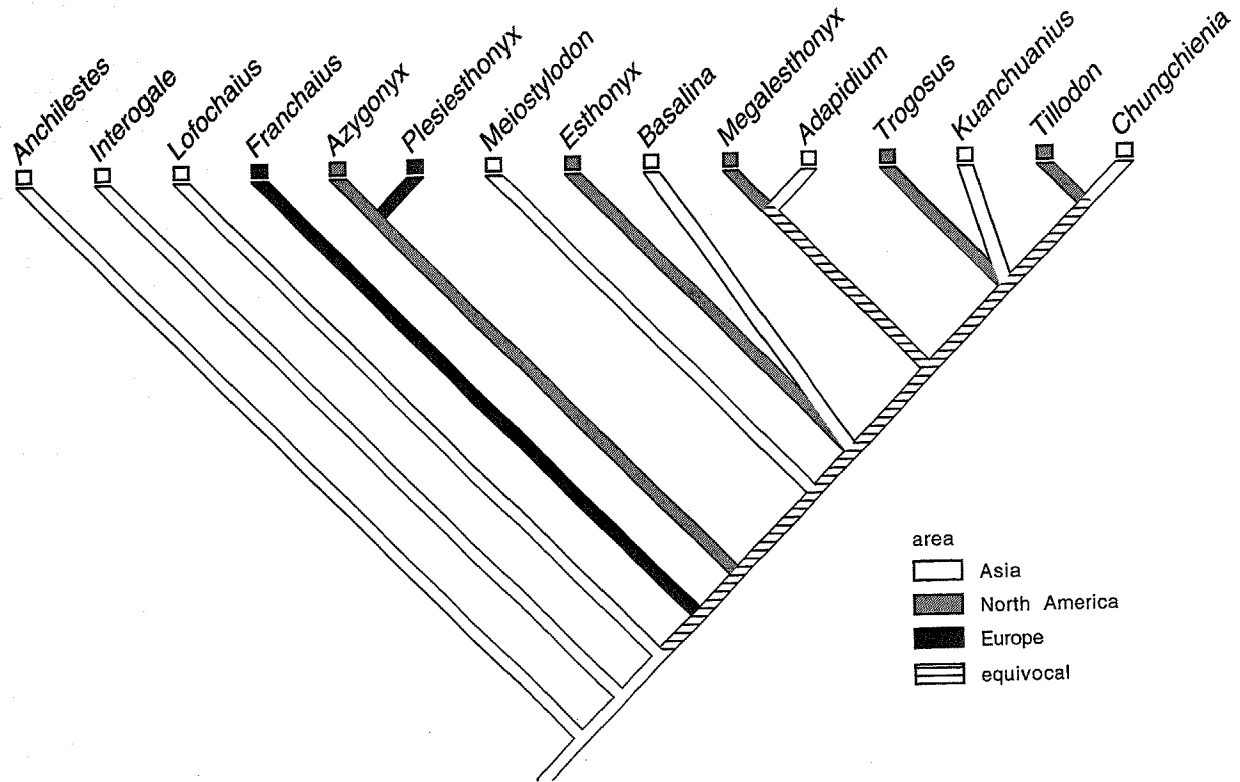
Fig. 8.—A phylogenetically derived biogeographic reconstruction for Tillodontia. Tree topology is based on Gaudry (1992) and Chow et al. (1996:fig. 3B). Note that an Asian origin for tillodonts is unambiguously supported.

Sparnacian, respectively; see Gingerich and Gunnell, 1979; Rose, 1981; Gaudry, 1992), whereas the order is represented in faunas as old as Shanghuan in Asia (e.g., Ting, 1998). Most recent workers acknowledge the likelihood of an Asian origin for tillodonts, given their early fossil record on that continent (e.g., Stucky and Krishtalka, 1983; Ting and Zheng, 1989; Krause and Maas, 1990; Gaudry, 1992; Lucas and Williamson, 1995).

Based on the phylogenetic reconstruction for tillodonts published by Gaudry (1992) and modified by Chow et al. (1996:fig. 3B), an Asian origin for the order is unambiguously favored (Fig. 8). As noted above, the fossil record is clearly in accord with this phylogenetically derived biogeographic reconstruction, such that an Asian origin for tillodonts is a robust biogeographic hypothesis indeed.

DINOCERATA

Undoubted uintatheres are restricted to Asia and North America, where they are recorded in rocks as old as Gashatan and late Tiffanian, respectively (Tong and Lucas, 1982; Schoch and Lucas, 1985; Thewissen and Gingerich, 1987). The South American Paleocene genus Carodnia is frequently cited as a close relative or even as a member of Dinocerata (Simpson, 1935; de Paula Couto, 1952; McKenna, 1980; Gingerich, 1985). Previous hypotheses regarding the continent of origin for Dinocerata have focused on Asia (Schoch and Lucas, 1985) and South America (Gingerich, 1985; Sloan, 1987).

A phylogenetically derived biogeographic reconstruction of the continent of origin for Dinocerata fails to yield an unambiguous result, because both Asia and North America are equally parsimonious optimizations for the node at the base of Dinocerata (Fig. 9). However, no recent worker has seriously considered the possibility that Dinocerata originated in North America, because the order appears suddenly in the North American fossil record during late Tiffanian zone Ti5 and potential sister taxa or close relatives of Dinocerata remain unknown from North America prior to that time. On the other hand, two aspects of the fossil record of early uintathere evolution support an Asian origin for this taxon. First, species of Asian Prodinoceras appear to retain certain characters that are more primitive than their counterparts among North American species of Probathyopsis. For example, Prodinoceras lacks the reduction in size of upper and lower first molars
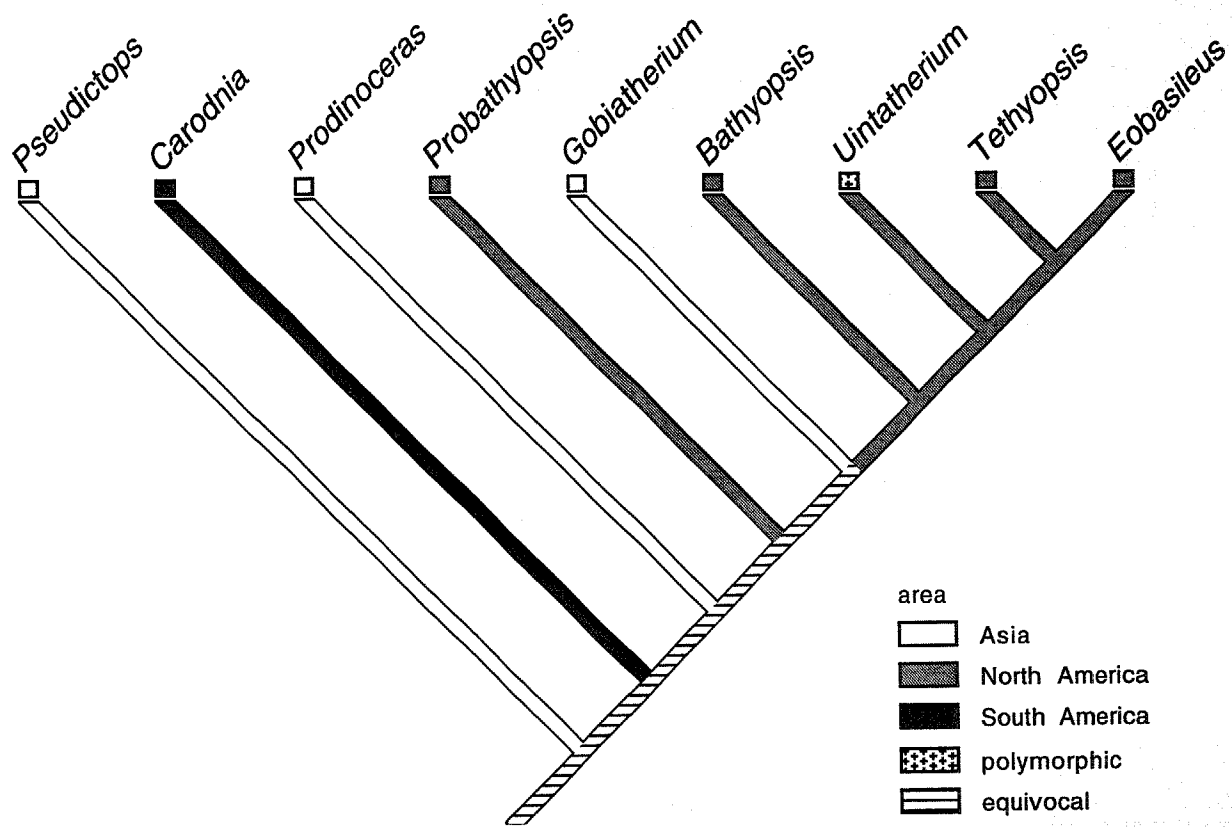
Fig. 9.—A phylogenetically derived biogeographic reconstruction for Dinocerata and their presumed allies. Tree topology is based on Schoch and Lucas (1985:fig. 3), with the addition of North American *Probathyopsis* as a genus distinct from Asian *Prodinoceras*, following Thewissen and Gingerich (1987). As in Figure 6, geographic character states were treated as "ordered," on the assumption that dispersal between Asia and South America must have involved North America as an intermediary. Note that optimization of the center of origin for the order is ambiguous, with both North America and Asia being equally parsimonious solutions.

seen in North American *Probathyopsis* (Thewissen and Gingerich, 1987:fig. 10B). Second, in contrast to the situation in North America, where potential sister taxa for Dinocerata remain unknown, the endemic Asian family Pseudictopidae has been cited as a possible sister taxon of Dinocerata on the basis of dental traits (e.g., Tong and Lucas, 1982; Schoch and Lucas, 1985; Lucas, 1993). If this hypothesis can be corroborated by other data, an Asian origin for Dinocerata would become plausible indeed.

ARCTOSTYLOPIDAE

Arctostylopids are known only from Asia and North America, where the earliest forms occur in faunas of Nongshanian and late Tiffanian age, respectively (Cifelli et al., 1989; Ting, 1998). Traditionally, arctostylopids have been allied with South American notoungulates (for review, see Gingerich, 1985), but thorough study of this issue led Cifelli et al. (1989) to doubt this relationship. In either case, Arctostylopidae appear to represent a valid

clade. Previously, both Asia (e.g., Matthew and Granger, 1925; Cifelli et al., 1989) and North America (by way of a South American notoungulate; see Gingerich, 1985; Sloan, 1987) have been cited as potential centers of origin for arctostylopids.

Based on the phylogenetic reconstruction for Arctostylopidae published by Cifelli et al. (1989:fig. 11), an Asian origin for this clade is strongly preferred (Fig. 10). This phylogenetically derived biogeographic reconstruction agrees with the fossil record of Arctostylopidae in Asia and North America, because the Nongshanian records of early arctostylopids in Asia likely antedate the late Tiffanian FAD for *Arctostylops* in North America (Wang et al., 1998; contra Gingerich, 1985:134–135).

RODENTIA

The most ubiquitous and diverse of all living orders of mammals, rodents today enjoy a virtually worldwide distribution (e.g., Nowak and Paradiso, 1983). While it would thus be difficult to recon-
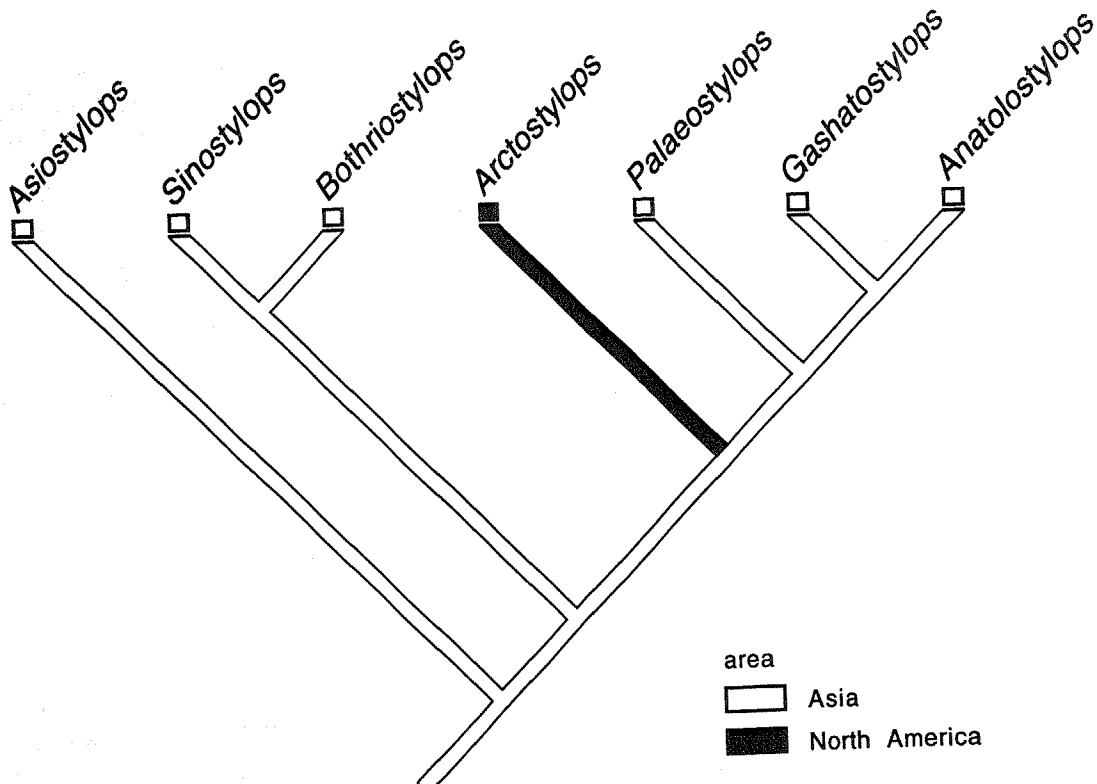
Fig. 10.—A phylogenetically derived biogeographic reconstruction for Arctostylopidae. Tree topology is based on Cifelli et al. (1989: fig. 11). Note that an Asian origin for arctostylopids is unambiguously supported, with subsequent dispersal to North America of *Arctostylops*.

struct the continent of origin for Rodentia on the basis of neontological evidence alone, consideration of fossil taxa limits the viable options considerably. As a result, no modern worker has seriously considered the possibility of a geographic origin for Rodentia outside of North America and Asia. Indeed, the hypothesis that rodents may have originated in the southern part of North America (Sloan, 1969; Wood, 1977) is now largely discredited. Rather, more recent discoveries of basal rodents and potential rodent sister taxa in Asia make the latter continent a much more plausible candidate for the ancestral rodent homeland (Li, 1977; Li and Ting, 1993; Meng et al., 1994; Tong and Dawson, 1995; Dawson and Beard, 1996).

Phylogenetic relationships among basal rodents and their close relatives as reconstructed by Dawson and Beard (1996) provide unambiguous support for an Asian origin for the order (Fig. 11). This phylogenetically derived biogeographic reconstruction is concordant with the fossil record of early rodents in Asia and North America, although the order Rodentia itself is defined in various ways vis à vis such phylogenetically basal taxa as *Heomys* and Alago-

myidae (Wyss and Meng, 1996). Regardless of such semantic issues, the demonstrably older occurrences of basal rodents (or rodent sister taxa, depending upon one's preferred definition of the order) in Asia corroborate the Asian origin for rodents suggested by phylogenetic data. In particular, the early rodent or rodent sister taxon *Heomys* is known from the Shanghuan of the Qianshan Basin, Anhui Province, China, an interval that is millions of years older than the North American FAD for the order at the beginning of the Clarkforkian (Ting, 1998; Wang et al., 1998). Similarly, the early alagomyid *Tribosphenomys* is known from the Gashatan Bayan Ulan beds of the Erlian Basin, Nei Mongol Autonomous Region, China (Meng et al., 1994, 1998). Although correlation of the Asian Gashatan with the North American sequence of land mammal ages is controversial (see below), Asian *Tribosphenomys* is probably older than the North American early Clarkforkian FAD for rodents (Dawson and Beard, 1996; also see Wang et al., 1998).

ALAGOMYIDAE

First described only recently by Dashzeveg (1990), the basal rodent family (or rodent sister tax-
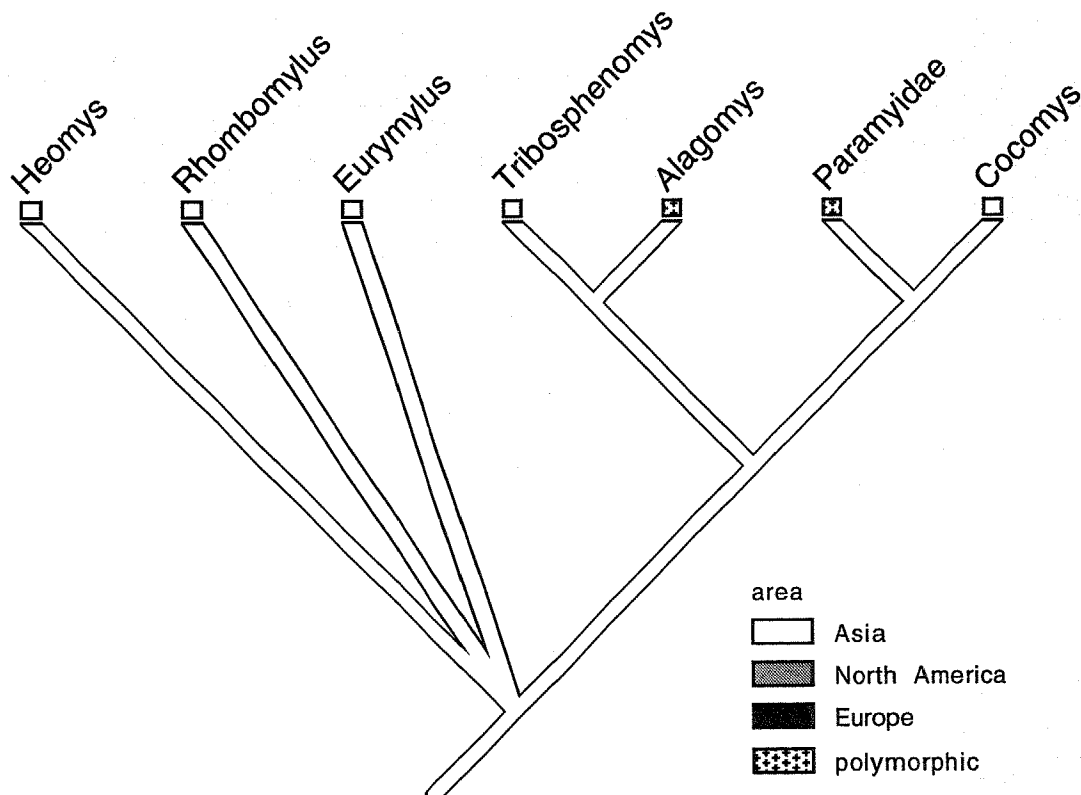
Fig. 11.—A phylogenetically derived biogeographic reconstruction for Rodentia and their presumed allies. Tree topology is based on Dawson and Beard (1996:fig. 1). Note that an Asian origin is unambiguously supported for both the order Rodentia and the family Alagomyidae (*Tribosphenomys* + *Alagomys*).

on; see above) Alagomyidae is now known from the Gashatan Bayan Ulan beds of Nei Mongol Autonomous Region, China (Meng et al., 1994), Bumbanian localities in the Nemegt Basin of southern Mongolia (Dashzeveg, 1990) and the Wutu Basin, Shandong Province, China (Tong and Dawson, 1995), and a single site in North America—the Clarkforkian Big Multi Quarry in the Washakie Basin of southern Wyoming (Dawson and Beard, 1996). Dawson and Beard (1996) attributed the sole North American record of *Alagomys* to immigration from Asia, thereby implying an Asian origin for the family. The possibility that alagomyids originated in North America has never been seriously entertained.

Phylogenetic reconstruction of alagomyids and their close relatives offers clearcut support for the hypothesis that alagomyids originated in Asia, with subsequent dispersal of *Alagomys* to North America (Fig. 11). The fossil record of alagomyids does not contradict this assessment, because the Gashatan record of *Tribosphenomys minutus* in Nei Mongol Autonomous Region, China, probably antedates the

Clarkforkian FAD for Alagomyidae in North America (see above). Interestingly, in Asia *Alagomys* is known only from Bumbanian faunas (Dashzeveg, 1990; Tong and Dawson, 1995), while the sole record of this genus in North America occurs in a Clarkforkian fauna. If alagomyids originated in Asia as is argued here, one would not expect *Alagomys* to occur earlier in North America than in Asia. Accordingly, traditional correlations of the basal Bumbanian in Asia with the basal Wasatchian in North America require reevaluation (see below).

LAGOMORPHA

Despite their nearly cosmopolitan distribution today, lagomorphs have long been considered to have originated in Asia by virtue of their precocious fossil record on that continent (e.g., McKenna, 1982; Li and Ting, 1993). Based on current knowledge of the major features of lagomorph phylogeny (M. R. Dawson, personal communication), a biogeographic reconstruction for Lagomorpha unequivocally supports the traditional hypothesis that lagomorphs originated in Asia (Fig. 12). Because such basal
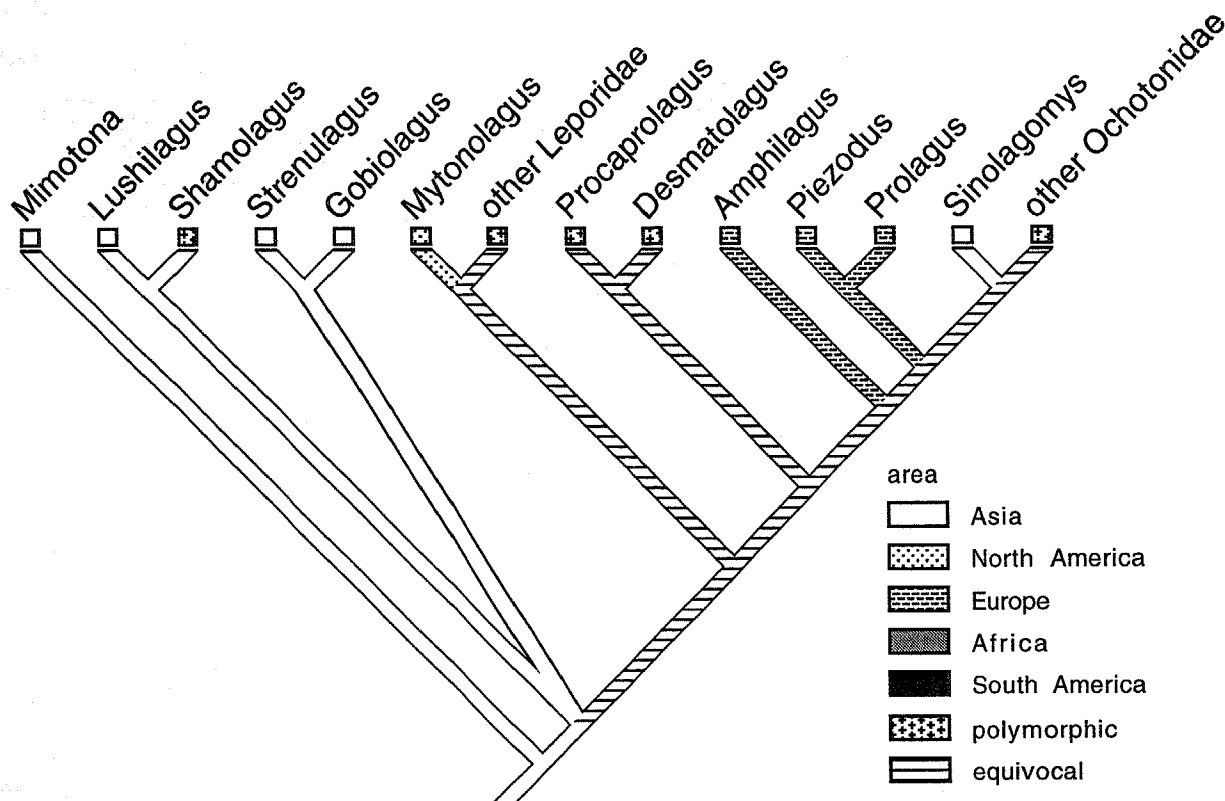
Fig. 12.—A phylogenetically derived biogeographic reconstruction for Lagomorpha. Tree topology is that preferred by M. R. Dawson (personal communication). Note that an Asian origin for lagomorphs is unambiguously supported.

Asian lagomorphs (or lagomorph sister taxa) as *Mimotona* from the Shanghuan and Nongshanian of the Qianshan Basin, Anhui Province, China, are considerably older than the earliest lagomorphs known from other continents, the fossil record of lagomorphs is in complete accord with the phylogenetically derived biogeographic reconstruction shown in Figure 12. Therefore, the hypothesis advocating an Asian origin for Lagomorpha is very strongly corroborated.

PRIMATES

On the three Holarctic continents, undoubted primates (i.e., excluding fossil "plesiadapiforms," see Beard, 1993a, 1993b) are documented as early as the Bumbanian in Asia, the Wasatchian in North America, and the Sparnacian in Europe. According to Dashzeveg (1982, 1988) and Krause and Maas (1990), these FADs on the northern continents may be synchronous (but see below). This pattern of Holarctic occurrences for Primates therefore resembles that known for Perissodactyla and Artiodactyla. The primate *Altiatlasius koulchii* is recorded at the Adrar Mgorn 1 locality in Morroco, which is

thought to be Thanetian in age, making *Altiatlasius* the world's oldest undoubted primate (Sigé et al., 1990). The FAD for Primates in South America is Deseadan (late Oligocene) in age (Kay et al., 1995).

Given the similar pattern of occurrence shown by Primates, Perissodactyla, and Artiodactyla on the Holarctic continents, it is unsurprising that biogeographic reconstructions for these taxa have varied along the same general lines. In particular, early hypotheses advocating an origin for Primates in the southern part of North America (Sloan, 1969; Gingerich, 1976; Schiebout, 1979) have not been corroborated by more recent examination of faunal change across the Clarkforkian–Wasatchian boundary on that continent (Gingerich, 1986, 1989, 1993; Krause and Maas, 1990). As a result, most workers have looked to other continents in searching for the geographical origin of Primates. Discovery of the Thanetian primate *Altiatlasius* in North Africa has strengthened the hypothesis that Primates may have originated on that continent (Gingerich, 1986, 1990; Sigé et al., 1990). Alternatively, Krause and Maas (1990) hypothesized an origin for Primates on the Indian Noah's Ark prior to its collision with Asia.
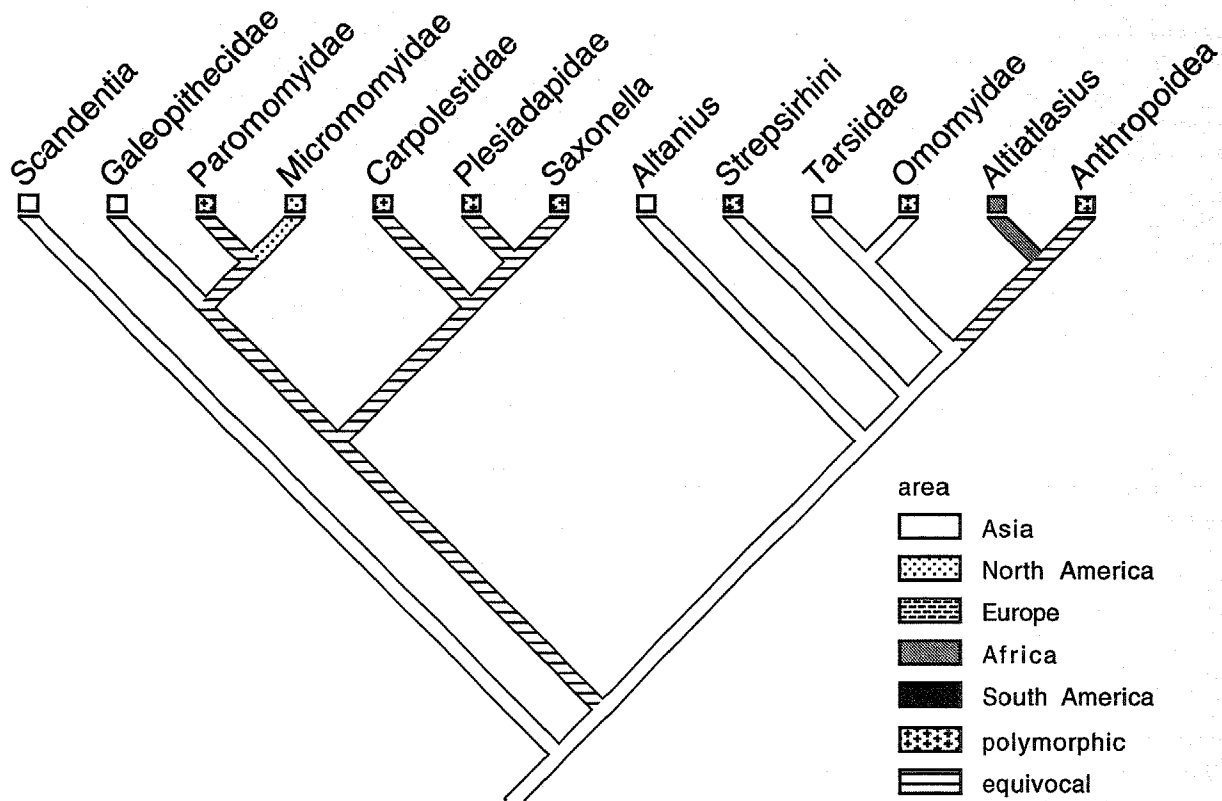
Fig. 13.—A phylogenetically derived biogeographic reconstruction for Primatomorpha + Scandentia. Tree topology is based on Beard (1993*b*) and Beard and Wang (1995) with respect to living and fossil Dermoptera, Gingerich et al. (1991) with respect to *Altanius*, and Beard and MacPhee (1994), Beard et al. (1996), and Beard (1998) for all other primates. Note that an Asian origin for Primates is unambiguously supported.

Finally, based on the poorly known Paleocene taxon *Decoredon anhuiensis* from the Qianshan Basin, Anhui Province, China, Szalay and Li (1986) proposed an Asian origin for Primates. However, the primate affinities of *Decoredon* have been questioned by several workers (Gingerich et al., 1991; Rose and Bown, 1991; Rose et al., 1994; Rose, 1995), so that the earliest record of undoubted primates in Asia remains Bumbanian.

Many details regarding higher-level relationships among primates and their close relatives continue to be vigorously debated. However, my earlier hypothesis advocating the monophyly of a Primates + Dermoptera clade called Primatomorpha (Beard, 1989, 1990, 1991, 1993*a*, 1993*b*) receives continued support here. Molecular phylogenetic studies suggest that Scandentia are closely related to Primatomorpha (e.g., Cronin and Sarich, 1980; Adkins and Honeycutt, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Stanhope et al., 1993), in agreement with the long-standing hypothesis of a close relationship between tree shrews and primates

(e.g., Luckett, 1980; Novacek et al., 1988). Accordingly, Scandentia are accepted as the sister taxon of Primatomorpha here. Relationships among living and fossil dermopterans are based on the work of Beard (1993*b*) and Beard and Wang (1995). Relationships among undoubted primates are reconstructed following the work of Gingerich et al. (1991) for *Altanius* and Beard and MacPhee (1994), Beard et al. (1996), and Beard (1998) for all other taxa.

Based on the phylogenetic relationships depicted in Figure 13, an Asian origin for the order Primates is unequivocally supported. However, this phylogenetically derived biogeographic reconstruction may be in conflict with the primate fossil record as it is currently understood. The Thanetian taxon *Altiatlasius* from Morocco is almost certainly older than the Bumbanian FAD for undoubted primates (in the form of *Altanius orlovi*) in Asia. However, the enigmatic Nongshanian taxon *Petrolemur brevirostre* from the Nanxiong Basin, Guangdong Province, China, was originally described as a pri-

mate by Tong (1979). Although its primate affinities have proven to be controversial (e.g., Szalay and Li, 1986; Rose, 1995), the antiquity of *Petrolemur* is probably similar to that of Moroccan *Altiatlasius*. If *Petrolemur* ultimately proves to be a primate, the Asian origin for Primates supported by the phylogenetic relationships depicted in Figure 13 would be consistent with the fossil record for the order. Otherwise, either the phylogenetically derived biogeographic reconstruction depicted in Figure 13 is flawed or the fossil record of early primates in Asia remains incompletely sampled.

HYAENODONTIDAE

Hyaenodontid creodonts are common carnivorous mammals in Paleogene faunas of North America, Europe, Asia, and Africa. Along with perissodactyls, artiodactyls, and primates, hyaenodontids first occur in North America at the beginning of the Wasatchian. Their FAD in Europe occurs at the beginning of the Sparnacian, which may be synchronous with the North American FAD for this same suite of taxa (Dashzeveg, 1982, 1988; Gingerich, 1989; Krause and Maas, 1990). Important records of early hyaenodontids in Asia are now known from the Gashatan Bayan Ulan fauna of Nei Mongol Autonomous Region, China (Meng et al., 1998), and the Gashatan Naran Member of the Naran Bulak Formation in the Nemegt Basin, southern Mongolia (Dashzeveg, 1988). The earliest hyaenodontid known from Africa is the late early Eocene *Koholia atlasense* from El Kohol, Algeria (Crochet, 1988). Earlier African records of indeterminate hyaenodontids and/or creodonts are based on specimens that are too fragmentary for confident taxonomic allocation (Gheerbrant, 1995).

Previous hypotheses on the area of origin for hyaenodontids have been closely tied to paleobiogeographic reconstructions for the mammal taxa that appear with them at the beginning of the Wasatchian and Sparnacian in North America and Europe, respectively. Because of their sudden appear-

ance in Europe and North America, most workers have argued for an origin of hyaenodontids outside the confines of either of these continents. Two regions in particular, Africa and the Indian subcontinent, have been cited as the most likely areas of origin for Hyaenodontidae. For example, Gingerich (1976, 1989) and Gingerich and Deutsch (1989) argued for an African origin for Hyaenodontidae on the basis of their abundance and diversity in late Paleogene faunas of North Africa. Following the same lines of evidence they marshalled for Perissodactyla, Artiodactyla, and Primates, an origin for hyaenodontids on the Indian subcontinent prior to its collision with Asia was favored by Krause and Maas (1990).

Knowledge of hyaenodontid phylogeny remains sketchy because many taxa are represented by only fragmentary fossils, outgroup relationships are poorly resolved, and a synthetic treatment of the entire clade has yet to be achieved (Polly, 1996). Based on the recent phylogenetic reconstruction of selected hyaenodontids by Polly (1996), identification of the continent of origin for Hyaenodontidae is equivocal (Fig. 14). Both North America and Europe are equally parsimonious optimizations of the basalmost node on the cladogram in Figure 14. However, as noted above, these continents are precisely those that many paleontologists agree are least likely to include the center of origin of hyaenodontids. In either case, this phylogenetically derived biogeographic reconstruction conflicts with the fossil record of early Hyaenodontidae because the world's earliest members of this clade are now known from the Gashatan of central Asia (Meng et al., 1998). Accordingly, either the phylogeny depicted in Figure 14 is incorrect or the early fossil record of hyaenodontid evolution is poorly documented at present. The latter possibility seems likely indeed in the case of Asia, where Bumbanian hyaenodontids have yet to be reported, and Africa, where only the enigmatic taxon *Koholia atlasense* documents the presence of the group prior to the late Paleogene (Crochet, 1988).

EAST OF EDEN: ITERATIVE TRANS-BERINGIAN DISPERSAL AND THE NORTH AMERICAN FOSSIL RECORD

There is a long tradition in paleontology of viewing the North American continent as a vital epicenter of mammalian evolution and diversification. That is, for many years the ancestry of numerous mammalian orders and other higher taxa was sought among older North American mammals (e.g.,

Wood, 1957; Van Valen, 1963, 1971, 1978, 1988; Radinsky, 1966; Sloan, 1969; Gingerich, 1976). This notion pervades a great deal of the literature on early Cenozoic mammal evolution, particularly that before about 1990, although it is frequently difficult to cite specific cases to illustrate the point.
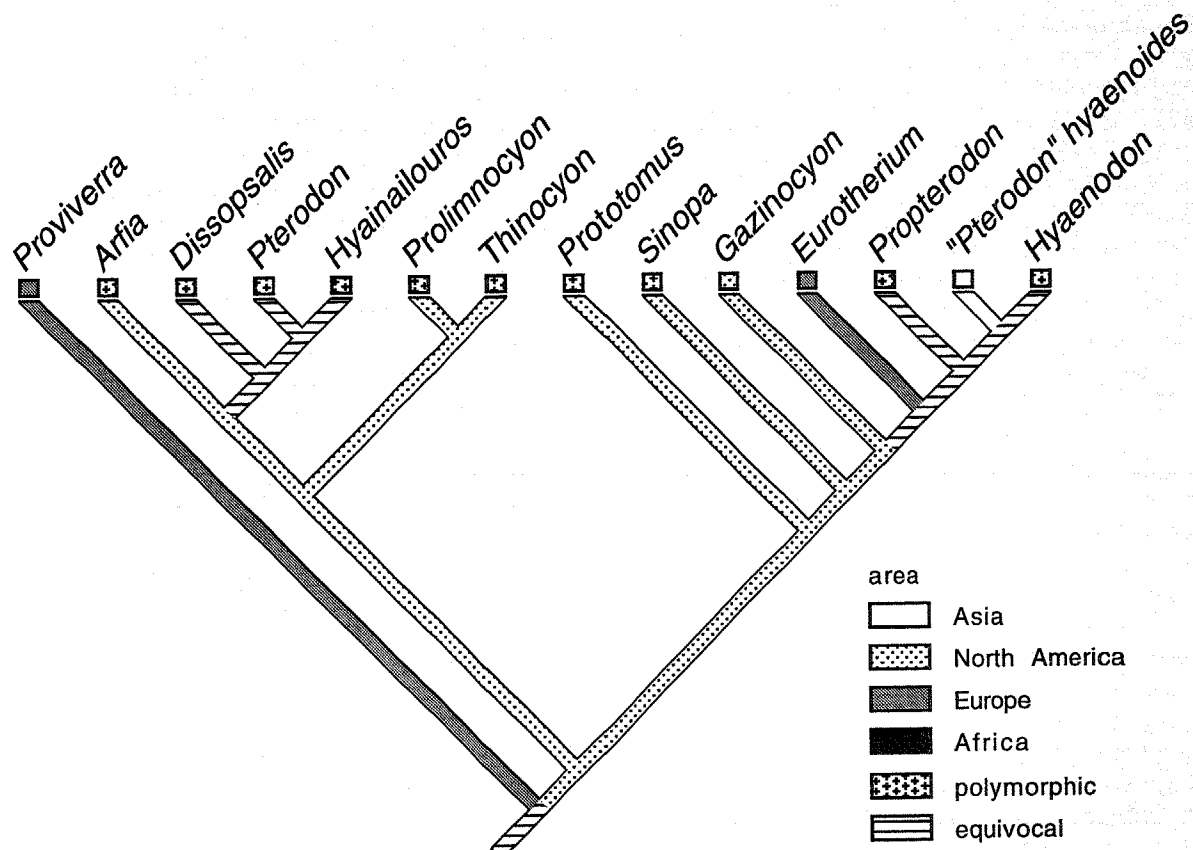
Fig. 14.—A phylogenetically derived biogeographic reconstruction for Hyaenodontidae. Tree topology is based on Polly (1996:fig. 10). Note that optimization of the center of origin for the clade is ambiguous, with both North America and Europe being equally parsimonious solutions. See text for further discussion.

However, Van Valen's (1988:47) statement that "... most mammalian evolution in the Paleocene of North America seems to have been autochthonous" is a revealing example of this general attitude. As knowledge of the phylogeny and biostratigraphy of early Tertiary mammals in North America has improved, the significance of intercontinental dispersal in shaping the North American mammal fauna has come to be increasingly appreciated (e.g., Rose, 1981; Archibald et al., 1987; Krishtalka et al., 1987; Gingerich, 1989; Krause and Maas, 1990; Stucky, 1992; Maas and Krause, 1994; Maas et al., 1995; Woodburne and Swisher, 1995). Nonetheless, ideas regarding the geographic source areas of these mammalian immigrants to North America have been diverse (Krause and Maas, 1990; Woodburne and Swisher, 1995; also see above) and frequently unconstrained by phylogenetic, geophysical, or biostratigraphic data.

In light of the data and interpretations presented above, a new and more cohesive paleobiogeographic model can be presented to account for the dra-

matic changes in the North American mammal fauna that are seen throughout much of the early Cenozoic. Under this "East of Eden" model, the vast majority of taxa that appear suddenly in the North American mammal record, with no clear evidence of earlier ancestry on that continent, are viewed as the result of iterative trans-Beringian dispersal from Asia. Highly distinctive taxa that appear suddenly in the fossil record are, by definition, excellent index taxa for purposes of biostratigraphy. As such, the East of Eden model has important implications not only for reconstructing paleobiogeography, but also for biostratigraphic correlation (see next section). Here, I will focus on the East of Eden model as a means of explaining modernization of the North American mammal fauna from the late Tiffanian through the Uintan. Rather than viewing North America as an epicenter of mammalian evolution and anatomical innovation, the East of Eden model treats North America as a biogeographical cul-de-sac that received repeated innoculations of

more "progressive," "modern," or "advanced" taxa from Asia.

Major immigrants to North America during the late Tiffanian include Arctostylopidae and Dinocerata (Archibald et al., 1987; Thewissen and Gingerich, 1987; Cifelli et al., 1989). Based on both phylogenetic and biostratigraphic evidence, the FAD for Arctostylopidae in North America almost certainly resulted from dispersal from Asia (Cifelli et al., 1989; also see above). As noted earlier, phylogenetic and biostratigraphic data currently provide only weak support for an Asian origin for Dinocerata. However, the simultaneous appearance of Dinocerata with Arctostylopidae in North America strengthens the case that uintatheres immigrated from Asia at this time as well.

The onset of the Clarkforkian NALMA (North American Land Mammal Age) is marked by the apparently simultaneous FADs of Rodentia, Tillodontia, and Coryphodontidae (Rose, 1980, 1981; Archibald et al., 1987). Reconstructed phylogenetic relationships and the fossil record agree that an Asian origin for Rodentia and Tillodontia is extremely likely. Paleobiogeographic reconstructions are more ambiguous in the case of Coryphodontidae, but the fact that coryphodontids first appeared in North America in association with two other taxa that are believed to have dispersed from Asia increases the likelihood that coryphodontids followed this route as well.

The beginning of the Wasatchian NALMA is characterized by the simultaneous appearance of Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae—certainly among the more impressive (and vigorously debated) immigration events in the Cenozoic history of North America (Rose, 1981; Gingerich, 1989; Krause and Maas, 1990). Phylogenetically derived biogeographic reconstructions unambiguously support an Asian origin for Perissodactyla and Primates, and an Asian origin for Artiodactyla seems likely as well, depending in part on the phylogenetic position of the Wutu suiform (see above). The fossil record, in the form of the Nongshanian perissodactyl-like taxon *Radinskya yupingae* (McKenna et al., 1989) and the Gashatan hyaenodontid species *Prolimnocyon chowi* (Meng et al., 1998), supports an Asian origin for Perissodactyla and Hyaenodontidae. Similar data are ambiguous in the case of Artiodactyla and Primates because of inadequate controls on intercontinental correlation at this time (see below). Thus, the North American Wasatchian FADs for Perissodactyla, Primates, Artiodactyla, and Hyaenodontidae appear to

conform with the East of Eden model in resulting from trans-Beringian dispersal from Asia. The case for an Asian origin for these four mammalian higher taxa is strongest for Perissodactyla (supported by both phylogenetic and biostratigraphic data), less strong for Primates (supported by phylogenetic data; biostratigraphic data are ambiguous at best) and Hyaenodontidae (supported by biostratigraphic data; phylogenetic data do not currently support an Asian origin for this clade), and weakest in the case of Artiodactyla. However, many workers (e.g., Gingerich, 1989:90) have assumed that all four of these taxa must have originated in the same geographic region, following the same route of dispersal. Considering all four taxa at once, the case for an Asian origin is far stronger than that which can be made for any alternative biogeographic reconstruction.

If dispersal from Asia to North America does indeed account for the distinctive reorganization of the North American fauna at the Clarkforkian/Wasatchian boundary, it seems likely on paleogeographic grounds that the same wave of immigrant mammals proceeded at high latitudes across North America to colonize western Europe. A similar paleobiogeographic hypothesis was advanced previously by Gaudry (1992) with respect to tillodonts, which first appear in Europe in the Sparnacian (after the Thanetian hiatus). However, this scenario for the origin of Europe's Sparnacian immigrant mammals runs counter to the biogeographic reconstructions of workers such as Hooker (1980), Godinot (1981, 1982), and Woodburne and Swisher (1995), who advocate dispersal from Europe to North America at this time. For purposes of reconstructing subsequent episodes of intercontinental faunal exchange, it is important to reiterate that rifting in the North Atlantic soon after the basal Wasatchian would have precluded later dispersal directly between North America and Europe (e.g., McKenna, 1983*b*; Stucky, 1992; Woodburne and Swisher, 1995; Ritchie and Hitchen, 1996). This tectonic isolation of North America from Europe virtually requires that all subsequent Paleogene (and most Neogene) immigrant mammals into North America arrived there via a trans-Beringian route, thus ensuring the primacy of the East of Eden model well into the late Cenozoic.

Although the phylogenetic and biostratigraphic data discussed earlier did not treat lower-level perissodactyl taxa, these forms have long played a prominent role in the biostratigraphic subdivision of the Wasatchian (see Gingerich [1991:205–206] for a recent review of this subject), so that some brief

remarks are in order here. Genera of special interest in this context are: 1) the isectolophid *Homogalax*, the FAD of which defines the onset of the Gray-bullian subage of the Wasatchian (= Wa3) in the usage of Gingerich (1991:table 3); 2) the basal ceratomorph *Heptodon*, the FAD of which defines the beginning of the Lysitean subage of the Wasatchian (= Wa6); and 3) the early brontothere *Lambdotherium*, the FAD of which defines the beginning of the Lostcabinian subage of the Wasatchian (= Wa7; see Krishtalka et al., 1987). Traditionally, these taxa have been viewed as evolving from earlier perissodactyl ancestors in situ in North America. Radinsky (1963:73), for example, thought that *Homogalax* and contemporary *Hyracotherium* are similar enough ". . . that immediate common ancestry seems quite probable." Likewise, *Homogalax* was interpreted by Radinsky (1963) as a stem genus from which the early ceratomorph *Heptodon* was probably derived.

Although this traditional view of autochthonous evolution of Wasatchian perissodactyls in North America cannot be completely refuted at present, the East of Eden model is more consistent with the known data. Trans-Beringian dispersal of *Homogalax* is required in any case, because *Homogalax wutuensis* occurs in the important Bumbanian Wutu fauna of Shandong Province, China (Chow and Li, 1965; Tong and Wang, 1998). Outstanding problems in intercontinental correlation preclude the independent determination of whether or not *Homogalax wutuensis* antedates the North American FAD for the genus (see below). However, Rose's (1996) finding that *Homogalax* retains primitive skeletal characters that have been transformed in *Hyracotherium* seriously weakens Radinsky's (1963) hypothesis of a close common origin between these two genera in North America. Likewise, the phyletic origin of *Heptodon* directly from *Homogalax* is extremely doubtful. More than 35 years of intensive collecting in early Eocene basins in western North America has failed to fill in the morphologic gap acknowledged by Radinsky (1963:75) to separate these genera. Furthermore, in terms of its postcranial skeleton, *Heptodon* seems to resemble *Hyracotherium* more closely than it does *Homogalax* (Rose, 1996). Such primitive Asian ceratomorphs as *Orientolophus hengdongensis* from the Bumbanian Hengdong fauna of Hunan Province, China (Ting, 1993), may represent more promising outgroups for *Heptodon* and its allies than does *Homogalax*. Finally, although it was originally described as a basal chalicothere by Wang (1995), I regard the Bumban-

ian perissodactyl *Danjiangia pingi* from the Yu-huangding Formation, Liguanqiao Basin, Hubei Province, China, as a primitive sister taxon of *Lambdotherium*. The East of Eden model is therefore fully consistent with the stratigraphic pattern of appearance of exotic perissodactyl taxa in North America during the Wasatchian. Indeed, the fact that these perissodactyl genera continue to prove useful in North American Wasatchian biostratigraphy suggests that they immigrated into that continent rather than having evolved in situ there.

Immigrants to North America at the beginning of the Bridgerian include the brontotheres *Palaeosyops* and *Eotitanops* (these genera are sometimes synonymized, but see Mader [1989]), the basal rhinocerotoid *Hyrachyus*, the tillodont *Trogosus*, and suiform artiodactyls in the form of *Helohyus* (Stucky, 1984). All of these taxa are interpreted here as conforming to the East of Eden model. The case for an Asian origin for suiform artiodactyls was discussed above, so that the FAD for this taxon in North America can be easily interpreted as the result of trans-Beringian dispersal. *Trogosus*, like *Megalesthonyx* from the Lostcabinian, possesses a sister taxon in Asia, suggesting multiple, temporally staggered trans-Beringian dispersals of tillodonts near the Wasatchian–Bridgerian boundary (Stucky and Krishtalka, 1983; Chow et al., 1996). The ancestry of the Bridgerian brontotheres *Paleosyops* and *Eotitanops* must be sought outside of North America, where only the autapomorphous *Lambdotherium* is known from earlier rocks. Asian *Danjiangia* is a plausible stem brontothere, suggesting that the broad North American radiation of this family also follows the East of Eden pattern. *Hyrachyus*, like Wasatchian *Homogalax*, is known from both shores of the Pacific (Russell and Zhai, 1987; Prothero et al., 1989), thus indicating trans-Beringian dispersal for this genus in any case.

The onset of the Uintan was defined by Flynn (1986) on the basis of the FAD of Amynodontidae (*Amynodon*). Amynodontids clearly originated in Asia, where both their earliest records (Averianov and Potapova, 1996) and basalmost taxa (Wall, 1989) are known. Certain other mammalian taxa that first appear in North America in the Uintan also can be attributed to trans-Beringian dispersal, and thereby conform to the East of Eden pattern. For example, the earliest North American record of the omomyid primate genus *Macrotarsius* occurs in the Wagonhound Member of the Uinta Formation (Krishtalka, 1978), which is early, but not earliest, Uintan in age (Flynn, 1986). This genus also occurs

in Fissure D at Shanghuang in southern Jiangsu Province, China (Beard et al., 1994), which is thought to be Irdinmanhan in age (Qi and Beard, 1996). The sudden appearance of *Macrotarsius* in North America, coupled with its possibly earlier occurrence in Asia, suggests that *Macrotarsius* may have dispersed into North America from Asia in typical East of Eden fashion.

A number of other mammals first appear in North America more or less synchronously with *Macrotarsius* and likewise appear to conform to the East of Eden pattern. Among these are the oldest undoubted chalicotheres from North America, *Eomoropus* and *Grangeria*, both of which also occur in China (Lucas and Schoch, 1989). Tong and Wang (1998) report fossils pertaining to a Bumbanian chalicothere from the Wutu Basin, Shandong Province, China, a record which, if substantiated, antedates the North American FAD for chalicotheres by millions of years. Otherwise, the oldest and phylogenetically most basal chalicothere currently known is *Litolophus gobiensis* from the Irdinmanhan of Nei Mongol Autonomous Region, China (Radinsky, 1964; Coombs, 1989). Both the alleged chalicothere from Wutu and *Litolophus* suggest an Asian origin for chalicotheres and conformity to the East of Eden pattern for North American *Eomoropus* and *Grangeria*.

Later in the Uintan (Ui2) occurs the North American FAD for the order Lagomorpha. Both phylogenetic and biostratigraphic data agree that lagomorphs originated in Asia (see above; Fig. 12), so that the late Uintan FAD for this order in North America also fits the East of Eden model. A diversity of other mammalian taxa appears for the first time in North America near the FAD for Lagomorpha (Krishtalka et al., 1987; Stucky, 1992; Woodburne and Swisher, 1995), but phylogenetic and biostratigraphic data remain so poorly resolved for these forms that it is premature to judge whether they too conform to the East of Eden biogeographic model.

Although the scope of the preceding discussion has been limited to mammals from the late Tiffanian through the Uintan, there is abundant evidence that the East of Eden model holds for both earlier and later intervals of time and for organisms other than mammals. The North American record of late Cretaceous dinosaurs illustrates the primacy of the East of Eden model during the latest Mesozoic, when ankylosaurids, ceratopsians, hadrosaurine and lambeosaurine hadrosaurs, and tyrannosaurid and troodontid theropods make their first appear-

ances on that continent (Russell, 1993; Sereno, 1997). With regard to these late Cretaceous dinosaurian taxa, Russell (1993:2007) notes that, "By Campanian–Maastrichtian time . . . the western subcontinent [of North America] had received so many groups of Asian dinosaurs . . . and other terrestrial vertebrates that, biogeographically speaking, it effectively merged with Central Asia. During the whole of the Cretaceous, no dinosaurian family is known to have originated in North America." Similarly, certain FADs for North American Paleocene mammals prior to the late Tiffanian may also conform to the East of Eden model. The North American FAD for Pantodonta (in the form of *Pantolambda*) in late Torrejonian zone To3 was identified as the result of dispersal from Asia in the preceding section. Lucas and Williamson (1995) argue for a much more significant episode (or episodes) of East of Eden dispersal near the Puercan–Torrejonian boundary, when they suggest Carnivora (in the form of *Protictis*), Mesonychia (in the form of *Dissacus*), and *Deltatherium* invaded North America from Asia. Of these taxa, perhaps the best case for compliance to the East of Eden model can be made for Mesonychia, because both early and phylogenetically basal mesonychians are known from Asia (Chow et al., 1973, 1977; Lucas and Williamson, 1995). In contrast, the case for an Asian origin for Carnivora was weakened by Fox and Youzwyshyn (1994), who reported fragmentary fossils of the alleged carnivoran *Ravenictis* from the Puercan Ravenscrag Formation, Saskatchewan, Canada. Phylogenetic relationships between North American *Deltatherium* and Asian Paleocene mammals are too poorly documented to permit confident assessment of whether or not conformity to the East of Eden model holds for this taxon. Like *Deltatherium*, a number of mammal taxa appear suddenly in the Paleocene fossil record of North America without having closely related or ancestral forms known from earlier horizons on that continent. These taxa (e.g., Palaeanodonta, Paromomyidae, Carpolestidae, Erinaceidae) too may eventually prove to uphold the dominance of the East of Eden paleobiogeographic model, but evidence remains scant.

Numerous examples of East of Eden dispersal events among mammals subsequent to the Uintan have been reviewed by Woodburne and Swisher (1995). These data demonstrate that Asia has served as a persistent source area for exotic mammalian immigrants to North America throughout the Cenozoic. No other continent has contributed

as many taxa over such an extended interval of time as Asia has to the North American mammal fauna. Future paleobiogeographic studies of plants and nonmammalian vertebrates are necessary to determine the primacy of the East of Eden model for those taxa.

IMPLICATIONS FOR THE BIOSTRATIGRAPHIC CORRELATION OF EARLY TERTIARY MAMMAL AGES OF ASIA

If Asia has indeed served as a biogeographic source area for many of the immigrant mammal taxa that are used for biostratigraphic purposes in North America, the possibility of inferring spuriously young correlations for Asian faunas containing such forms logically follows. For example, because pantodonts are unknown in North America prior to the late Torrejonian (To3), one could argue, as Ting (1998) has, that Shanghuan pantodont records in Asia are unlikely to antedate North American zone To3. However, such a correlation ignores the point that pantodonts, like all clades, must have originated somewhere on the face of the planet (rather than everywhere at once). If pantodonts originated anywhere other than North America, the possibility exists of a significant interval of endemism for pantodonts near the clade's center of origin prior to their dispersal to North America. In fact, given the strong evidence reviewed above that pantodonts originated in Asia, one should actually expect there to be Asian pantodont records that are demonstrably older than To3. Of course, in order to demonstrate an earlier age for at least some Asian pantodonts, an assessment of age that is independent of mammalian biostratigraphy is necessary. Unfortunately, most of the known early Tertiary mammal faunas of Asia are uncalibrated radiometrically (but see Wang et al., 1998), and correlation of Asian mammal faunas to the Geomagnetic Polarity Time Scale remains in its infancy (e.g., Kappelman and Gose, 1995; Xue et al., 1996). In this section the ramifications of the East of Eden model for biostratigraphic correlation of the Gashatan and Bumbanian Asian Land Mammal Ages (ALMAs) are explored. For current views on correlation of the Shanghuan and Nongshanian ALMAs, see Ting (1998) and Wang et al. (1998).

GASHATAN ALMA

The Gashatan ALMA is defined by Ting (1998) on the basis of the first appearance of Rodentia (in the form of the alagomyid Tribosphenomys). This definition is less than felicitous because Tribosphenomys is currently known from only one of the faunas (the Bayan Ulan fauna of Nei Mongol Au-

tonomous Region, China) that are widely acknowledged to represent the Gashatan ALMA (see Meng et al., 1998; Ting, 1998). Defining the Gashatan on the basis of the first appearance of the more commonly encountered Dinocerata (in the form of Prodinoceras) may provide more stability and ease of recognition for this ALMA in the future. In either case, the primary faunas referred to the Gashatan ALMA remain the same: the Bayan Ulan and Nomogen faunas from the Erlian Basin, Nei Mongol Autonomous Region, China; the faunas from the Zhigden and Naran members of the Naran Bulak Formation in the Nemegt Basin, southern Mongolia; and the Gashato fauna from the Ulan Nur Basin, also in southern Mongolia. Additional Chinese Paleocene faunas that may be referred to the Gashatan ALMA include the Taizicun fauna from Xinjiang, the Pinghu fauna from Jiangxi, and the Shuangtasi and Tujinshan faunas from Anhui (Wang et al., 1998).

Opinions regarding correlation of the Gashatan ALMA with the sequence of NALMAs have varied. Meng et al. (1998) and Ting (1998) regard the Gashatan ALMA as essentially correlative with the Clarkforkian NALMA. In contrast, Wang et al. (1998) suggest that the Tiffanian–Clarkforkian boundary lies within the Gashatan, so that the Gashatan is correlative in part with the latter part of the Tiffanian NALMA, although exactly how much of the Tiffanian correlates with the Gashatan was not discussed.

Consideration of the East of Eden model suggests that the correlation of the Gashatan ALMA advocated by Wang et al. (1998) is more likely. Because rodents are among the taxa that appear to have originated and dispersed in East of Eden fashion, the possibility that the FAD for Rodentia in Asia antedates the FAD for Rodentia in North America must be assumed. Indeed, Tribosphenomys from the Gashatan ALMA is more primitive than its close relative Alagomys, a genus known only from the Bumbanian ALMA and the Clarkforkian NALMA (Dawson and Beard, 1996). Superpositional relationships between Gashatan (below) and Bumbanian (above) faunas are demonstrable in the field in

the Nemegt Basin of southern Mongolia (Dashzeveg, 1982, 1988; Russell and Zhai, 1987). Accordingly, there is every reason to believe that the Gashatan record of *Tribosphenomys* in the Bayan Ulan fauna antedates the Clarkforkian record of *Alagomys* at Big Multi Quarry, Wyoming (Dawson and Beard, 1996). Consideration of Gashatan arctostylopid and dinoceratan records is consistent with this assessment, because both of the latter taxa first appear in North America during late Tiffanian zone Ti5 (Archibald et al., 1987; Thewissen and Gingerich, 1987; Cifelli et al., 1989). Like rodents, arctostylopids appear to have originated and dispersed in conformity with the East of Eden model, such that the earliest Asian records of this clade (which occur in the Nongshanian ALMA) must be expected to antedate zone Ti5, which they seem to do. Therefore, the Gashatan ALMA is regarded here to be partly correlative with approximately the latter half of the Tiffanian NALMA. The Gashatan may also correlate with the early part of the Clarkforkian NALMA, but it seems unlikely that the entire Clarkforkian can be accommodated within the Gashatan.

If the correlation of the Gashatan advocated here is correct, then two records of mammals from the Bayan Ulan fauna of Nei Mongol Autonomous Region, China, become important for determining whether or not the clades they represent also follow the East of Eden pattern. These taxa are the *Lambdotherium*-like perissodactyl and the hyaenodontid *Prolimnocyon chowi* (see Meng et al., 1998). Because both Perissodactyla and Hyaenodontidae first appear at the beginning of the Wastachian/Sparnacian in North America and Europe, their occurrence in an Asian fauna of seemingly greater antiquity supports the hypothesis that both of these clades also conform to the East of Eden model.

BUMBANIAN ALMA

The Bumbanian ALMA is defined by Ting (1998) on the basis of the first appearance of Perissodactyla (in the form of *Orientolophus*). Such a definition seems reasonable, but Ting's (1998) proposed zonation of the Bumbanian, based on perceived evolutionary trends among Asian perissodactyls, is not supported by superpositional relationships observable in the field and may well be overturned by future work. In particular, there is no evidence to support a greater age for Ting's *Orientolophus* Interval Zone than for her *Homogalax* Interval Zone. As such, there is no biostratigraphic basis for inferring that the Wutu fauna (referred to the *Homogalax* Interval Zone) is younger than ei

ther the Bumban or Hengdong faunas (both of which are ascribed to the *Orientolophus* Interval Zone). Ting's (1993:205) claim that "The Hengdong specimens [i.e., *Orientolophus*] represent a more primitive ceratomorph than *Homogalax* and *Cardiolophus*" is based on her analysis of dental characters alone, which conflicts with the retention of primitive skeletal traits in *Homogalax* as documented by Rose (1996). Morphological evidence supporting the ceratomorph affinities of *Homogalax* and other isectolophids is weak, and the possibility exists that Isectolophidae comprises the sister group of a much larger clade of perissodactyls (perhaps even all other undoubted perissodactyls).

Virtually all recent workers have considered the Bumbanian ALMA to correlate, in whole or in part, with the North American Wasatchian and the European Sparnacian (e.g., Dashzeveg, 1982, 1988; Krause and Maas, 1990; Ting, 1998). In light of the East of Eden model elaborated above, this correlation likely underestimates the antiquity of at least some Bumbanian mammal faunas, which more likely correlate with the Clarkforkian NALMA.

Phylogenetic and biostratigraphic data supporting an Asian origin for Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae—all of which share North American FADs at the beginning of the Wasatchian NALMA and European FADs at the beginning of the Sparnacian—were reviewed above. If these taxa did indeed originate in Asia, there is no reason to assume that their earliest records on that continent are synchronous with their North American and/or European FADs. Indeed, two of the four taxa (Perissodactyla and Hyaenodontidae) are known from the Gashatan Bayan Ulan fauna (Meng et al., 1998), which is highly unlikely to correlate with North American faunas younger than Clarkforkian (see above). Likewise, phylogenetically derived biogeographic reconstructions unambiguously point to Asia as the center of origin for Primates (Fig. 13) and, less firmly, Artiodactyla (Fig. 4B).

Closer inspection of some Bumbanian records of primates and artiodactyls reveals why correlation with the Clarkforkian NALMA is not so radical as it might appear at first glance. For example, the primate *Altanius orlovi*, from the Bumban Member of the Naran Bulak Formation, has been the subject of considerable debate because it shows anatomical characters that are exceedingly primitive if this taxon is an undoubted primate as opposed to a "plesiadapiform" (Dashzeveg and McKenna, 1977; Rose and Krause, 1984; Gingerich et al., 1991; Rose et al., 1994; Rose, 1995). Gingerich et al.

(1991) reconstructed the phylogenetic position of *Altanius* as comprising the sister group of all other undoubted primates. If this phylogenetic reconstruction is correct, there is no logical requirement for *Altanius* to be as young as North American and/or European primates, all of which would then be nested higher up the primate cladogram. Similarly, the suiform artiodactyl known from the Wutu fauna (see Tong and Wang, 1998) almost certainly lies outside the clade of neoselenodont artiodactyls (including *Diacodexis* spp.) that first appears in North America and Europe at the base of the Wasatchian and Sparnacian, respectively. As such, there is no reason to assume that the Wutu suiform is as young as these more inclusively nested artiodactyls known from Europe and North America.

Perhaps the best case for correlating an Asian Bumbanian fauna with the Clarkforkian NALMA can be made for the diverse mammal fauna being collected from the Wutu Basin in Shandong Province by Tong Yongsheng, Wang Jingwen, and their colleagues (see Tong and Wang, 1998). Several taxa known from Wutu, including the carpolestid plesia-dapoids *Chronolestes simul* and *Carpocristes oriens* (Beard and Wang, 1995), the alagomyid rodent *Alagomys oriensis* (Tong and Dawson, 1995), and the neoplagiaulacid multituberculate *Mesodmops dawsonae* (Tong and Wang, 1994), suggest correlation with pre-Wasatchian faunas in North America, where carpolestids, alagomyids, and the nearest neoplagiaulacid relatives of *Mesodmops* are unknown from faunas as young as Wasatchian (Archibald et al., 1987; Beard and Wang, 1995; Dawson and Beard, 1996). The only data supporting correlation of the Wutu fauna with the Wasatchian NALMA is the occurrence of artiodactyls and perissodactyls there. As noted above, both of these taxa appear to conform to the East of Eden paleobiogeographic model, and therefore are not adequate grounds for advocating a Wasatchian correlation for the Wutu mammal fauna. Thus, although an independent means of estimating the age of the Wutu mammals is sorely needed, correlation with the Clarkforkian is fully consistent with the entirety of its mammalian fauna, particularly in light of the East of Eden paleobiogeographic model developed here.

DISCUSSION

TEMPO AND MODE OF FAUNAL INTERCHANGE

The East of Eden model holds that, since at least late Cretaceous time, Asia has been a persistently important source area from which new clades have repeatedly dispersed into North America. In North America this iterative pattern of immigration resulted in episodic modernization of its mammalian fauna. Subsequent to the initial rifting of the North Atlantic in the early Eocene, continued faunal links between North America and the Eurasian landmass were only maintained via trans-Beringian dispersal. Moreover, the vast majority of successful trans-Beringian dispersal events occurred in East of Eden fashion, that is, from Asia to North America. What factors account for this repeating pattern of East of Eden dispersal through time, and how does this long-term pattern of faunal interchange between Asia and North America compare with other examples of intermingling of previously separated faunas?

From the late Cretaceous until the Recent, Beringia has always been a potential avenue for dispersal between Asia and North America, at least in the sense that deep marine trenches have never separated what is today the Russian Far East from the Alaskan mainland (e.g., McKenna, 1983a; Worrall, 1991). However, the high-latitude location of this region clearly functioned as a significant filter to dispersal, at least during intervals of cooler climatic conditions. Trans-Beringian dispersal is potentially controlled by three partly interrelated factors: eustatic sea level, regional tectonics, and climate. Data compiled by Woodburne and Swisher (1995) suggest that, at least for the interval encompassing the late Tiffanian through basal Wasatchian, climate may have been the most important of these three variables. A major sea-level lowstand during the middle Tiffanian (TA2.1) witnessed little or no trans-Beringian dispersal, while three closely staggered East of Eden events occurred during the late Tiffanian (Ti5; Dinocerata, Arctostylopidae), basal Clarkforkian (Cf1; Rodentia, Tillodontia, Coryphodontidae), and basal Wasatchian (Wa0; Perissodactyla, Artiodactyla, Primates, Hyaenodontidae), when eustatic sea level was uniformly higher (Woodburne and Swisher, 1995:fig.1). Perhaps, then, the repetitive nature of the East of Eden model derives largely from the fact that dispersal was controlled by climatic fluctuations: whenever climatic conditions allowed Asian endemic taxa to expand their ranges sufficiently northward, nothing pre-

vented them from invading North America. Because the interval from the late Tiffanian through basal Wasatchian was characterized by increasing mean annual temperatures and decreasing latitudinal temperature gradients (e.g., Zachos et al., 1994; Wing et al., 1995), the three episodes of East of Eden dispersal into North America during this interval may have occurred in response to this single sustained warming trend.

By the same token, were it not for the fact that the only potential route for dispersal between Asia and North America is located at such high latitude, interchange between the two continents would likely have been even more extensive and more nearly continuous, preventing the development of significant endemism on either landmass. Dispersal via lower-latitude corridors, such as that between Asia and western Europe at the time of the Grand Coupure and that between North and South America at the time of the Great American Interchange, typically result in broader and more nearly synchronous faunal interchange (e.g., Webb, 1976, 1985; Heissig, 1979; Marshall, 1988; Berggren and Prothero, 1992; Legendre and Hartenberger, 1992).

The strong trend for Asian endemic taxa to colonize North America successfully, but not vice versa, conforms with patterns established during the Grand Coupure and the Great American Interchange. In both of the latter examples taxa hailing from the larger landmass comprised the great majority of successful invaders, while those from the smaller landmass were able to swim against the current much less frequently. Explaining why this pattern should hold—whether because of competitive superiority, MacArthur-Wilson equilibrium theory, or other factors—is debatable (cf. Marshall, 1988), and this subject will not be considered further here.

CLIMATE CHANGE, TIMING OF DISPERSAL, AND
PALEOBIOGEOGRAPHY IN ASIA

The hypothesis that three episodes of East of Eden dispersal spanning late Tiffanian through basal Wasatchian time were caused by a single sustained warming trend was advanced in the previous section. If this hypothesis is accurate, it should be possible to infer something about the paleobiogeographic distributions of the taxa involved in these three closely staggered dispersal events. That is, in light of the prolonged warming trend and the reconstructed pathway of dispersal, it stands to reason that those taxa dispersing first (Dinocerata and Arctostylopidae) ranged into relatively high latitudes within Asia during the early Tertiary. At the same time, taxa dispersing later (Perissodactyla, Artiodactyla, Primates, Hyaenodontidae) must have been confined to lower latitudes on the Asian landmass. Taxa involved in the intermediate episode of East of Eden dispersal (Rodentia, Tillodontia, and Coryphodontidae) should have ranged farther north than perissodactyls, artiodactyls, primates, and hyaenodontids during the early Tertiary, but not so far north as early in time as uintatheres and arctostylopids. In this way continued warming, or at least further breakdown of latitudinal temperature gradients, would have allowed successive waves of Asian endemic taxa to expand northward until their ranges included the western margin of Beringia, when dispersal to North America became feasible. Timing of dispersal would therefore have been largely a function of climate, which also defined the northern boundaries of taxon ranges.

How does this theoretical model compare with real data regarding taxonomic distributions in the early Tertiary? Unfortunately, nothing is known of the early Tertiary mammals that must have once inhabited the vast region that today comprises the Russian Far East, Alaska, and adjacent parts of northwestern Canada. However, Gashatan faunas of the Mongolian Plateau (the most northerly mammal faunas currently known from the early Tertiary of Asia) are notable for preserving a diversity and abundance of uintatheres and arctostylopids (Dashzeveg, 1982, 1988; Russell and Zhai, 1987; Cifelli et al., 1989; Meng et al., 1998), in agreement with the model's predictions. Also represented at Gashatan localities on the Mongolian Plateau are some of the taxa that dispersed into North America subsequent to the arrival of uintatheres and arctostylopids there. These include alagomyid rodents (Meng et al., 1994, 1998), coryphodontid pantodonts (Dashzeveg, 1982, 1988), a perissodactyl (Meng et al., 1998), and at least one species of Hyaenodontidae (Dashzeveg, 1982, 1988; Meng et al., 1998). Tillodonts, artiodactyls, and primates have yet to be reported from Gashatan localities of the Mongolian Plateau, and earlier Tertiary mammal faunas remain undocumented there. Hence, in the absence of more northerly Gashatan (or earlier) mammal localities on the Asian landmass, it is impossible to test the model's prediction that early uintatheres and arctostylopids ranged to higher latitudes than did contemporary rodents, coryphodontids, perissodactyls, and hyaenodontids. However, the absence of tillodonts in Gashatan localities of the Mongolian Plateau is probably significant paleobiogeographically, because this clade is docu-

mented as early as the Shanghuan in southern China (see above). Primates, artiodactyls, and tillodonts remain unknown in northern China (Shandong Province) and/or the Mongolian Plateau prior to the Bumbanian (Dashzeveg and McKenna, 1977; Tong

and Wang, 1998). Interestingly, these three taxa are also undocumented among the high northern-latitude mammal faunas known from the early Tertiary of Ellesmere Island, Canada (Dawson, 1990).

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